Zoo Biology 26:27–39 (2007)

Research Article

Use of Novel Nest Boxes by Carmine Bee-Eaters (*Merops nubicus*) in Captivity

Jennifer J. Elston,* Jennifer Carney, Glorieli Quinones, Christy Sky, Chelle Plasse, and Tammie Bettinger

Disney's Animal Kingdom, Lake Buena Vista, Florida

Carmine bee-eaters make attractive additions to zoo aviaries but breeding programs have had challenges and limited success. The objectives of this study were to document nesting behavior of Carmine bee-eaters in a captive setting and compare reproductive success between a novel nest box (plastic, $17 \times 30 \times 22$ cm) and a PVC pipe model used previously (30 cm long, 8 cm in diameter). Three bee-eater pairs were given access to seven nest chambers (six novel boxes, one PVC model). Behavioral observations occurred during a 15-min period in the morning or afternoon before egg production and continued until chicks fledged for a total of 87 observation periods (21.75 hr). All occurrences by an individual bird entering or exiting a nest tunnel, food provision, and the time (min) spent inside a nest cavity were documented. Additionally, daily temperature within each nest chamber was recorded. Before eggs were produced the average daily temperature (23.02°C) within the nest chambers did not differ, suggesting that nest cavity choice was not influenced by temperature. No differences were detected among pairs in percent of observed time spent inside their nest cavities or number of times a nest tunnel was entered during the incubation or fledging periods. During incubation females spent a greater percent of observed time inside the nest cavity than males ($P = 0.02$). During the fledging period food provision did not differ between the pairs, however males entered their nest tunnels more often per hour than females ($P = 0.03$), and males tended to provide food more often than females ($P = 0.053$). Two pairs nested in novel nest boxes and successfully fledged one chick each. The pair that nested in the PVC model did not fledge a chick. A nest box that aids in keeping eggs intact is essential for breeding bee-eaters in captivity, and maintaining captive populations will provide opportunities for zoo

*Correspondence to: Jennifer Elston, PhD, Disney's Animal Kingdom, P.O. Box 10000, Lake Buena Vista, Florida 32830. E-mail: Jennifer.J.Elston.-ND@disney.com

Received 14 March 2006; Accepted 23 September 2006

DOI 10.1002/zoo.20118
Published online 25 January 2007 in Wiley InterScience (www.interscience.wiley.com).

visitors to enjoy these birds and will reduce the need to remove birds from the wild. Zoo Biol 26:27–39, 2007.

Keywords: Carmine bee-eater; *Merops nubicus*; reproduction; behavior; captive propagation

INTRODUCTION

Carmine bee-eaters (*Merops nubicus*) are striking birds that make colorful additions to zoo aviaries. These birds are sexually monomorphic, possessing a bright pink breast, red wings and tail, and blue-green head and undertail. Native to the rivers, savanna woodlands, and grass plains of Africa, they are opportunistic, insectivorous birds that forage aerially, consuming locusts, honeybees, grasshoppers, and flying ants [Fry, 1984, Fry et al., 1992]. Because of their natural aerial feeding behavior, bee-eaters can provide an entertaining and educational display for zoo visitors.

