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Nest Building in Captive Gorilla gorilla gorilla

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ABSTRACT

Although various aspects of gorilla nest building have been described in wild populations, nest-building behavior of captive gorillas has not been subject to much scientific review. We observed nest building in 17 gorillas during three periods: summer baseline, winter baseline, and winter treatment, in which the amount of available nesting material was doubled. We conducted observations exclusively in the indoor holding area in the hour following evening departure of animal care staff. During baseline, gorillas engaged in nest-building on 3.1% of scans and were on a constructed nest on 27.9% of scans. Overall, gorillas spent significantly more time on elevated nests than on floor nests. There were no statistically significant sex, age class, or rearing history differences in nest building, time spent on a nest, or nest location preference. Nest building consisted of both gathering and manipulating materials. The gorillas spent significantly more time building nests in winter than in summer. Additionally, they were more often on elevated nests during winter than summer. Doubling the amount of nesting material did not increase nest building, but it increased the number of floor nests. Our results suggest that providing adequate materials to captive gorillas for nest building may facilitate performance of species-typical nest-building, minimize competition among individuals for nesting sites and materials, and permit individual thermoregulation.

INTRODUCTION

Like all great apes, gorillas build both day and night nests for sleeping (*Gorilla berengei:* Bolwig, 1959; Donisthorpe, 1958; Schaller, 1963; *G. g. gorilla:* Jones and Sabater Pi, 1971; Mehlman and Doran, in press; Remis, 1993; Tutin *et al*., 1995; Tutin and Fernandez, 1984; *G. b. graueri:* Casimir, 1979; Fruth and Hohmann, 1996; Hall *et al*., 1998; Yamagiwa, 2001). Although day and night nests may be composed of similar materials (Schaller, 1963), night nests may be more elaborately constructed than day nests (captive *Gorilla gorilla gorilla*, Bernstein, 1962; wild *Pan troglodytes,* Brownlow *et al*., 2001; wild *P. paniscus*, Fruth and Hohmann, 1993; wild *G. berengei*, Schaller, 1963) and should be distinguished in studies of nesting behavior (Brownlow, *et al*., 2001). Although various aspects of gorilla night nest building have been described in wild populations, nest-building behavior of captive gorillas has not been subject to much scientific review (Bernstein, 1962, 1969; Weiche, 2000). We studied characteristics of nest building in captive gorillas by describing motor patterns of nest construction, evaluating seasonal differences in nest building and location, and measuring effects of increased nesting material on nest-building behavior. In addition, we evaluated the effects of age, sex, rearing history, and infant presence on nest building.

Nest Building in Wild Gorillas

Counts of night nests, and fecal matter contained within, have been used to conservatively estimate population demographics in the absence of visual observation of gorillas (Bolwig, 1959; Hall *et al.*, 1998; Tutin *et al.*, 1992, 1995). Of the great apes, only gorillas regularly defecate in a nest (Casimir, 1979; Fruth and Hohmann, 1996; Schaller, 1963), but there appears to be variation in this habit between subspecies. For example, Schaller (1963) found dung in 99% of 2,451 mountain gorilla nests, but Jones and Sabater Pi (1971) found dung in only 43% of 410 western lowland gorilla nests (26% had dung dropped outside the nest and 31% had no feces in or outside the nest). Unlike mountain gorillas, that build predominantly terrestrial nests (Donisthorpe, 1958; Schaller, 1963), lowland gorillas regularly build both terrestrial and arboreal nests. Comparative analyses of nest building in gorillas suggest variability in nest type and location between gorilla subspecies and populations (Mehlman and Doran, in press; Remis, 1993; Yamagiwa, 2001). Gorillas do not always construct nests per se. Instead there is a variety of nest types, including bare-earth nests (no construction), ground nests (minimal or full construction), and arboreal nests (Mehlman and Doran, in press; Remis, 1993; Schaller, 1963). Remis (1993) reported $\geq$ 65% of nest sites contained at least one bare-earth nest.

The tendency for gorillas to build nests at varying heights or to construct nests at all may be influenced by group size (Remis, 1993), habitat type (Bolwig, 1959; Hall *et al*., 1998; Jones and Sabater Pi, 1971; Mehlman and Doran, in press; Remis, 1993; Tutin *et al*., 1995; Yamagiwa, 2001); season (Remis, 1993; Tutin *et al.*, 1995), proximate rainfall or maximum daily temperature (Mehlman and Doran, 2001). For example, at the Dzanga-Sangha Reserve in Central African Republic (CAR), Remis (1993) reported that gorillas built more tree nests in the wet season and more bare-ground nests in the dry season, but cautioned against interpreting the findings as evidence of a thermoregulatory function for nests because the increased use of tree nests during the wet season corresponded with increased arboreal feeding on fruit. At Lope Reserve in Gabon, Tutin *et al*. (1995) also found the frequency of tree nests to be correlated positively with rainfall, but the results were confounded by seasonal variation in the use of different types of habitats. Contrarily, Mehlman and Doran (in press) found significant, independent relationships between temperature, proximate rainfall (12 hrs previous to nest construction), and nest construction at Mondika Research Site in Central African Republic and Republic of Congo. Gorillas slept on bare-earth nests more often when temperatures increased and built more nests when proximate rainfall increased. Unlike Remis (1993), Mehlman and Doran (manuscript submitted for publication) found no relationship between the use of large fruit trees and construction of arboreal nests.

There are sex differences in gorilla nest construction in the wild. Western gorilla females generally build nests higher and more frequently than silverbacks do (Mehlman and Doran, in press; Tutin *et al.,* 1995). Silverbacks use ground nests more often than non-silverbacks do (Mehlman and Doran, 2001; Remis, 1993), though Tutin *et al*. (1995) reported that silverbacks occasionally nest in trees at heights $\leq$ 34m above ground. Male gorillas may spend more time than females do on ground nests because many trees lack structural support for the larger bodily size of silverbacks (Remis, 1995, 1999).

