



## Original Investigation

Seasonal, diel, and ontogenetic patterns of within-den behavior in beavers (*Castor canadensis*)Cy L. Mott<sup>a,b,\*</sup>, Craig K. Bloomquist<sup>a,c</sup>, Clayton K. Nielsen<sup>a</sup><sup>a</sup> Cooperative Wildlife Research Laboratory, Department of Zoology, Southern Illinois University, Carbondale, IL 62901-6504, USA<sup>b</sup> Department of Biology, Kentucky Wesleyan College, 3000 Frederica Street, Owensboro, KY 42301, USA<sup>c</sup> USDA-APHIS-Wildlife Services, Midway AMC Bldg., 6201 Laramie Ave., Chicago, IL 60638, USA

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## ABSTRACT

Despite the ubiquity of denning as a natural history strategy among terrestrial vertebrates, little is known regarding basic patterns of within-den behavior, how such patterns are influenced by demographic and environmental parameters, or how within-den behavioral repertoires relate to activities performed in external environments. Den usage is believed to facilitate increased expression of behaviors that compromise fitness in external environments, though empirical data validating these assumptions are generally lacking. Relative isolation from external light cues within dens has been linked to temporal patterns of den use, yet few studies examine associations between photoperiod and rhythmicity strictly for within-den behavior. Also, for denning species with relatively equivalent parental investment, conclusions regarding sex-specific behavior have been equivocal, and no studies have examined potential segregation of parental activity within dens. We videorecorded 1506 h of within-den activity from 23 beaver (*Castor canadensis*) colonies and characterized behavioral patterns based on sex and age over daily and monthly intervals. Within-den time-activity budgets were equivalent among male and female adult beavers, with feeding, sleeping, allogrooming, and individual grooming accounting for more than 95% of all recorded behaviors. Behavioral repertoires within dens exhibited distinct seasonality and were influenced by temporal variation in external conditions associated with food availability, indicating linkages between activities within and outside of dens. Lastly, beaver age classes varied considerably in their associations between diel activity patterns and photoperiod, with adults and kits exhibiting single and multiple sleep-wake cycles, respectively.

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## Introduction

Denning behaviors occur among 70% of terrestrial vertebrate orders, representing families from all continents, excluding Antarctica, in all terrestrial biomes (Duellman and Trueb, 1986; Pough et al., 1998; Nowak, 1999; del Hoyo et al., 2008). Such activities include den construction and maintenance, food caching, feeding, breeding, play, and agonism, among others. Reliance on den sites varies from permanent colonization to construction of temporary retreats and exploitation of natural cavities, and, consequently, den structure ranges from rudimentary shelters to elaborate above-ground structures or subterranean burrow systems (Duellman and Trueb, 1986; Pough et al., 1998; Nowak, 1999; del Hoyo et al., 2008). The impact of denning activities on behavior may be considerable,

as a den's internal structure creates a suite of conditions distinct from external surroundings with respect to predation risk (Tietje and Ruff, 1980), availability of food (Smith and Reichman, 1984), and light intensity (DeCoursey, 1986), and such environments promote expression of behaviors not exhibited outside of dens (Rogers, 1974).

Previous research regarding denning activities has focused almost exclusively on denning chronology and site selection (e.g. Dieter and McCabe, 1989; Schooley et al., 1994). Few studies have described within-den behaviors for otherwise intensively researched denning species, and even rarer are studies that characterize seasonal patterns of within-den behavior. These data, however, are critical in assessing the influence of den conditions on behavioral repertoires and social interaction in confined environments in which individuals spend considerable portions of their lives. The scarcity of within-den behavioral data is due largely to difficulties in: (1) observing behavior without altering den structure; (2) observing organisms without disrupting natural behavior; and (3) observing species that use dens intermittently and synthesizing these data into a cohesive summary representative of 'typical'

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den behaviors. However, recent advances in remote videography technology have facilitated such studies, as video cameras thus employed are increasingly lightweight, weather-resistant, economical, and capable of extended operation (Sykes et al., 1995; Delaney et al., 1998; Bloomquist and Nielsen, 2009).

Den use has been hypothesized to facilitate novel behavioral repertoires relative to external environments, resulting primarily from reduced needs for vigilance and competitive behaviors within dens. Consequently, activities such as self-maintenance, play, feeding, and sleeping should be preferentially displayed within dens because, in general, such behaviors outside of dens are associated with reduced vigilance and consequent decreases in fitness (*sensu* Clutton-Brock et al., 1999; Dennis and MacDonald, 1999). In addition, denning species exhibit considerable interspecific variation in biological rhythms in response to photoperiod, as their connectivity to external conditions varies widely dependent upon den design and associated isolation from external stimuli (Rieter, 1974; DeCoursey, 1986). As a result, time-activity budgets of denning species may be closely associated with internal clock mechanisms, ambient photoperiod, or both, in addition to seasonal variation in external conditions (Kowalczyk et al., 2003).