Carmine bee-eaters are gregarious birds and nest in colonies in high sandy cliffs or steep riverbanks [Fry, 1984]. The birds excavate tunnels (1–2 m long, 6 cm wide) and produce a clutch of between two to five eggs, depending on latitude [Fry et al., 1992]. Carmine bee-eaters are generally not territorial, however, when perched at its nest entrance a bird may lunge aggressively at birds stationed at nearby nest cavities [del Hoyo et al., 2001]. Male bee-eaters tend to guard their female partner during the breeding season, however, males and females may mate with others if provided an opportunity, and females may lay eggs in a nest cavity for another pair to rear [del Hoyo et al., 2001]. The incubation period of bee-eaters in general is approximately 20 days and the fledging period spans approximately 23–30 days [Fry, 1984; Brooke and Birkhead, 1991]. Wrege and Emlen [1991] studied several colonies of white-fronted bee-eaters (*Merops bullockoides*) in Kenya and found that intraspecific nest parasitism played a role in egg rejection, accounting for 24% of egg loss because parasitizing females tended to remove host eggs from the nest, and host females frequently discarded or abandoned eggs that were not their own. Additionally, bee-eaters do not line their nest cavities with any type of substrate so broken shells are common and also contribute to egg loss [Fry, 1984]. Eggs are generally laid approximately 2 days apart so nestlings vary in size after hatching (i.e., asynchronous hatching), and in clutches greater than two the youngest nestling is often subject to starvation and death [Fry, 1984]. Wrege and Emlen [1991] found that starvation was a major factor in pre-fledging mortality of white-fronted bee-eaters, accounting for 48% of all hatchling deaths. Within the nest cavity, adults and hatchlings drop insect remains and defecate, and additionally, deceased nestlings are not removed so nests become heavily soiled throughout the nesting period [Fry, 1984]. Just before fledging begins, parents tend to decrease the provision of food to the young, but after fledging, parents continue to feed their young for up to 6 weeks [Fry, 1984]. It is unknown whether or not Carmine bee-eaters have helpers at the nest, but in other species of bee-eaters helpers may aid in nest excavation and feeding of nestlings, and are usually offspring from the previous year, birds without mates, or birds with failed nests [Fry, 1984]. Emlen and Wrege [1988] found that in 50% of nest attempts by white-fronted bee-eaters the breeding pairs were assisted by helpers, with related birds more likely to act as helpers than non-related birds.

In 2004, Disney's Animal Kingdom, Lake Buena Vista, Florida housed a pair of Carmine bee-eaters who successfully fledged a chick, making it the only facility in North America to experience a successful parent-rearing of a Carmine bee-eater chick. Disney's Animal Kingdom also housed two additional pairs in 2004 that each had one clutch of two eggs, however, those eggs succumbed to breakage. Five nest chambers were provided, each consisting of PVC pipe (8 cm in diameter, 30 cm long) attached inside a $2 \times 1 \times 1$ m plywood box with an 84 cm PVC pipe tunnel. The chambers and tunnels were filled with a sand/clay mixture to provide birds the opportunity to excavate the pipes themselves. The chambers were difficult for keeper staff to keep clean and additionally, had no holes for air ventilation. As a result, the nest chambers became extremely soiled over the course of the fledging period. Although unclean nest cavities are common in the wild, they are undesirable in zoo settings where control of parasites and disease is crucial. Some anecdotal evidence exists among aviary managers suggesting that bee-eaters require a certain temperature in the nest. A study by White et al. [1978] showed a uniform temperature of 25°C among nests in a colony of European bee-eaters. At Disney's Animal Kingdom the restricted airflow in the PVC pipe nest chambers may have inhibited the maintenance of the desired temperature. In addition, the quarters were fairly small, and it was speculated that some of the egg breakage could have been the result of adult movement in the restricted space. For these reasons, Disney's Animal Kingdom keeper staff introduced novel nest boxes during the 2005 breeding season in an attempt to increase the reproductive success of the Carmine bee-eaters.

The objectives of this study were to document nesting behavior of Carmine bee-eaters in a captive setting and compare reproductive success between a new nest box design and the original PVC pipe model used at Disney's Animal Kingdom. Specific goals of this study were to determine if differences in parental behavior exist among pairs and whether males and females exhibit differential parental care. Because egg/chick loss could result from nest chamber design or egg/chick damage by unrelated conspecifics, an additional focus of this study was to determine frequency of visits to a nest cavity by unrelated birds and the subsequent effects on egg and chick survival. Two additional objectives of this study were to document temperature during the reproductive period and determine whether temperature within the nest chambers played a role in nest cavity choice among the birds.

MATERIALS AND METHODS

Animals

Nine Carmine bee-eaters (five male, four female) were housed together in a mixed-species, off display, $6 \times 9 \times 2$ m outside aviary at Disney's Animal Kingdom, Lake Buena Vista, Florida. Birds also had access to space in an attached aviary ($3 \times 3 \times 2$ m) that contained the holding box for the nest chambers. Additional species housed in the aviary included Marianas fruit doves (*Ptilinopus roseicapilla*; n = 2) and crested wood partridges (*Rollulus roulroul*; n = 2). Bee-eaters were fitted previously with colored leg bands for individual identification. Eight birds ranged from 7–11 years of age. One male was the offspring of the pair that had reproduced successfully in 2004 and was approximately 1 year of age. Birds were fed a diet of dog food (Science Diet, Hill's Pet Nutrition, Inc., Topeka, KS), parrot pellets