There are no systematic behavioral studies of gorilla nest construction techniques in the wild. Fruth and Hohmann's (1996) summary and comparison of published data from 10 field sites suggests direct observation rarely occurs in studies of western gorillas, and information is lacking on ontogeny of nest building, duration of nest construction, and activities of wild gorillas when on nests. Comprehensive analyses of nest building, such as those conducted by Fruth and Hohmann (1993) on wild bonobos, have yet to be conducted in wild populations of gorillas.

Nest Building in Captive Gorillas

Systematic analyses of nest building in captive gorillas are scarce. Weiche (2000) reported that changes in group composition influenced sleeping sites and preferred nesting neighbors for captive gorillas, but did not review nest construction techniques. Bernstein (1969) described captive gorillas transporting materials to a nest site and using construction techniques only at the nest site. Overall, motor patterns used to carry, play with, fluff, separate, and otherwise manipulate nesting material were similar among the three ape species in Bernstein's (1969) study, but comparisons on the development and incidence of nest building among species were confounded by age differences in subjects.

Although there are guidelines for meeting the psychological and behavioral needs of captive primates (United States Department of Agriculture, 1999), there is no standard requiring that captive apes be provided with ample and varied materials to build day or night nests. The lack of information on nest building in captive gorillas may be attributed to variations in management across institutions housing apes. The extent to which captive gorillas build nests is largely dependent on the amount and type of materials provided to them by caretakers (Bernstein, 1969; Maple and Hoff, 1982). Provision of nesting materials may vary among institutions with differing natural or financial resources and within institutions over time. Some facilities provide apes with hay, straw, mulch, and cut pieces of natural vegetation in addition to artificial materials such as paper, burlap, or cardboard boxes for nest building. Other institutions regularly provide only one type of bedding material, or none.

To provide a more systematic characterization of nest building in captive gorillas, we studied 5 social groups at Zoo Atlanta. We collected data after the departure of human caretakers at the end of the day in the night-time holding facility only. The purpose of the study was to ascertain the incidence of night nesting, to quantify the motor patterns of nest construction, and to examine sex differences in nest building. In addition, we sought to examine seasonal differences in nest building and to determine whether increasing the amount of available nest building material influenced nesting behavior. Because the structural strength of elevated areas in Zoo Atlanta's nighttime holding facility was designed to support even the largest gorillas, we hypothesized there would be no constraint on, and therefore no sex difference in, nest location preferences. Considering Bernstein's (1969) suggestion that nesting competency increases with age, we expected adult wild-caught gorillas to exhibit more nest-building behavior than captive-born, subadult gorillas would. Finally, if nest building indeed serves a thermoregulatory function for gorillas, we hypothesized there would be more nest building in winter than in summer.

METHOD

Subjects and Housing

The subjects were 17 western gorillas at Zoo Atlanta: 3 silverbacks, 9 adult females, and 5 subadults (Table I). Infants < 2 years old were not in the study. Subjects were housed in 5 social groups, including 3 mixed-sex breeding groups, an all-female group, and an all-male group. Just before the final phase of the study, 2 females from the all-female group moved into one of the breeding groups (Table I).

The gorillas occupied outdoor, naturalistic exhibits between 1000 and 1700 h (Ogden *et al.*, 1990, 2002). Between 1630 and 1730, gorilla groups sequentially entered into an indoor holding facility composed of 14 rooms, which are interconnected with a series of overhead passageways and doorways (Winslow *et al.*, 1992). The composition of each social group was maintained in the indoor holding facility with each group occupying 1–3 rooms. Each room was outfitted with climbing structures such as ropes and hammocks, manipulable items such as crates and balls, and nesting/forage material such as straw, hay, and natural browse (bamboo, willow, mulberry, etc.) when seasonally available. Natural browse was provided no more than once weekly. In the *ca.* 30 min after a gorilla group entered the holding facility, keepers visually examined the subjects and individually administered commercial primate biscuits, a beverage (Lukas *et al.*, 1999), and medicine or nutritional supplements to group members before leaving for the night. The amount of time that elapsed between the first gorilla group entering the building and keepers dispersing usually varied between 30 min and 2 hr.

Data Collection

We observed 5 groups containing 17 subjects 8 hr in summer baseline, 7 hr in winter baseline, and between 7 and 9 hr in winter treatment. We observed Ivan's group of 2 subjects only 6 hr in the winter treatment condition. We collected data between 1730 and 1930 h in the indoor holding facility. A total of 5 observers, who obtained interobserver agreement with 90% reliability, collected data on 2–3 gorilla groups each evening. Data collection commenced after keepers left the building, usually $<$ 1h after gorillas first entered the building. All observers were familiar to the gorillas and were instructed to sit or stand $>$ 2.5m ft from the front of the holding cage, to avoid making eye contact with subjects, and to remain silent and unresponsive to gorillas before, during, and after data collection.

Sampling methods included 3 elements:

i. Group-scan sampling of substrate, posture, and behavior at 2-min intervals for individuals in a focal group during 1-h observation sessions;
ii. All-occurrence sampling of elimination behavior and displacement or agonistic behavior related to nesting during the same 1-h observation sessions; and
iii. One-time scans of location and substrate for all subjects at the end of each data collection session. We plotted each subject's location on a map of the holding facility and noted the substrate.

Behavior categories for substrate and posture contained exhaustive and mutually exclusive behavior lists. Only 2 or 3 groups were observed on any given day, but we conducted one-time scans on all 17 subjects at the end of every session on evenings data were collected.