Beavers (*Castor canadensis* and *C. fiber*) are arguably two of the most intensively researched denning mammals, due to their commercial value, complex social structure (Wilsson, 1968, 1971; Nowak, 1999; Baker and Hill, 2003; Crawford et al., 2008), multi-generational cooperative parenting system (Hodgdon and Lancia, 1983; Patenaude, 1983), and ecologically valuable construction activities (Nummi and Hahtola, 2008). However, behavioral patterns within dens (i.e. lodges and bank dens) are virtually unknown for beavers, as are the influences of den environments on activity and the formation of adult behavioral repertoires through ontogeny. Den conditions differ remarkably from the external environment with respect to such factors as temperature variation (Stephenson, 1969), conspecific density (Novak, 1977), and light cues, all of which have been shown to exert considerable behavioral influences among other mammalian taxa (Wolff, 1993; Beery et al., 2007; Dearing et al., 2008). An examination of within-den behavior is critical to understanding the influence of den conditions on social interaction, and to determining how within-den behavior may differ from that exhibited in external environments, as well as the ecological consequences of such variation. In examining these issues, we employed remote videography in this study to quantify within-den beaver behaviors and characterize seasonal and ontogenetic behavioral patterns among both sexes.

### Behavior outside of dens

Nearly all studies of beaver behavior are based on observations outside of lodges, with primary foci on territoriality (Muller-Schwarze and Heckman, 1980; Schulte, 1998; Sun and Muller-Schwarze, 1998), dam and lodge construction (Richard, 1983), and functions as ecosystem engineers (Nummi and Hahtola, 2008). The following accounts deal solely with patterns observed outside dens. Also, our review of behavioral patterns represents collective observations of both *C. canadensis* and *C. fiber* as is customary in beaver behavioral research.

Beavers are most active from spring to fall, when ice cover is absent from ponds and lakes. Individuals exhibit an active period of 11–13 h (Hodgdon and Lancia, 1983), typically between 1700 and 0800 h (Tevis, 1950; Busher, 1980; Lancia, 1979; Hodgdon and Lancia, 1983; Buech, 1995), during which time major activities include traveling and foraging (Sharpe and Rosell, 2003). Seasonal behavioral patterns are also evident, with increased construction and food caching occurring in autumn; these changes are associated

with obtaining fat reserves retained through periods of reduced resource availability (Richard, 1983).

Male and female beavers exhibit different behaviors depending on season. Sharpe and Rosell (2003) reported time budgets did not differ among sexes for most activities, but males exhibit longer daily activity periods and increased traveling behaviors associated with territory defense. Hodgdon (1978) observed females dedicate greater time to lodge maintenance than males, attributing this behavior as part of the ‘nesting instinct’; however, Busher (1980) observed the converse, with males exhibiting more frequent maintenance activities. Seasonal variation in territorial behaviors is also evident, correlating with the dispersal of subadults in spring (Rosell et al., 1998).

Finally, observations of both wild and captive, hand-reared individuals reveal ontogenetic patterns of behavior development. Lancia and Hodgdon (1983) reported that most behaviors exhibited by adults develop quite early in newborns; such activities include swimming, grooming, wrestling, and self-feeding, which are observed less than three weeks after birth. In addition, subadults and juveniles exhibit adult behaviors associated with construction and maintenance of lodges and dams prior to their dispersal from the natal colony (Hodgdon and Lancia, 1983).

### Research objectives and experimental hypotheses

Our first objective was to construct diel, monthly, sex- and age-specific time-activity budgets for male and female adult beavers and their kits. Based on previous findings of relatively equivalent parental behaviors between males and females (Sharpe and Rosell, 2003), we hypothesized that time-activity budgets for within-den adult behaviors would not differ by sex. However, based on general tendencies for increased feeding and sleeping among newborn mammalian taxa, we hypothesized that beaver kits would display greater frequencies of these activities relative to adults. Due to reduced needs for vigilance, we also hypothesized that behaviors observed rarely outside of dens, such as play, intraspecific aggression, and grooming, should be prevalent. With respect to temporal behavioral trends in beavers, few actions have been shown to vary seasonally, and activities that do vary are linked to aspects of territoriality (Sharpe and Rosell, 2003). Therefore, we hypothesized that the relatively consistent environmental conditions within dens would result in little seasonal variation in within-den behavior. Similarly, we hypothesized that diel variation in within-den activity would not be observed, as beavers within dens are somewhat isolated from variable light and temperature cues that typically influence behavior cycles. In testing these hypotheses, we characterize the development of social and other behaviors through ontogeny and across seasons. Our second objective was to qualitatively compare behavioral patterns of beavers within lodges to those observed previously by other researchers outside of lodges. Given the paucity of data concerning long-term patterns of within-den behavior, we utilized the null hypothesis that the most prevalent activities observed in external environments in previous studies should match those observed within dens in the present study. Finally, we examine these differences in the context of the influence of den environments on social and other behaviors.