(Mazuri Parrot Breeder, PMI Nutrition International, St. Louis, MO), commercial meat (Toronto Zoo Carnivore Diet) mixed with bird pellets (Mazuri Small Bird Breeder), shredded carrots, crickets, and waxworms (0800 and 1200 hr), and also received superworms coated with a vitamin and mineral mix (Nekton-S and Lafeber's Emeraid Nutri-support) and Roxanthin Red (Sensient Technologies) for color supplementation (between 1500 and 1630 hr). Body weights were obtained opportunistically for all adult birds during 2001 through spring 2005. Nest chambers were checked daily by keeper staff during the incubation and fledging periods to monitor egg and chick status. Additionally, a feather was collected from each chick >20 days of age and submitted for gender determination via laboratory analysis (tissue sexing; Avian Biotech International, Tallahassee, FL).

Nest Chambers

Seven nest chambers (six novel boxes, one original PVC pipe model) were available for birds to choose from. The novel nest boxes were plastic, $17\times 30\times 22$ cm, with a wire mesh floor. The boxes contained two sliding doors along the back to allow keeper access to the chamber. Additionally, small holes were drilled along the top of the boxes to facilitate air movement. The nest chamber that housed the offspring that survived in 2004 was left in its original state (PVC pipe; 30 cm long, 8 cm in diameter). The nest chambers were placed within three rows in a $2\times 1\times 1$ meter plywood holding box (Fig. 1) that was positioned 1.2 m off of the ground. This holding box was the same box used during 2004, and was modified to include the six novel nest boxes. All nest cavities were numbered for identification. Birds gained access to an individual nest chamber through a hole leading into a PVC pipe tunnel from the outside of the holding box. Small wooden blocks were attached at the front of each hole to provide a platform for birds to land on before entering a tunnel. Each access hole was 8 cm in diameter. There were three access holes along

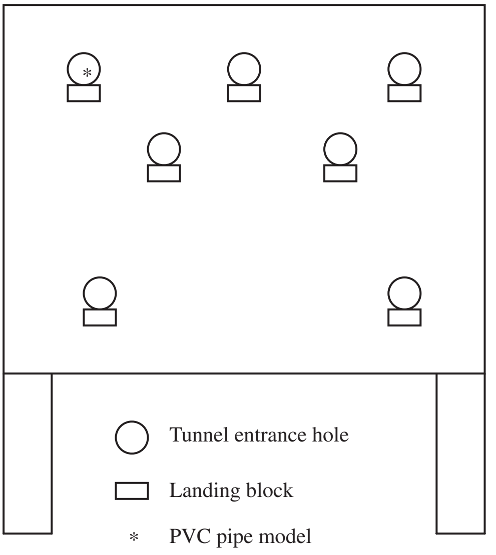

Fig. 1. Diagram of nest holding box (front view) used by Carmine bee-eaters during the 2005 breeding season at Disney's Animal Kingdom (note: not to scale).

the top row, 50 cm apart, 1.7 meters from the ground. The middle row contained two access holes that were 30 cm below the top row, 50 cm apart, and 1.4 m from the ground. The bottom row contained two access holes that were 46 cm below the second row, 61 cm below the top row, 84 cm apart, and 1.2 m from the ground. The original PVC pipe model was positioned inside the top left of the holding box, with 84 cm long PVC pipe (8 cm in diameter) attached as a tunnel. Five novel nest boxes were placed within rows inside the holding box, and also had 84 cm long PVC pipe tunnels attached. One novel nest box was placed inside the holding box with only an 8 cm long PVC pipe attached to create a shorter tunnel. This box was positioned inside the bottom left of the holding box. All tunnels and nest chambers were packed completely with a sand/clay mixture (50:50) to provide excavation opportunities for the birds. After all nest chambers were excavated by the birds, a small hole was drilled in each nest box and a probe from a HOBO data logger (Onset Computer Corporation, Bourne, MA) was inserted to record hourly temperatures within each nest chamber. Additionally, one data logger was set up inside the holding box to record the ambient temperature surrounding the nest chambers.