A nest is a structure of hay or other manipulable material constructed by gorillas for resting or sleeping. For a structure to be labeled a nest, the data collector must have either observed a gorilla exhibiting one or more defined nest-building behaviors while making it or the structure must have been substantially developed beyond the initial scattering of hay distributed by caretakers. When they were not on a nest, we scored gorillas as occupying a bare substrate (floor or elevated surface with no or very little hay or other nesting material beneath the body), a hay-scattered substrate, floor or elevated surface with more than a few strands of hay or other nesting material beneath the body), or on another substrate, i.e., rope, hammock, ledge or doorway.

The study occurred in three phases: summer baseline, winter baseline, and winter treatment. Summer baseline occurred during August and September 1996, when the temperature in the indoor holding facility during data collection averaged 26.9˚C (range 25.0-28.6˚C).Winter baseline occurred in November and December 1996, when the temperature in the indoor holding facility during data collection averaged 20.7˚C (19.0-22.2˚C). During baseline, the amount of hay was standardized to one flake (*ca.* 1.1 kg) per gorilla. Winter treatment occurred in January 1997 when the temperature in the indoor holding facility during data collection averaged 19.7˚C range 15–22.7˚C). In this phase, keepers doubled the amount of hay to two flakes (*ca,* 2.3 kg) per gorilla.

Table I. Subject information

Group[a]	Name	North American Studbook number	Sex	Rearing history[b]	Age in years (1996)	Adult or subadult[c]	Stage class[d]
1	Willie B	115	M	WC	39	Adult	Silverback
1	Choomba	180	F	WC	33	Adult	Adult female
1	Kinyani	820	F	CB, HR	13	Adult	Adult female
1	Kudzoo	T1002	F	CB, MR	2	Subadult	Infant
1	Mia Moja	1109	F	CB, MR	7	Adult	Adult female
2	Ozoum	175	M	WC	35	Adult	Silverback
2	Banga	224	F	WC	32	Adult	Adult female
2	Paki	191	F	WC	33	Adult	Adult female
3	Ivan	710	M	WC	32	Adult	Silverback
3	Shamba	221	F	WC	37	Adult	Adult female
4⟶1	Kashata	1294	F	CB, MR	3	Subadult	Infant
4	Katoomba	168	F	WC	34	Adult	Adult female
4	Kuchi	870	F	CB, MR	12	Adult	Adult female
4⟶1	Machi	609	F	CB, MR	30	Adult	Adult female
5	Kekla	1108	M	CB, MR	7	Subadult	Juvenile
5	Stadi	1186	M	CB, MR	5	Subadult	Juvenile
5	Taz	1110	M	CB, MR	7	Subadult	Juvenile

[a] Machi and Kashata were removed from Group 4 and introduced to Group 1 just before the winter treatment condition.

[b] WC = wild-caught; CB = captive-born; MR = mother-reared (never removed from mother for>24 h to receive care by humans); HR = hand-reared (removed from mother > 24 h to receive care by humans).

[c] Adult = females > 64, males > 104; Subadult = females 0–54, males 0–94 (Schaller, 1963).

[d] Silverback = males > 104; Adult female = females > 64; Juvenile/Adolescent = males 3–104, females 3–64; Infant < 34 (Schaller, 1963).

Data Analysis

First we calculated the mean number of scans on which each behavior was observed for each individual in each baseline ($M = \Sigma X/N$, X = number of scans on which behavior was scored within each observation session and N = number of observation sessions [i.e., 8 in summer baseline, 7 in winter baseline]) and then we averaged them across the two baseline conditions for each individual. We conducted statistical tests via individual mean values. We calculated group means (and standard errors) from individual means for each behavior. We only converted group means to percentages (*M*/30*100%) as a final step so that we could present the mean percentage of scans that gorillas engaged in each behavior during baseline. We similarly summarized all occurrence data as mean hourly rates of behavior. We used nonparametric statistical tests when inter-group comparisons resulted in decreased sample sizes within comparative classes, and we used parametric statistical tests when conducting repeated measures analyses on all 17 gorillas. Accordingly, we used nonparametric tests (Mann-Whitney *U* test for two samples) to evaluate sexual differences, age class differences (adult vs. sub-adult), and rearing history differences (wild-born vs. captive-born) in nesting behavior and to compare behavior of adult females with infants to those without them.

To compare nesting behavior among conditions, we summarized group-scan samples to reflect the mean number of scans in which an individual gorilla exhibited each behavior during each condition. We summarized all-occurrence data as individual mean hourly rates for each phase. For each behavior, we conducted paired *t*-tests to make two sets of comparisons: (1) between summer and winter baselines and (2) between winter baseline and winter treatment. We used a Bonferroni's correction (Bakeman and Gottman, 1986) to determine which alpha level to apply to each test. This resulted in an adjusted alpha of 0.025; accordingly, we considered p-values between 0.025 and 0.05 to be trends. To determine if the total number of gorillas that built a nest each night changed between conditions, we first determined the total number of gorillas on nest during the one-time evening scans for each day. Then we determined the mean number of gorillas that built a night nest for each condition and compared them via 2-sample *t*-tests with a Bonferroni correction.

We used paired *t*-tests to compare use of nests versus non-nest (hay-scattered and bare) substrates and use of bedded (nest and hay-scattered) versus bare substrates. To compare use of varied substrate types, we performed a multivariate analysis of variance for repeated measures across 6 substrate types: floor-bare, floor-hay-scattered, floor-nest, elevated-bare, elevated-hay-scattered, and elevated-nest. Then we conducted 3 comparisons post hoc between floor-bare vs. elevated-bare, floor-hay-scattered vs. elevated-hay-scattered, and floor-nest vs. elevated-nest. Bonferroni's correction resulted in an adjusted alpha of 0.017 for each test.