### Material and methods

#### Study area and subjects

We observed within-den beaver behavior at the Union County Conservation Area (UCCA), southwestern Illinois, USA (Universal Transverse Mercator Zone 16 414000N, 290000E) between

February 2005 and October 2006, though observations were not continuous across months because they were a secondary component of a larger study (Bloomquist, 2007; Bloomquist and Nielsen, 2010) and dependent on study site accessibility. The UCCA lies within the Mississippi River floodplain and is characterized by interconnected networks of wetlands and drainage ditches interspersed with agricultural fields and bottomland hardwood forests composed of green ash, *Fraxinus pennsylvanica*, black willow, *Salix nigra*, cottonwood, *Populus deltoides*, sweetgum, *Liquidambar styraciflua*, pecan, *Carya illinoensis*, and pin oak, *Quercus palustris* (Kjolhaug, 1986). The primary aquatic flora includes buttonbush, *Cephalanthus occidentalis*, elodea, *Elodea* spp., and water lily, *Nymphaea* spp. (McNew, 2003). Beavers in this region experienced precipitous declines in the late 19th and early 20th century, but have since recovered (Pietsch, 1956). Harvest of beavers was prohibited on the UCCA; therefore, colonies were representative of an unexploited population (Bloomquist and Nielsen, 2010).

We live-captured beavers at the UCCA using snares prior to behavioral observations (McNew et al., 2007) from September to December in 2004 and 2005. We weighed beavers in crates hung on a spring scale (accurate to 0.3 kg), and assigned individuals to 1 of 4 age classes based on weight (McTaggart, 2002): kits (<11 kg), yearlings (1 year old; 11–16 kg), subadults (1–2 years old; >16–19 kg), and adults (>2 years old; >19 kg). However, due to difficulties in establishing age via video recordings, all individuals other than kits were grouped into the “adult” age class when characterizing within-den behavior patterns. We immobilized captured individuals using an intramuscular injection of a 9:1 mix (6–12 mg/kg) of ketamine hydrochloride and xylazine hydrochloride (Bloomquist, 2007). We sexed immobilized adults by palpating for bacula (Osborn, 1955) and fitted selected adults with a monel #4 ear tag (National Band and Tag Co., Newport, KY, USA) and a tail-mounted tag utilized for individual identification. Plastic tail-mounted tags were formed in distinctive shapes, coated with reflective tape, and mounted on the tail in specific locations such that individuals could be identified by location and shape of tail tags or the number on ear tags (Bloomquist, 2007). We attached identification tags by drilling an 8-mm hole through the tail proximal to the midline (Rothmeyer et al., 2002). We marked beavers from 4 colonies (7 males and 7 females) in such a manner.

#### Behavioral observations

We recorded within-den behaviors in 23 colonies (17 lodges and 6 bank dens) using burrow probe systems (Fuhrman Diversified, Seabrook, TX, USA); this apparatus and aspects of its use have been described in detail previously and have been determined not to disturb den structure or alter beaver behavior (Bloomquist and Nielsen, 2009). We recorded within-den behaviors over 30, 60, or 90-h intervals in sequential fashion, such that after all 23 colonies had been sampled, the entire recording process was repeated beginning with the first lodge initially sampled. Using this sequential sampling method, we recorded each of the 23 lodges between 60 and 180 h. All colonies were not sampled equally due to seasonal variation in site accessibility and the goals of an additional study which required repeated observations in certain colonies but not others (Bloomquist, 2007). All colonies selected in the first year of the study were recorded for 90 h, with all discrepancies between 30, 60, or 90 h recording intervals occurring during the second year. Within each recording session, the VCR was programmed to operate for two 5-h bouts and five 4-h bouts, with intervals between bouts used to exchange VCR tapes.

We classified behaviors according to previously established ethograms (Wilsson, 1971; Patenaude and Bovet, 1983; Patenaude, 1984; Buech, 1995; Sharpe and Rosell, 2003), but we did not observe all behaviors exhibited in previous studies (Table 1). We recorded

**Table 1**

Categories of observed beaver behavior and their descriptions.