Behavioral Observations

Birds were observed during the pre-laying period after excavation of the cavities and throughout the incubation and fledging periods. To minimize disturbance to the birds, observations of the entire holding box occurred through a window from inside a small building that adjoined the aviary. Observations took place during the morning (between 0800 and 1200 hr) and afternoon (between 1300 and 1700 hr) for a 15-min period. Birds interacting with the holding box were identified, as well as the associated nest cavity. All occurrences of holding box visits, entering or exiting a nest tunnel, and food provision (Table 1) were documented via behavioral sampling [Martin and Bateson, 1993] using a digital voice recorder (Sony Corporation, model ICD-MS515).

Data Analyses

The number of holding box visits by a bird per hr, the number of times a bird entered and exited a nest tunnel per hr, and the length of time (min) each bird spent inside a nest cavity were calculated to determine totals and means for each pair and means for each gender during the pre-laying, incubation, and fledging periods. The number of times food provision occurred per hr by each bird was calculated during the fledging period to determine totals and means for each pair and means for each

TABLE 1. Carmine bee-eater ethogram used at Disney's Animal Kingdom in 2005

Behavior	Description
Holding box visit	Arrival/presence on the plank in front of a nest chamber entrance hole
Enter nest tunnel	Movement by bird (all or parts of its body) into tunnel
Exit nest tunnel	Bird emerges from tunnel
Food provision	Bird has food item in beak when enters nest cavity

gender. Additionally, mean daily temperature and minimum and maximum daily temperatures within each nest chamber and within the holding box were calculated during the pre-laying, incubation, and fledging periods. Analysis of Variance [SPSS, 2004] was used to compare activity means among the three pairs and a Student's *t*-test [SPSS, 2004] was used to compare activity means between males and females during the incubation period. A Student's *t*-test was used to compare activity means between the two pairs and between the sexes for the fledging period. Analysis of Variance was used to compare temperature means among the seven nest chambers and the holding box during the pre-laying period and a Student's *t*-test was used to compare temperature means between occupied and unoccupied nest chambers during the incubation and fledging periods.

RESULTS

Behavior

All birds began showing an interest in the nest cavities (investigating tunnel entrances, mild pecking of the sand/clay mixture) in late March 2005. By mid-April 2005 tunnel excavation was well underway and was finished by mid-May 2005. Birds were observed over 87 observation periods for a total of 21.75 hr. Birds chose the same partners they previously paired with in 2004, forming three distinct male-female pairs. Mean body weights ranged from 46.1 ± 0.85 g for females (n = 3) to 48.1 ± 1.23 g for males (n = 3). The paired birds nested in adjoining cavities and are identified as Pair 1, Pair 2, and Pair 3 hereafter. Pair 1 nested in the original PVC pipe model chamber and Pairs 2 and 3 nested in the novel nest boxes. The two males that were unpaired (including the 2004 offspring) were removed after all tunnels had been excavated to avoid the risk of potential aggressive encounters with the paired birds. The unpaired female was also separated from the flock due to her age (>10 years) and health status.

Pre-laying period.

During the pre-laying period Pairs 1, 2, and 3 visited their chosen nest cavity by either landing on the entrance block or physically entering the tunnel a total of 21.5, 1.5, and 9.1 times/hr, respectively. The female of Pair 1 entered the tunnel occupied by Pair 3 once and engaged in excavation, and the female of Pair 2 landed on the entrance of Pair 3's cavity once, but did not enter.

Incubation period.

Eggs were produced by late-May, and eggs within a clutch were laid asynchronously, approximately 1–3 days apart. The number of eggs produced by each female was 3, 2, and 3, respectively. Two eggs from Pair 1 and one egg from Pair 2 sustained cracks during the incubation period and thus did not hatch. During the incubation period, the male of Pair 2 entered Pair 1's tunnel once and remained inside approximately 7 min while the female of Pair 1 was also inside the cavity. The male of Pair 2 also entered Pair 3's tunnel once during incubation and remained inside for >1 min. There were no differences among pairs in mean percent of observed time spent inside their nest cavities, mean number of times their nest tunnels were entered, or mean length of time spent inside their cavities per visit (Table 2). Females spent a

TABLE 2. Reproductive activity of three Carmine bee-eater pairs at Disney's Animal Kingdom in 2005