To compare use of elevated (>0.3 m off the floor) versus floor substrates we measured floor spaces and nesting platforms within the holding area. Although ropes and a few hammocks were available in some of the holding quarters, the usable space estimates are based on fixed architectural elements only. Accordingly, estimates of usable elevated spaces do not include the amount of space afforded by temporary and moveable climbing or perching mechanisms and therefore slightly underestimate the total usable elevated space. Some groups occupied alternate holding areas throughout the study, and in the winter treatment condition 2 individuals were introduced to another group and thus occupied different holding areas. Therefore, we first calculated expected values for space distribution for each gorilla in each holding condition. For the 9 individuals in >1 holding condition, we weighted expected values by the amount of observations in each holding configuration and then averaged them so there is one set of expected values for each individual.

To compare gorilla behavior within the hour following departure of care staff per group-scan data and at one hour after departure of care staff per one-time scan data, we calculated the percentage of scans gorillas were observed on each substrate type and in each posture in the baseline conditions for both data types. Then we compared the percentages via paired *t*-tests.

We analyzed use of the holding area from the map location data. We divided the individual holding rooms into quadrats 0.9 x 0.9 m. We noted the number of times each gorilla was in each quadrat and used the datum to calculate the coefficient of variation (CV) (Ogden *et al.*, 1990; Rasmussen, 1980; Stoinski *et al.*, 2001). A high CV corresponds with habitual use of few quadrats and a low CV corresponds with distributed use of many quadrats. For the 9 individuals observed in >1 holding condition, we first calculated CVs for each animal in each holding condition and then averaged them, weighted by the amount of observations in each holding configuration.

Except where adjusted as noted above, we used an alpha level of 0.05 for all statistical tests, and for nonparametric tests only, we report probabilities between 0.05 and 0.10 as trends. We performed all analyses via Systat® 7.0.

RESULTS

Nest-building During Baseline Conditions

Group Scan Data

Table II is a summary of substrate use, posture and behavior during baseline periods. In baseline, gorillas engaged in nest building during a mean 3.1% of observations and occupied a constructed nest in a mean 28% of observations. There were no sex, age class, or rearing history differences in building or occupying nests.

Table II. Summary of results on substrate use, posture, behavior, and social proximity from data collected during focal group observation sessions during baseline (individual behaviors averaged over summer baseline and winter baseline)[a]

Group scan data: mean percentage of scans	Mean (SE)
Substrate	
Floor substrate	54.5% (5.3)
Floor – Bare	34.4% (3.9)
Floor – Hay-scattered	11.9% (1.7)
Floor – Nest	8.2% (1.8)
Elevated substrate	38.3% (5.3)
Elevated – Bare	2.9% (1.5)
Elevated – Hay-scattered	15.6% (3.8)
Elevated – Nest	19.7% (2.9)
Bare substrate (floor/elevated combined)	37.3% (3.9)
Hay-scattered substrate (floor/elevated combined)	27.5% (3.1)
Nest (floor/elevated combined)	28.0% (3.7)
Other substrate	3.1% (1.3)
Not visible	4.1% (2.2)
Posture	
Reclining	42.3% (4.3)
Sitting/crouching	43.8% (4.0)
Standing	5.7% (1.3)
Locomoting	3.8% (1.0)
Not visible	4.3% (2.3)
Behavior	
Nest building	3.1% (0.6)
All occurrence data: mean number per hour	Mean (SE)
Behavior	
Elimination (urination or defecation)	0.53 (0.10)
Displace another from nest	0.07 (0.03)
Non-contact aggression related to Nesting	0.04 (0.01)
Contact aggression related to nesting	0.00 (0.00)

[a] N=17 subjects.

Overall, there was no difference in the percentage of scans gorillas occupied the floor (54.5% of scans) versus an elevated substrate (38.3%), and they spent 7.2% of scans on an unidentified substrate (hammock, threshold of a doorway, not visible, etc.). However, when we estimated the amount of usable terrestrial and elevated space and adjusted the values to only include scans in which use of elevated or floor areas could be confirmed, gorillas spent significantly less time on the floor (58.9%) than might be predicted if all areas of the holding area were used equally (87.4%, $t(16)=5{:}514$, $p<0{:}001$). Accordingly, gorillas spent significantly more time on elevated substrates (41.1%) than would be predicted by chance (12.6%, $t(16)=5{:}514$, $p<0{:}001$). The likelihood of a gorilla spending more time on an elevated substrate versus the floor is not associated with sex, age class, or rearing history.

Overall, gorillas occupied constructed nests less often than non-nest substrates (27.9% vs. 64.8%, $t(16)=-5{:}393$, $p<0{:}001$), but there was no difference in the percent time gorillas were on constructed nests (27.9%) versus hay-scattered substrates (27.5%). Gorillas were more often on bedded substrates (nests and hay-scattered substrates) than on bare substrates (55.4% vs. 37.3%, $t(16)=2{:}245$, $p=0{:}039$).

Although there was more space for gorillas to build floor nests, they were more often on elevated nests (19.7%) than floor nests (8.2%, $F(1,16)=12.933$, $p=0.002$) and more often on bare terrestrial substrates (34.4%) than bare elevated substrates (2.9%, $F(1,16)=48.405$, $p<0.001$). There was no difference in time spent on elevated- versus floor-hay-scattered substrates. There was no statistically significant sex, age class, or rearing history difference associated with nest location.

Gorillas displaced others from nests a mean 0.07 times per hour, and there was little aggression displayed toward other gorillas in nests (Table II). Overall, there was no statistically significant sex, age class, or rearing history difference in the rate of these behaviors. Four adult female gorillas—Banga, Choomba, Machi, and Mia Moja,—were housed with their infants ($\leq$3 yrs of age). There was no difference in nesting behavior or nest location for them versus other adult females, but there was a trend toward females with infants displacing others from nests ($n=4$, $M=0.103$ per hour) more often than those without infants did ($n=5$, $M=0.029$ per hour, Mann-Whitney U test statistic = 16.500, $p=0.096$).