Category	Description
Sleep/recumbent	Sitting or laying with no visible activity, or stretching
Feeding	Suckling, eating leaves or bark, or bringing food to the mouth
Individual grooming <sup>a</sup>	Grooming with forepaws, combing with double claw and hindpaw, grooming with teeth, or shaking
Allogrooming	Grooming another with forepaws, teeth or hindpaw
Lodge maintenance	Pushing sticks or mud with forepaws, picking up and removing sticks from chamber, gnawing or scratching at chamber walls, or making wood strippings for bedding
Locomotion	Quadrupedal or bipedal walking, galloping, or swimming
Exploration	Simultaneous smelling, scanning inside of den, touching of objects, with or without movement
Play	Climbing on each other without aggression or tumbling
Agonism	Chasing, wrestling, and biting
Unknown	Unable to determine the activity
Camera-related	A behavior in response to the presence of the camera
Other	Adults carrying kits, kits attempting to suckle one another, kits stealing twigs from one another

<sup>a</sup> Although body postures suggestive of coprophagy were evident from video data, such activities were not quantified because they were not components of the ethograms initially used to construct the ethogram presented here. Consequently, we made no distinction between the two behaviors, and instances of coprophagy were most likely classified as “individual grooming”.

the type, duration, and time of behaviors of both marked and unmarked individuals using focal sampling (Altmann, 1974), and we treated all beavers observed in the burrow probe’s field of view as focal individuals. In the case of multiple individuals performing actions simultaneously, we rewound video tapes until behaviors of all visible individuals were documented.

#### Data analyses

Prior to creation of time-activity budgets and subsequent statistical analyses, we eliminated behaviors associated with camera placement and use (<1% of all behaviors) or when behaviors were unknown due to beavers or vegetation blocking the field of view (~15% of all behaviors). Initially, we constructed time-activity budgets to identify behavior patterns associated with sex, age, time, and season. To distinguish between males and females in constructing sex-based time-activity budgets, we utilized only known individuals that had been sexed and tagged as previously described (7 males, 7 females). We omitted additional untagged individuals from these analyses, as their sex could not be determined. In constructing age-based time-activity budgets, we divided individuals into either “adult” (adult + subadult + juvenile) or kit age classes. We included subadults and juveniles within the ‘adult’ dataset as the specific ages of these three age categories could not easily be determined from video data, but we differentiated kits based on our abilities to witness birth events within colonies. Consequently, all behavioral data presented on “kits” from here onward include only those individuals recognized through video data as newly-born (not kits from the previous year), and assignment as “kits” persisted only until it became impossible to differentiate these individuals from juveniles from the previous year. To characterize diel patterns of within-lodge behaviors, we subdivided adult and kit behaviors separately into hourly intervals comprising a 24-h clock; we then created time-activity budgets for each interval. Finally, to identify seasonal behavior patterns, we subdivided adult and kit

**Table 2**

Hours of video footage for sexed and unsexed beavers (*Castor canadensis*) obtained from within-den cameras in southern Illinois, USA, operating between February 2005 and October 2006. Behaviors for certain demographics and months could not be obtained (denoted as NA).

Month	All adults	Sexed adults	Kits
February	67	19	NA
March	72	4	12
April	198	60	33
May	289	64	291
June	232	66	211
July	23	NA	3
October	75	3	NA
Subtotal	956	216	550
Total (adult + kits)	1506		

behaviors separately by month, with each month characterized by an individual time-activity budget.

We initially tested data for each behavior category for homogeneity of variances and normality using Levene and Kolmogorov–Smirnov tests, respectively, with the proportions of focal behaviors performed during each recording interval in each lodge as individual observations. We attempted to remedy deviations from equal variance and normality using logit transformations; if unsuccessful, we utilized equivalent nonparametric analyses. We first determined if behaviors were performed unequally throughout the study duration (i.e. if certain behaviors were performed over others) utilizing a Chi-square goodness-of-fit test. To test the null hypothesis that time-activity budgets for within-den behavior would not differ between males and females, we utilized paired *t*-tests (or Wilcoxon sign rank tests) of the proportions of each focal behavior (Table 1) displayed by each sex. To test for differences in the proportions of focal behaviors by age (adult or kit), time of day (each hour of a 24-h clock), and month, we utilized separate ANOVAs or Kruskal–Wallis tests for each variable, with the proportion of each focal behavior as the response variable. All statistical analyses were conducted using SAS version 9.1 (SAS Institute Inc., Cary, NC, USA), and only  $P < 0.05$  were deemed significant.

## Results

Between February 2005 and October 2006 we recorded 2830 h of video data from beaver lodges and bank dens. From this footage, we observed 1506 h of beaver behavior (Table 2).