	Pair 1		Pair 2		Pair 3		
	Pair	Individual	Pair	Individual	Pair	Individual	
Activity	Total	Mean ± SEM	Total	Mean ± SEM	Total	Mean ± SEM	*P*-value
Incubation period							
% of time spent inside nest cavity	35.1	17.6 ± 5.7	50.2	25.1 ± 9.5	45.9	23.0 ± 14.7	0.9
No. of times per hr entered cavity	3.9	1.9 ± 0.2	4.5	2.3 ± 0.5	4.8	2.4 ± 0.3	0.6
Time (min) spent inside cavity per visit	—	5.6 ± 2.3	—	6.3 ± 1.3	—	5.4 ± 2.6	0.96
Fledging period							
% of time spent inside nest cavity	—	—	20.5	10.2 ± 1.4	18.52	9.26 ± 2.5	0.97
No. of times per hr entered cavity	—	—	7.0	3.5 ± 0.9	7.2	3.6 ± 1.6	0.9
Time (min) spent inside cavity per visit	—	—	—	2.1 ± 0.8	—	1.8 ± 0.3	0.8
Food provision per hr	—	—	5.4	2.7 ± 1.0	4.3	2.1 ± 1.8	0.5

TABLE 3. Reproductive activity[a] of Carmine bee-eaters at Disney's Animal Kingdom in 2005

Activity	Males	Females	*P*-value
Incubation period[b]			
% of time spent inside nest cavity	11.9 ± 2.1	31.8 ± 4.4	0.02
No. of times per hr entered cavity	2.0 ± 0.1	2.4 ± 0.3	0.31
Time (min) inside cavity per visit	3.7 ± 0.6	7.8 ± 0.1	0.003
Fledging period[c]			
% of time spent inside nest cavity	10.3 ± 1.5	9.2 ± 2.5	0.7
No. of times per hr entered cavity	4.8 ± 0.4	2.4 ± 0.1	0.03
Time (min) inside cavity per visit	1.4 ± 0.1	2.5 ± 0.4	0.1
Food provision per hr	3.8 ± 0.1	1.0 ± 0.7	0.053

[a]Mean $\pm$ SEM.
[b]n = 3 males and 3 females.
[c]n = 2 males and 2 females.

greater percent of observed time inside the nest cavity than males ($P = 0.02$; Table 3). The number of times per hr females entered their nest tunnels did not differ from the number of times the males entered, however, on tunnel entry, females remained inside the nest cavity longer than males ($P = 0.003$). The incubation period lasted approximately 21 days for Pairs 1 and 3 and 20 days for Pair 2.

Fledging period.

One chick hatched from Pair 1, but died after only 2 days. Necropsy of the nestling showed a bacterial infection. One chick hatched from Pair 2 and three chicks hatched from Pair 3, however, Pair 3's first chick was euthanized because of medical problems (its yolk sac had been exposed) and the second chick died at 17 days of age after suffering trauma when it fell out of the nest tunnel onto the ground. Its sibling fell out of the tunnel as well, but was unharmed by the event. Chicks weighed an average of 4.77 g on the date of hatching (n = 2) and grew steadily throughout the fledging period (Fig. 2). Between Days 15–18 chicks weighed an average of 72 g (n = 3), and decreased in weight approximately 16% to an average of 60.61 g (n = 2) at Days 24 and 27, just before fledging. Pair 2's chick was female and fledged after approximately 26 days and Pair 3's chick was male and fledged after approximately 28 days. At fledging, chicks were around 22% heavier than the average adult weight. Chicks were weighed again at approximately 2.7 months of age, and by this time average body weight (47 g) was similar to the average adult weight.

The female of Pair 1 was not observed associating with any nest cavity after her brood failed, however, the male continued to land on (but not enter) his tunnel entrance and the entrances of the other two occupied tunnels for 8 days after his deceased hatchling was found. There were no differences between Pairs 2 and 3 in mean percent of observed time spent inside their nest cavities, mean number of times their nest tunnels were entered, or mean length of time spent inside their cavities per visit (Table 2). Pairs 2 and 3 were observed entering their tunnels with a food item during 77% and 59% of visits, respectively, and food provision did not differ between the pairs. Males entered their nest tunnels more often per hr than females ($P = 0.03$; Table 3), however, there were no differences between males and females for percent of observed time spent inside the nest or for the average length of visit