Hay was the only material the gorillas used to build nests. Natural browse items were only rarely provided to them, but when present, they never incorporated it into nests. Nest building had 2 behavioral components: gathering materials (40%) and manipulating them (60%). Of the 40%of nest building in which gorillas gathered materials, they spent 18% in a stationary posture, pulling nearby materials toward their bodies; 17% locomoting, pushing or pulling nesting material along the ground toward the nesting site; and 5% carrying nesting material, in arms while walking or with crossed legs while engaged in suspensory locomotion. Of the 60% of observations in which gorillas manipulated materials, 19% involved tucking hay beneath the body, 24% fluffing hay upward around the body, 9% parting materials on the ground with hands or legs, 3% placing hay on the head or body, and 5% in some other fashion.

On average, gorillas urinated or defecated 0.53 times per hour (SE=0.10). Across the two baseline conditions, we observed a total of 135 elimination events. Gorillas eliminated in a nest only 3 times and moved from a nest to urinate or defecate 15 times. When not on a nest, they moved to an alternative position or location to urinate or defecate 68 times. This usually entailed moving to an elevated location such as a shelf or ledge, from which urine or feces would drop. However, gorillas also urinated or defecated without moving to a different location 49 times. Urination or defecation was easily indicated by a shift in posture that allowed for easy flow and minimal body contact with the waste matter. The likelihood of a gorilla urinating or defecating within or outside of a nest was not associated with age class, sex, or rearing history.

End of Evening Scans

One-time scans of posture, substrate, and location at the end of each observation session occurred between 1830 and 1930 h, most of which occurred at 1830 h (52.9%) or 1845 h (23.5%). We conducted a total of 34 (20 summer baseline, 14 winter baseline) one-time scans on all 17 subjects during baseline and 19 one-time scans in the treatment condition. Table III is a comparison of results obtained during the one-time scans with results obtained during hour-long, group scan observation sessions. Gorillas were more often on elevated substrates by the end of the evening versus the previous hour. They decreased use of bare terrestrial substrates, increased use of elevated hay-scattered substrates, and decreased use of elevated nests at the end of the evening. End-of-evening scans also indicated that they were predominantly lying down or sitting then rather than standing or locomoting (Table III). Gorillas were more likely to be lying down by the end of the evening versus the previous hour, and they were significantly less likely to be sitting or locomoting then.

Table III. Comparison of behaviors during the hour following care staff departure (data collected on focal groups during group-scan sampling sessions) and behaviors observed just before observer departure (data collected on all subjects during one-time, end-of-evening scans on all days data were collected) via paired *t*-tests (a

	Group scan data (from Table I)	End-of-evening scans	*t*(16)	p-value
Substrate (% of scans)				
Floor substrate	54.5% (5.3)	45.8% (5.3)	4.183	p=0.001
Floor – Bare	34.4% (3.9)	25.0% (4.4)	3.869	p=0.001
Floor – Hay	11.9% (1.7)	13.1% (2.1)	-0.754	*ns*
Floor – Nest	8.2% (1.8)	7.7% (2.2)	0.611	*ns*
Elevated substrate	38.3% (5.3)	47.8% (5.3)	-4.675	p<0.001
Elevated – Bare	2.9% (1.5)	2.5% (1.6)	0.809	*ns*
Elevated – Hay	15.6% (3.8)	28.7% (3.9)	-6.106	p<0.001
Elevated – Nest	19.7% (2.9)	16.7% (2.5)	2.321	p<0.05
Bare substrate (floor/elevated combined)	37.3% (3.9)	27.5% (4.8)	4.060	p=0.001
Hay substrate (floor/elevated combined)	27.5% (3.1)	41.8% (3.5)	-6.230	p<0.001
Nest substrate (floor/elevated combined)	28.0% (3.7)	24.4% (3.6)	2.513	p<0.05
Other substrate	3.1% (1.3)	1.3% (0.5)	1.522	*ns*
Not visible	4.1% (2.2)	5.0% (2.6)	-1.277	*ns*
Posture (% of scans)				
Reclining	42.3% (4.3)	59.1% (4.6)	-4.968	p<0.001
Sitting/crouching	43.8% (4.0)	30.5% (4.3)	4.248	p=0.001
Locomoting	3.8% (1.0)	0.9% (0.3)	3.501	p<0.01
Not visible	4.3% (2.3)	5.9% (2.9)	-1.368	*ns*

[a] Machi and Kashata were removed from Group 4 and introduced to Group 1 just before the winter treatment condition.

There were too few gorillas in each class—silverback, adult female, juvenile, infant—to compare them statistically, but we report the mean, standard error, and range for nest-building in each class in Table IV. As the final record of nesting each day, the one-time, end-of-evening scans provide the best comparison of captive gorilla nesting habits to wild gorillas. To enable a better comparison to data reported on nest use in wild gorillas among silverbacks, adult females, juveniles, and infants, we summarized data for each individual across the two baseline periods and report the mean, standard error, and range for each nest type by class in Table IV.

Finally, the map location data revealed that during the baseline periods only, the mean CV for individual gorillas in the holding area is 3.461 (SE = 0.184), with a range from 2.469 to 5.389. There was no difference in CV values in the baseline conditions that could be attributed to differences in age class, sex, or rearing history.

Seasonal Differences in Nest Building and the Effect of Increasing Nesting Materials on Behavior

A univariate analysis of variance revealed a significant difference in temperature across the 3 conditions ($F(2, 47)=121.073$, $p<0.001$). A matrix post hoc of pairwise comparisons (with Bonferroni adjustment) revealed summer temperature differed significantly from winter baseline (pairwise mean difference = - 11:116, df =47, $p<0.001$), but there was no difference in temperature between the two winter conditions. Means, standard errors, and test statistics for behaviors that changed significantly between conditions are in Table V.