**Table 3**

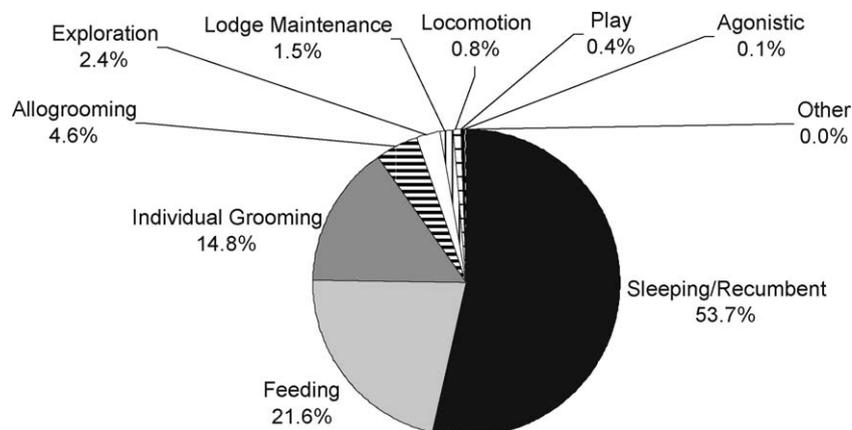
Results of separate Kruskal–Wallis tests for monthly changes in adult males and females and unsexed kits for each of 10 focal behaviors observed within beaver (*Castor canadensis*) lodges and bank dens in southern Illinois, USA, between February 2005 and October 2006. Degrees of freedom (df) values  $< 6$  for adults and  $< 3$  for kits indicate that these behaviors were not observed in all months for these life stages. ‘Other’ behaviors among kits were only observed in a single month and, consequently, no analyses of monthly changes in these behaviors could be conducted.

	Behavior	$\chi^2$	df	<i>P</i>
Adults	Agonistic	3.00	2	0.223
	Allogrooming	30.93	6	$< 0.001$
	Exploration	29.79	6	$< 0.001$
	Individual grooming	67.96	6	$< 0.001$
	Feeding	18.38	6	0.005
	Lodge maintenance	20.24	6	0.003
	Locomotion	34.34	6	$< 0.001$
	Other	0.38	1	0.539
	Play	7.55	4	0.110
	Sleeping/recumbent	17.86	6	0.007
Kits	Agonistic	2.86	2	0.239
	Allogrooming	8.35	3	0.039
	Exploration	12.29	3	0.007
	Individual grooming	11.95	3	0.008
	Feeding	9.07	3	0.028
	Lodge maintenance	2.52	2	0.283
	Locomotion	23.42	2	$< 0.001$
	Other	NA	NA	NA
	Play	25.12	2	$< 0.001$
	Sleeping/recumbent	27.96	3	$< 0.001$