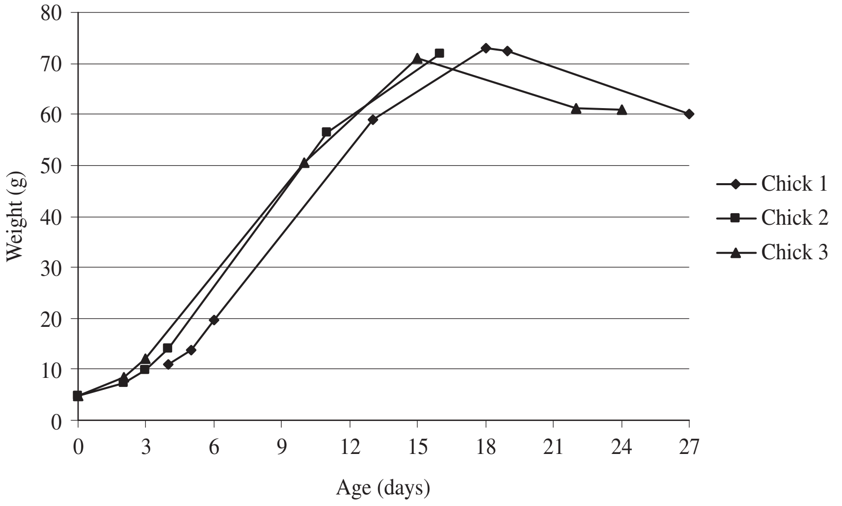

Fig. 2. Carmine bee-eater chick (n = 3) growth rate during the 2005 fledging period at Disney's Animal Kingdom.

once inside the nest. Although not significant, males tended to enter their tunnels with a food item more often than females ($P = 0.053$). The female of Pair 2 entered Pair 3's tunnel once during the fledging period but only remained inside for 5 sec.

Temperature

Pre-laying period.

The average daily temperature within the seven nest chambers (23.02°C) did not differ among one another, nor did the temperature differ between the nest chambers and the inside of the holding box (22.89°C; $P = 0.77$). The average minimum daily temperature within the nest chambers was 18.67°C, and did not differ among chambers or with the holding box (18.27°C; $P = 0.99$). The average maximum daily temperature within the nest chambers was 27.17°C and did not differ among chambers or with the holding box (27.46°C; $P = 0.11$).

Incubation period.

The average daily temperature ranged from 25.39–27.25°C among nest chambers and was 25.87°C inside the holding box. The average daily temperature of the three nest chambers that were occupied by the pairs was warmer than the unoccupied nest boxes ($P = 0.03$) during the incubation period (Table 4). Additionally, the minimum daily temperature and maximum daily temperature of the three occupied nest chambers were higher than the unoccupied nest boxes ($P = 0.03$ and $P = 0.05$, respectively).

Fledging period.

The average daily temperature ranged from 26.0–27.35°C among nest chambers and was 26.35°C inside the holding box. The average daily temperature of the two nest boxes that contained nestlings was warmer than the empty nest

TABLE 4. Temperature (°C)[a] within nest boxes used by Carmine bee-eaters during incubation and nestling periods at Disney's Animal Kingdom in 2005

	Occupied	Unoccupied	*P*-value
Incubation period[b]			
Average daily temperature	26.68 ± 0.29	25.75 ± 0.17	0.03
Minimum daily temperature	23.59 ± 0.27	22.82 ± 0.09	0.03
Maximum daily temperature	30.0 ± 0.35	28.86 ± 0.28	0.05
Fledging period[c]			
Average daily temperature	27.18 ± 0.17	26.32 ± 0.12	0.01
Minimum daily temperature	24.48 ± 0.16	23.74 ± 0.07	0.003
Maximum daily temperature	30.15 ± 0.20	29.14 ± 0.26	0.08

[a]Mean ± SEM.
[b]n = 3 occupied and 4 unoccupied.
[c]n = 2 occupied and 5 unoccupied.

chambers ($P = 0.01$) during the nestling period (Table 4). The average minimum daily temperature of the two nest boxes that contained nestlings was higher than the unoccupied nest chambers ($P = 0.003$), however, the average maximum daily temperature of the boxes with the nestlings did not differ from the empty chambers.