Table IV. Comparison of nest-building and substrate during the two baseline periods between members of each age/sex class[a]

	Mean (SE), range				
	Overall N = 17	**Silverbacks N = 3**	**Adult Females N = 9**	**Juveniles N = 3**	**Infants N=2**
	Group scan data: Mean percentage of scans				
Behavior					
Nest Building	3.1% (0.6) 0.0 – 9.1%	4.6% (2.4) 0.0 – 8.3%	2.3% (0.4) 1.0 - 4.3%	4.9% (2.1) 2.6 - 9.1%	1.8% (0.4) 1.6 - 2.1%
	One-time, end-of-evening scans: Mean percentage of scans				
Substrate					
Floor – Bare	30.4% (5.4) 0.0 – 65.4%	49.0% (10.0) 29.4 – 61.8%	21.2% (5.9) 2.9 – 58.8%	45.6% (15.1) 16.0 – 65.4%	21.0% (21.0) 0.0 – 41.9%
Floor – Hay-scattered	15.1% (2.3) 18.4% (2.2)	13.7% (7.0) 0.0 – 23.5%	17.3% (3.5) 0.0 – 38.2%	7.6% (2.2) 4.0 – 11.5%	18.4% (2.2) 16.1 – 20.6%
Floor – Nest	8.3% (2.4) 0.0 – 27.3%	8.8% (5.1) 0.0 – 17.6%	9.0% (3.6) 0.0 – 27.3%	2.5% (1.3) 0.0 – 3.8%	13.2% (13.2) 0.0 – 26.5%
Elevated (Bare, Hay-scattered, and Nest combined)	46.2% (5.6) 8.8 – 97.1%	28.4% (9.8) 8.8 – 38.2%	52.6% (8.0) 11.8 – 97.1%	44.2% (18.4) 19.2 – 80.0%	47.4% (5.5) 41.9 – 52.9%

[a]Group-scan data collected during 1-h focal group sessions; one-time, end-of-evening scans conducted on all subjects at the end of each day that data were collected (means calculated excluding Not Visible and Other values).

There was a significant decrease in the percent of time gorillas occupied the bare floor and sections of floor scattered with hay between summer and winter baseline (Table V). Conversely, there was a significant increase in the percent of time gorillas occupied elevated nests in the winter versus the summer baseline. The only difference in substrate use that resulted from the increased provision of hay was an increased use of floor nests: group-scan data indicated gorillas spent nearly twice as much time on floor nests when the amount of hay was doubled compared to winter baseline. One-time scans on all 17 subjects indicated more gorillas occupied elevated nests during winter (M=5.1, S=2.4) than summer (M=0.6, S=0.8; $t(32)=2.307$, Bonferroni adjusted $p<0.001$), and more gorillas built floor nests during the treatment phase (M=2.3, S=1.2), versus winter baseline (M=0.9, S=0.7; $t(31)=3.736$, Bonferroni adjusted $p<0.001$).

Table V. Mean (and standard error) for behaviors that differed significantly between conditions and results of paired *t*-tests[a]

				Paired *t*-test α =0.025	
	Mean (SE)			**Summer Baseline vs. Winter Baseline**	**Winter Baseline vs. Winter Treatment**
	Summer Baseline	**Winter Baseline**	**Winter Treatment**		
Substrate					
	Group scan data: Mean percentage of scans				
Floor – Bare	52.7% (6.3)	16.1% (3.4)	11.8% (2.1)	p < 0:001 *t*(16) = 5.665	*ns*
Floor – Hay	18.1% (2.8)	5.7% (1.2)	5.4% (1.2)	p < 0:001 *t*(16) = 4:771	*ns*
Floor – Nest	8.8% (2.9)	7.7% (3.0)	15.0% (5.5)	*ns*	
Elevated – Nest	3.5% (1.7)	36.0% (6.0)	45.2% (5.5)	p < 0:001 *t*(16) = -5.015	*ns*
Behavior					
Nest Building	1.2% (0.3)	5.0% (1.1)	6.4% (1.4)	p = 0:004 *t*(16) = -3:331	*ns*
Map Data	Mean (SE)	Mean (SE)	Mean (SE)		
Location					
Coefficient of Variation	2.719 (0.238)	4.203 (0.252)	3.816 (0.237)	p < 0:001 *t*(16) = -4.572	*ns*

[a] (Bonferroni adjustment to alphaD0.05 for conducting 2 comparisons resulted in adjusted alpha = 0.025; trends reported for 0.05<p<0.025).

All gorillas engaged in nest-building at least once during the study, and an increase in nest-building occurred between summer and winter baseline conditions (Table V). This overall increase in nest-building was influenced by trends toward increased time spent carrying materials ($t(16)$= -2:332, p=0.033) and tucking hay beneath the body ($t(16)$= -2:302, p=0.035) and a significant increase in time spent fluffing hay around the body ($t(16)$= -3.795, p=0.002) during winter. There was no additional increase in time spent nest building when the amount of hay was doubled during the treatment condition.

A comparison of location data across the 3 conditions revealed that the gorillas exhibited more habitual use of the same spaces during the winter conditions versus summer baseline (Table V), but there was no change in spatial clumping as a result of the increase in hay during winter treatment. There was no difference in posture—sit, stand, lie—or rates of all-occurrence behaviors, such as displacing another from a nest, eliminating habits, or engaging in nest-related agonistic behavior, among conditions.

DISCUSSION

At Zoo Atlanta, gorillas regularly constructed night nests in an indoor holding facility during the hour after keepers departed for the evening. They used a variety of motor patterns to gather and to manipulate material to form nests. No statistical difference in time spent in nest construction or nest location was based on sex, age class, or rearing history. Whether on a nest or not, the gorillas spent more time than expected by chance occupying elevated substrates. When nesting, gorillas were on an elevated substrate more often than on the floor, but doubling the amount of hay seemed to have little effect on behavior except to increase construction of floor nests.