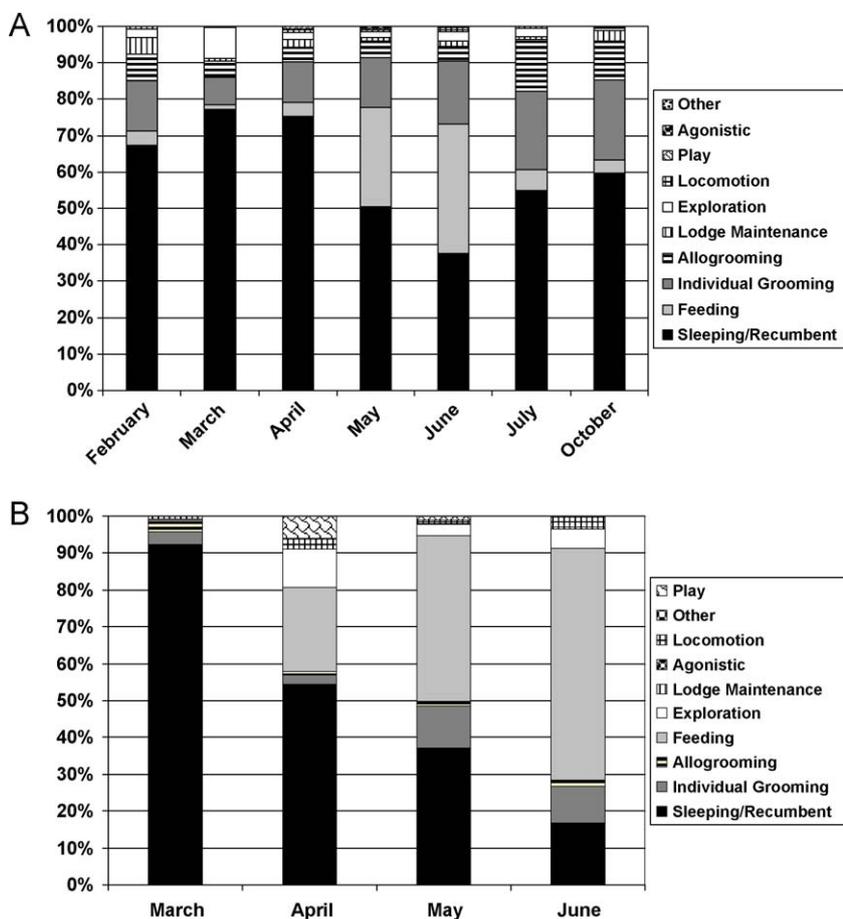
### Behavior of adults

No significant differences were found in behavior between adult males and females ( $\chi^2$  and *P* range = 0.00–1.80 and 0.18–1.00, respectively), thus data were pooled for all adults. Adult beavers did not allocate time equally among all behaviors ( $\chi^2 = 120,440,613$ ,  $df = 9$ ,  $P < 0.001$ ). The primary activities recorded among adults were sleeping/recumbent, feeding, individual grooming, and allogrooming, which, when combined, accounted for  $> 95\%$  of all within-den behaviors (Fig. 1). The prevalence of remaining focal behaviors ranged from 2.4% for exploration to  $< 0.01\%$  for ‘other’, which included: (1) adults carrying kits into the den; (2) kits attempting to suckle one another; and (3) kits stealing twigs from one another.

Significant seasonal differences existed in the frequency of many focal behaviors (Table 3 and Fig. 2A). Although sleeping/recumbent behaviors were most dominant during all months, the prevalence of these activities declined by 49% between March and June, followed by a subsequent increase to levels near those recorded in late winter and early spring. During this summer period of reduced



**Fig. 1.** Time-activity budget for adult beaver (*Castor canadensis*) within-den behaviors in southern Illinois, USA, among all sampling months combined from February to October 2005 to 2006, omitting unknown and camera-related behaviors.



**Fig. 2.** Monthly time-activity budgets for (A) adult beaver and (B) beaver kit (*Castor canadensis*) within-den behaviors for lodges and bank dens in southern Illinois, USA, recorded between February 2005 and October 2006 and omitting unknown and camera-related behaviors. Behaviors are stacked from top to bottom in order of increasing average frequency.

sleeping and resting, remaining hours were filled largely with significant increases in feeding, while the prevalence of most other behaviors remained relatively constant. As sleeping/recumbent behaviors began to increase in late summer and early fall, feeding was reduced by 83–89%, while individual grooming and allogrooming became 29–175% and 57–250% more common, respectively, than at any other time during the previous months. Exploration activities were 200–800% more common in March than during any other month, and significant seasonal differences were also observed for lodge maintenance and locomotion behaviors. Lodge maintenance activities peaked during the first and last months of observations, during which time they were 50–300% more common than in any other month. Locomotion was significantly higher in April and June relatively to other months, though this behavior was overall uncommon.