DISCUSSION

Pair 1 nested in the original PVC pipe model and did not fledge a chick, whereas Pairs 2 and 3 nested in the novel nest boxes and successfully fledged one chick each. This resulted in an increase in chick production at Disney's Animal Kingdom compared to 2004. Although it cannot be stated unequivocally that the new nest box design used in this study increased reproductive success in this population of bee-eaters, the results suggest that a nest box with these features (larger space, ventilation) would improve the chances of egg survival and the ability of parents to rear and fledge chicks. It is reasonable to assume that acclimation of the birds to the aviary conditions and previous experience with mate-pairing, egg production, and the holding box played a role in the successful reproduction of these bee-eaters. However, it is also conceivable that the novel nest box conditions contributed to the success by helping to keep the eggs intact and providing appropriate conditions to allow for parental care of the chicks.

Pairs did not differ in the percent of time spent inside their nest chambers during the incubation period and egg loss occurred as a result of shell damage, indicating that egg failure was not a result of differential care among pairs. Pair 1, which nested in the original PVC pipe model, lost two eggs to damage, whereas Pair 2 lost only one egg and Pair 3 lost no eggs. Both of the latter pairs nested in the novel nest boxes. It is possible that the original PVC pipe nest chamber contributed to egg failure by rendering eggs susceptible to damage because less space was available for parents once inside the chamber.

The incubation and fledging periods of the chicks were consistent with previous findings for bee-eaters [Fry, 1984, Brooke and Birkhead, 1991]. Chick growth rate seemed normal with regard to the typical weight gain of altricial young for some species [Winkler, 2004]. Chick mortality was not a result of inadequate parental care, but occurred because of other biologic issues (complications with a yolk sac and a bacterial infection) and an unfortunate accident. In fact, Pairs 2 and 3 both fledged chicks and did not differ in the number of visits made to their respective cavities or the number of times food was provided during the fledging period, which indicates that both pairs were providing sufficient care for their chicks.

During the incubation period, females spent a greater percent of time inside the nest cavity than males, suggesting that females may spend more time incubating and tending to the eggs whereas males may play a greater role in guarding the cavities. Indeed, males were often observed perched nearby the holding box during this period. In addition, the percent of time spent inside the nest cavity during incubation may be underestimated for females during this study, because females were observed in the aviary less often than males. The nest chambers were not checked for bird presence before or after the observation periods to minimize disturbance to the birds, so if a bird was not observed entering or exiting a nest tunnel its activity was not documented. On many occasions it is possible that females were inside their respective cavities before observation began, remaining inside throughout the data collection period and therefore unseen by the observer. Differential behavior between the genders also occurred during the fledging period, when males were found to enter their nest cavities more often than females and also showed a tendency (nonsignificant trend) to provide food more often than females. It is possible, given these results, that these behaviors are part of a natural shift in parental behavior. Females may take more responsibility in incubating the eggs and males may increase their responsibilities in caring for the chicks.

Throughout the entire reproductive season, all pairs associated almost entirely with their chosen nest cavity and visits by a bird to a cavity occupied by another pair were rare. Even before eggs were produced, birds seemed to be committed to their chosen cavities. During the incubation period when eggs were vulnerable observations did show that the male of Pair 2 entered both Pair 1 and Pair 3's tunnel once each. Although it would only take one visit by an unrelated bird to destroy an egg, it is unlikely that this male harmed the eggs of his conspecifics. All three of Pair 3's eggs hatched, and although two of Pair 1's eggs did not hatch, the observed visit to Pair 1's cavity by the male in question happened approximately 4 days before keepers discovering that an egg had shell damage. The female of Pair 2 entered Pair 3's tunnel one time during the fledging period, but did not remain longer than 5 sec and did not harm the chick that was present (evidenced by the fledging of that chick at a later date). Because the three unpaired birds (2.1) were removed from the aviary before eggs were present in the nest, it is unknown if those birds would have had access to any of the nest chambers or debilitated the eggs or hatchlings in any way, or if they (particularly the 2004 offspring) would have engaged in assisting the parent birds in care of the chicks. In white-fronted bee-eaters fledging success is increased when breeders have assistance from their relatives [Emlen and Wrege, 1988]. However, in a captive situation where food resources are plentiful, assistance from helpers is probably not as crucial for rearing, as evidenced by the reproductive success of the two pairs at Disney's Animal Kingdom.