Comparison With Nest Building in Wild Western Gorillas

Our data permit some comparisons to nest building in wild gorillas. Zoo Atlanta gorillas built more elevated nests in colder weather and spent more time on bare floor substrate in warmer weather. These findings relate directly to those of Mehlman and Doran (in press), who reported that wild western gorillas also built more nests in colder weather and fewer nests in warmer weather. They suggested that their findings support two hypotheses: (1) proximate climatic factors significantly influence nesting behavior, and (2) nest construction may be a thermoregulatory adaptation to insulate gorillas against cold temperatures.

Differences in arboreal and terrestrial nest locations in natural habitats may be reflected in a relative preference for elevated substrates to floor substrates in captivity. To compare our data to nest types of wild gorillas (Mehlman and Doran, 2001; Remis, 1993; Schaller, 1963), we consider floor – bare to be comparable to bare-earth nests; floor – hay to be equivalent to minimally constructed ground nests; floor – nest to resemble fully constructed ground nests; and all 3 elevated substrates—elevated – bare, elevated – hay-scattered, and elevated-nest—counter parts of arboreal nests.

On average, western gorillas at Mondika (Mehlman and Doran, in press) and Bai Hokou (Remis, 1993) sleep on bare-earth nests approximately 45% of time, constructed ground nests 35% of time, and arboreal nests 20% of time. If we average reports on nest construction types at Dzanga-Sangha, Central African Republic (CAR), Ndakan (CAR), Lope (Gabon), and Belinga (Gabon) (Remis, 1993, p. 249), this subgroup of western gorillas occupy bare-earth nests approximately 3% of time, constructed ground nests 83%of time, and arboreal nests 14% of time. Results of the one-time evening scans (Table IV) indicate Zoo Atlanta gorillas slept on the bare floor 30% of time, constructed floor nests or slept on hay-scattered floor substrates 24% of time, and slept on elevated substrates 46% of time. Accordingly, the distribution of Zoo Atlanta night nest locations suggests that the gorillas slept on bare terrestrial substrates less often than gorillas at Mondika and Bai Hokou did but more often than gorillas at Dzanga-Sangha, Ndakan, Lope, and Belinga did. Zoo Atlanta gorillas also appear to build terrestrial nests less often, and sleep on elevated surfaces more often, than gorillas did at the 6 field sites.

Mehlman and Doran (in press) reported silverbacks were observed on bare-earth nests 54% of time, minimally constructed ground nests 13% of time, fully constructed ground nests 31% of time, and arboreal nests a only 2% of time. In contrast, non-silverbacks were on bare-earth nests 44% of time, minimally constructed ground nests 8% of time, fully constructed ground nests 27% of time, and arboreal nests 21% of time. Results of the one-time end of evening scans (Table IV) indicate that Zoo Atlanta silverbacks slept on the bare ground 49% of time, hay-scattered floor substrates 14% of time, floor nests

9% of time, and elevated substrates 28% of time. Although our sample size is small, this comparison might suggest that captive silverbacks can more readily reap the thermoregulatory benefits of elevated nesting than their wild counterparts if they are given access to artificial nesting platforms that fully support their weight. Our results also suggest that adult females and infants exhibit similar nesting profiles and may occupy elevated nests more often than wild western gorillas did (Mehlman and Doran, 2001). In contrast, the 3 Zoo Atlanta subadult (juvenile) male gorillas were almost equally occupying bare floor substrates (46%) and elevated substrates (44%), resembling captive silverbacks in bare floor preference (49%) but captive infants in preference for elevated spaces (47%).

Our results also suggest some differences between captive and wild gorillas in nest-building. At Zoo Atlanta, nesting behavior and location did not vary systematically by age or sex, in contrast to accounts of nest building in wild gorillas that predict that females build nests higher and more frequently than males (Mehlman and Doran, in press; Remis, 1993; Tutin, *et al.,* 1995). Remis (1999) reported that tree size, shape, and structure influence sexual differences in wild gorilla arboreal feeding behavior, which might have implications for sexual differences in nest location as well. However, the captive gorillas of both sexes exhibited equal use of elevated versus terrestrial nests. Because the elevated spaces in the captive environment are not trees of varying size and structure but reinforced steel and mesh nesting platforms designed to support large male gorillas, it is perhaps not surprising that males and females use the spaces equally.

At Zoo Atlanta, gorillas enter freshly cleaned holding areas each night so, like their wild counterparts, they do not reuse night nests. Accordingly, one might expect to observe similar nest soiling habits. However, the capative gorillas did not often urinate or defecate in nests while settling down for the evening. Schaller (1963) found 99% of gorilla night nests in his study contained feces. In contrast, at Zoo Atlanta only 2% of elimination occurred inside nests. We did not examine night nests the following morning to look for feces or urine that may have occurred overnight, so our results may underestimate the incidence of nest soiling by gorillas in captivity. However, the gorillas predominantly avoided soiling nests and often moved from a resting position (when in a nest or otherwise) to urinate or defecate. Keepers at Zoo Atlanta reported that feces is occasionally in nests in the morning, but not on a daily basis.

Gorillas at Zoo Atlanta did not use the full range of nesting materials available to them, e.g., when natural browse items were seasonally offered. Because browse is a relatively rare and preferred food item for captive gorillas, they may have preferred to eat it rather than to use it in nests, especially since standard nesting material was readily available. Captive gorillas might exhibit opportunistic use of diverse and abundant nest materials if they were systematically provided the range of materials that was offered to chimpanzees by Bernstein (1962). An opportunity to observe sex- and age-related variation in nesting behavior in captive gorillas may depend on gorillas having access to the wide variety of nesting resources typically available to wild gorillas including verdant, woody, or herbaceous materials.