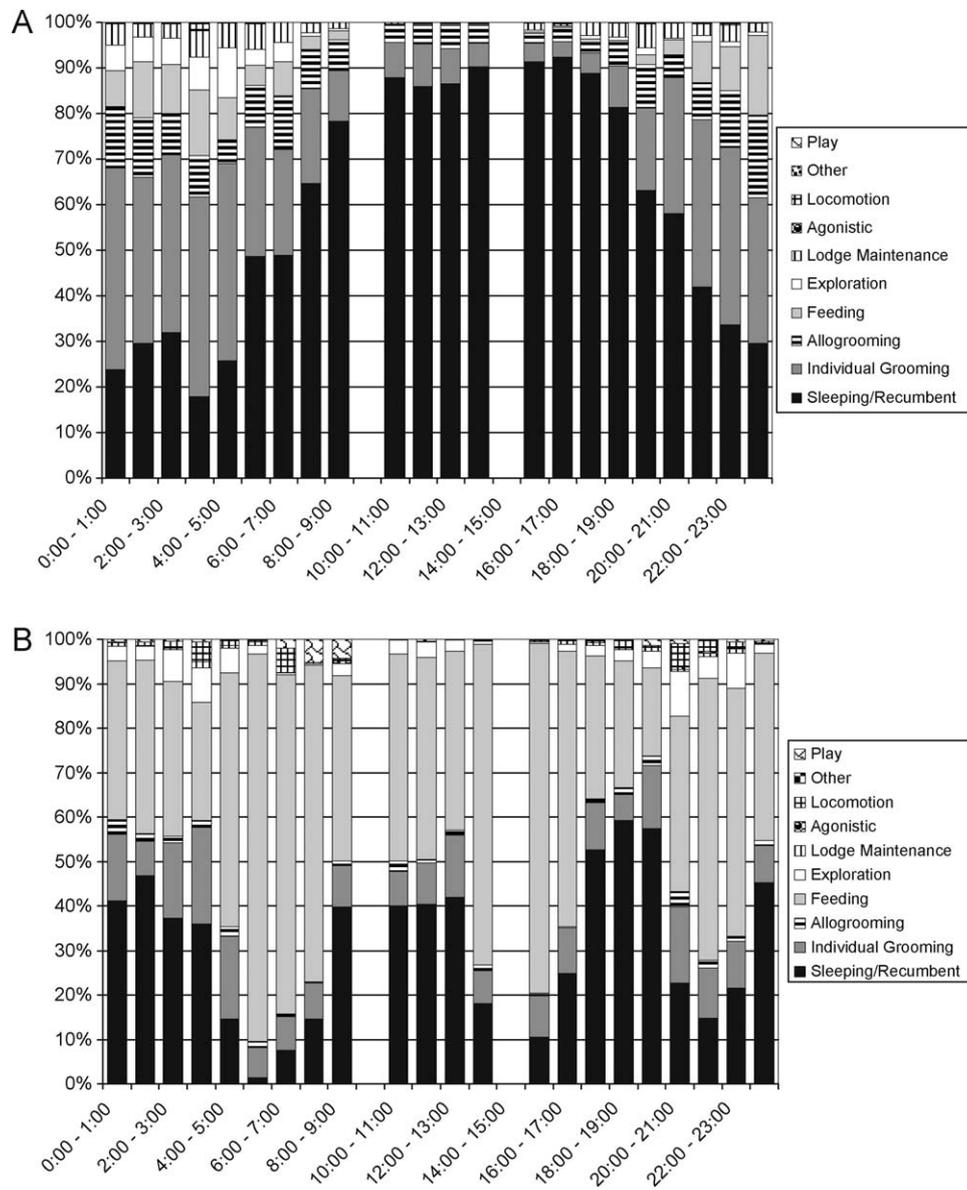
In addition to seasonal patterns in adult behaviors, distinct diel rhythms were apparent and characterized by fluctuations in the prevalence of several behaviors (Table 4 and Fig. 3A). A distinct sleep interval was apparent between ~0500 and 2100 h, during which times sleeping/recumbent activities dominated all other behaviors. However, a 'complete sleep' period, or one in which all colony members slept simultaneously, was not evident, as both individual grooming and allogrooming comprised 9–13% of all behaviors during even the middle of the sleep cycle. In the hours immediately preceding and following sleep periods, behaviors were largely dominated by increased feeding, individual grooming, allogrooming, and lodge maintenance, yet these behaviors were virtually nonexistent (<1%) during the core portion of sleep periods.

Increases in exploration were observed only in the hours preceding the sleep interval, during which time they were more common than at any point during or after the middle of the sleep cycle. In only 1 h of the day did agonistic, locomotion, play, and other behav-

**Table 4**

Results of separate Kruskal–Wallis tests for hourly change in each of 10 focal behaviors observed within beaver (*Castor canadensis*) adults and kits among lodges and bank dens in southern Illinois, USA, between February 2005 and October 2006. Degrees of freedom (df) values < 21 indicate that these behaviors were not observed during all hours sampled.

	Behavior	$\chi^2$	df	P
Adults	Agonistic	4.00	3	0.262
	Allogrooming	66.39	21	<0.001
	Exploration	41.35	21	0.005
	Individual grooming	37.72	21	0.012
	Feeding	42.59	19	0.001
	Lodge maintenance	101.34	21	<0.001
	Locomotion	22.65	21	0.363
	Other	7.02	4	0.135
	Play	3.93	6	0.686
	Sleeping/recumbent	147.48	21	<0.001
Kits	Agonistic	14.66	8	0.066
	Allogrooming	28.52	21	0.126
	Exploration	37.13	21	0.016
	Individual grooming	35.40	21	0.026
	Feeding	210.76	21	<0.001
	Lodge maintenance	15.38	12	0.222
	Locomotion	67.15	21	<0.001
	Other	9.00	5	0.109
	Play	42.15	18	0.001
	Sleeping/recumbent	63.88	21	<0.001



**Fig. 3.** Hourly time-activity budgets for (A) adult beaver and (B) beaver kit (*Castor canadensis*) within-den behaviors for lodges and bank dens in southern Illinois, USA, recorded between February 2005 and October 2006 and omitting unknown and camera-related behaviors. Hourly intervals with no time budget shown were not video recorded due to changing of video cassette tapes at these prescheduled times, and behaviors are stacked from top to bottom in order of increasing average frequency.

iors combined constitute  $>0.07\%$  of all behaviors, and none of these activities exhibited diel trends.