Average daily temperature within the nest chambers before egg production and during the incubation and fledging periods seemed similar to the temperature documented for wild bee-eater nest cavities in Europe (25°C) [White et al., 1978]. Before egg-laying occurred, the average daily temperature inside the seven nest chambers did not differ, indicating that nest cavity choice among these birds was not likely influenced by the temperature within individual chambers. However, because the temperature within the chambers was similar to the temperature documented for wild nest cavities, it is possible that temperatures within this range may influence the birds' decision to produce eggs and rear young and should therefore be maintained during the breeding season. Differences in temperature between occupied and unoccupied nest chambers were likely attributable to the body heat produced by the occupants.

In addition to providing the appropriate environmental conditions (e.g., nest box, temperature, diet) to enhance reproduction of Carmine bee-eaters, it may also be necessary for managers to include time for a lengthy bird adjustment period in their breeding programs. Although 2004 and 2005 were successful breeding seasons at Disney's Animal Kingdom, the birds did not produce offspring in previous years, even though they had been obtained and acclimated to one another at least 2 years before (December 2001). The holding box with PVC pipe nests and tunnels had been provided for the 2002 breeding season, but no reproductive activity was observed. In 2003 the bee-eaters engaged in tunnel excavation, but did not produce eggs. It is possible that bee-eaters need to establish strong pair bonds before engaging in nesting attempts, which may require a lengthy period of time.

CONCLUSIONS

1. A nest box that enhances hygiene and provides more desirable nest components (space, air flow), aids in keeping eggs intact, and promotes the ability of parents to rear their young is essential for breeding Carmine bee-eaters in captivity.
2. The ability of zoologic institutions to maintain a captive population of reproducing Carmine bee-eaters will be beneficial in two ways: first, the need to remove birds from wild populations will be reduced and second, the public will have opportunities to enjoy these vibrant birds.
3. Maintaining a successful reproduction program for Carmine bee-eaters in captivity has implications for additional species of bee-eaters as well as other cavity nesting birds, which may help achieve a greater number of self-sustaining bird populations in zoos.

ACKNOWLEDGMENTS

We thank the Disney's Animal Kingdom Aviary Team, especially K. Graham and G. Roles for assisting with construction/maintenance of the holding box for nests and P. Schutz for acquiring the nest boxes. We also thank B. Burkhalter for administrative support and R. Fry and L. Matherne for technical support. Additionally, we extend thanks to J. Mellen for critical review of this manuscript.

REFERENCES

Brooke M, Birkhead T. 1991. The Cambridge encyclopedia of ornithology. New York, NY: Cambridge University Press. 362p.

del Hoyo J, Elliott A, Sargatal J. 2001. Family Meropidae (bee-eaters). In: Handbook of the birds of the world. Vol. 6. Mousebirds to hornbills. Barcelona: Lynx Edicions. p 286–325.

Emlen ST, Wrege PH. 1988. The role of kinship in helping decisions among white-fronted bee-eaters. Behav Ecol Sociobiol 23:305–15.

Fry CH. 1984. The bee-eaters. San Diego: Academic Press. 304p.
Fry CH, Fry K, Harris A. 1992. Kingfishers, bee-eaters, and rollers. Princeton, NJ: Princeton University Press. 324p.
Martin P, Bateson P. 1993. Measuring behavior: an introductory guide, 2nd ed. New York, NY: Cambridge University Press. 222p.
SPSS 13.0. 2004. LEAD Technologies, Inc.: Chicago, IL.
White FN, Bartholomew GA, Kinney JL. 1978. Physiological and ecological correlates of tunnel nesting in the European bee-eater, *Merops apiaster*. Physiol Zool 51:140–54.
Winkler DW. 2004. Nests, eggs, and young: breeding biology of birds. In: Podulka S, Rohrbaugh RW Jr, Bonney R, editors The Cornell lab of ornithology handbook of bird biology. 2nd ed. Princeton, NJ: Princeton University Press. p 107–17.
Wrege PH, Emlen ST. 1991. Breeding seasonality and reproductive success of White-fronted bee-eaters in Kenya. Auk 108: 673–87.