Comparison to Nest Building in Captive Western Lowland Gorillas

The variety of motor patterns observed in gorillas at Zoo Atlanta, including fluffing, tucking, parting, and otherwise manipulating nesting material, reflect the diversity with which both wild gorillas (Schaller, 1963) and captive gorillas and chimpanzees (Bernstein, 1962, 1969) have been observed constructing nests. For example, Bernstein (1962) reported chimpanzees commenced nest building by transporting materials to a selected location. Good nests contained a thin center and a thick rim, similar to a large bird nest (Bernstein, 1962). Captive gorillas also transported materials to a nesting spot, cleared a space, and sat in the center of the space to construct nests around their bodies (Bernstein, 1969).We found that captive gorillas would part hay around their bodies, tuck it beneath themselves and fluff it around their bodies and heads to create a recognizable nest.

Our results also expand upon earlier work conducted by Bernstein (1969), who described the ontogeny of nest-building behavior in captive gorillas. Although Zoo Atlanta 3 year-olds regularly bedded down with their mothers and presumably did not need to contribute to the construction of the night nest, they also engaged in nest-building. These findings suggest that the behavior is fairly advanced by the time gorillas sleep alone. Our results also suggest that nest building proficiency is not deficient in captive-born gorillas.

Implications for Captive Management

Our observations provide the first systematic analysis of night nest building in a large sample of captive gorillas and they have implications for captive gorilla management. First, to promote exhibition of species-appropriate behaviors, zoo managers should provide proper bedding material to apes that will construct nests in captivity (Poole, 1998): bonobos (Berle *et al.*, 1995), chimpanzees (Bernstein, 1962, 1969; Brent *et al*., 1991), gorillas (Bernstein, 1969; Maple and Hoff, 1982; Weiche, 2000), and orangutans (Grundmann and Bomsel, 2000; Maple, 1980). Nests not only provide a warm sleeping location but also increases the complexity of the captive environment. Nesting can improve maternal behavior in gorillas (Miller-Schroeder and Paterson, 1989) and can decrease abnormal behavior in chimpanzees (Baker, 1997). Providing regularly varying nesting materials may be one of the few ways in which managers can diversify opportunities for night nest building in structurally static environments.

Second, the increased spatial clumping in winter versus summer corresponds to a decrease in terrestrial space use and increase in elevated nesting. These results illustrate that a limited amount of elevated space may result in increased spatial clumping for gorillas that prefer elevated resting spots. By designing exhibit and holding facilities with numerous, widely placed nesting platforms, managers of captive gorillas may increase the quantity and diversity of gorilla nesting opportunities. Similarly, when elevated spots are limited, subordinate apes may be displaced from elevated nests to terrestrial substrates. We observed this happen after many gorillas had already built nests so that supplanted individuals had access to little nesting material. Because our data suggest adult females with infants may displace others from nests at a higher rate than those without infants, adult females without infants may experience insufficient nesting opportunities in environments with limited nesting resources. Providing more hay in the winter treatment condition may have either encouraged dominant animals to nest on the floor, thus opening up elevated nest space for subordinate individuals, or encouraged subordinate individuals to make nests on the floor. Gorillas also exhibited slightly more habitual use of space in the indoor holding facility than has been reported for the same subjects in the outdoor facility at Zoo Atlanta (N=19, mean CV=2.8, Stoinski, *et al.*, 2001). This finding may be expected because the indoor space is smaller and affords fewer opportunities for diversity in space use. It is unlikely that captive gorillas demonstrate more habitual use of night nest sites than day nest sites on exhibit.

Third, gorillas used nests significantly less often during the summer, when they instead cleared away pieces of hay before sitting or lying down on the bare floor. Presumably, the concrete floor provided cool relief for gorillas during the warm summer, when the temperature in the indoor holding facility averaged 26.7˚C. By comparison, the temperature in the indoor holding facility was much cooler on average (20.2˚C) throughout the winter periods. A nest presumably provided warmth and comfort for gorillas as they slept, especially when they were off the cold floor on nesting platforms. Our finding that gorillas spend more time in elevated nests when the temperature decreases suggests that, like some populations of wild western gorillas (Mehlman and Doran, 2001), captive gorillas may build nests as shelter from the cold. Doubling the hay did not substantially increase time gorillas spent building nests, but it permitted more gorillas to build floor nests and to receive insulation from the cold floor during the winter.

In general, very little information exists on the behavior of captive gorillas in night dens after caretakers have departed for the evening. Because we collected data via two different sampling techniques, we could compare gorilla behavior during the hour following evening departure of care staff and at one hour following their departure, presumably when the gorillas had settled down into sleeping positions. The gorillas were not mobile at that time but sitting or reclining. Our results also suggest that gorillas might build and occupy nests while they are settling down, but some may move off nests—voluntarily or because they are displaced—for the night. Gorillas may also locomote or sit on bare or hay-scattered floor surfaces in the hour following departure of staff but retire to elevated surfaces to recline on hay or nests for the evening.

In summary, nest building is an aspect of gorilla natural behavior that can be readily accommodated in the captive setting. All Zoo Atlanta gorillas had access to nesting materials and all exhibited some nest-building behavior. Although gorillas may not always construct night nests for sleeping, preferences for bedded to bare substrates should be taken into consideration, especially in colder weather. To facilitate natural behavior, to minimize competition among individuals for nesting sites and materials, and to permit individual thermoregulation, managers of captive gorillas should provide sufficient elevated nesting locations and materials to allow all individuals to build nests. Such provision should be encouraged for captive gorilla management (Shumaker, 1997) and additionally be recommended in documents and policies that set care and housing standards for apes.

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