#### Behavior of kits

As with adult beavers, kits exhibited monthly behavioral patterns (Table 3 and Fig. 2B). The most prominent monthly change in kit behavior was the decrease in sleeping/recumbent behaviors with a concomitant increase in feeding during March–June. During this interval, sleeping/recumbent activities decreased from  $>90\%$  to  $<20\%$  of all behaviors, while feeding increased from an initial  $<1\%$  in March to  $>60\%$  by June. We also observed monthly differences in play behaviors, which were  $>530\%$  more frequent in April than in any other month. Individual grooming activities, though present from birth through late summer when kits from the previous summer could no longer be differentiated from adults, became significantly more common through time, increasing by 150% between March and June. Allogrooming behaviors, although less common than individual grooming, showed temporal variation

as well, occurring 50–200% more often in March than in any subsequent month. Monthly changes were also observed for exploration and locomotion, though no distinct trends could be detected, and no monthly changes in agonistic behavior or lodge maintenance were detected.

Beaver kits demonstrated significant diel behavioral trends, though these patterns were not synonymous with those observed among adults (Table 4 and Fig. 3B). Although kits exhibited sleeping/recumbent behaviors during all hours, periodic bouts in these activities were clearly evident, with each of three separate sleep intervals lasting approximately 5 h. Feeding activities dominated the daily activity of beaver kits, representing 27–87% of all behaviors within a given hour and the dominant activity when kits were not primarily exhibiting sleeping/recumbent behaviors. Although kits performed exploration activities continually though the day, these behaviors were largely nocturnal in nature, occurring primarily between 1900 and 0500 h, and rates of exploration during this interval were about 200% more frequent than during daytime hours. In addition, increases in play were observed between 0600

and 0900 h, though at no other hours did play behaviors comprise >1% of all recorded behaviors. Significant diel differences in individual grooming and locomotion were also observed, though we could not identify distinct temporal patterns for these behaviors. No significant hourly changes in agonistic, allogrooming, lodge maintenance, or other behaviors were detected.

## Discussion

Beavers in our study exhibited distinct seasonal, diel, and ontogenetic patterns of within-den behaviors, though no differences were observed between sexes. Among adults and kits, dominant behaviors included those associated with sleeping, feeding, and grooming, but seasonal and diel behavioral patterns differed among age classes. Across both diel and seasonal scales, behavioral shifts primarily consisted of changes in frequencies of feeding and sleeping, though we observed temporal trends for most focal behaviors. This research is the first to provide quantitative assessments of within-den behavior in beavers and document behavioral variation among denning, social mammals attributable to demographic and temporal variables under conditions of limited external stimuli.

That beavers primarily exhibited sleeping, feeding, and self-maintenance behaviors is consistent with previous mammal research (Gelatt et al., 2002) and identifies the most basic of animal activities. Specifically, activity patterns observed among our colonies infer the development of behavioral adaptations necessary for herbivorous, semi-aquatic denning mammals. Feeding activities, which were both continuous throughout the day and a dominant behavior in most hourly intervals, likely reflect the relatively poor nutritional quality, low assimilation efficiency, and increased handling/processing time associated with herbivory (Sternler and Hessen, 1994). However, feeding behaviors were not necessarily related to available foraging habitat, as aquatic habitats remained essentially ice-free throughout the study, and colonies varied widely in the presence of absence of food caches (Bloomquist, unpublished). Beavers in this region exhibit maximum home range sizes during winter months (Bloomquist, 2007), likely in meeting their daily metabolic requirements in the face of reduced vegetative growth. This increased winter use of external environments could account for much of the reduced time spent feeding observed in lodges. The intensity of feeding may also be associated with a reduced need for vigilance and other protective behaviors within dens, as individuals could preferentially perform activities that would leave them vulnerable outside of dens. In the absence of predation risk or competitors within dens, individuals feed in relative safety, resulting in extended feeding bouts lasting several hours. Regarding the prevalence of self-maintenance behaviors, individual- and allogrooming are associated with extensive use of aquatic habitats and frequent lodge maintenance, both of which necessitate continuous pelage care to ensure critical properties of insulation and buoyancy (Scholander et al., 1950; Fish et al., 2002). Allogrooming also reinforces social bonds among colonial mammals (Schino et al., 2005), and such behaviors could reduce aggression within dens when conspecifics are densely aggregated.

Agonistic interactions were seldom observed within our colonies, and no seasonal, ontogenetic, or sex-biases in aggression were detected. However, as Hodgdon and Lancia (1983) noted, agonism among beavers is largely represented through vocal displays as opposed to physical violence, and the former could not be detected in our study. Nevertheless, the lack of physical aggression within dens suggests the operation of pacifying mechanisms, behavioral or otherwise, that reduce or prevent density-dependent increases in agonism noted in other vertebrate taxa (Van Buskirk and Smith, 1991; Holbrook and Schmitt, 2002). That little aggression was observed prior to subadult dispersal supports the assertion

that dispersal is instinctual and not mediated by agonistic interactions. However, the role of adult aggression in initiating dispersal may also rely on the availability of quality resources for subadults, as offspring may resist dispersing when food is scarce.

The overall behavioral similarities between males and females supports our hypotheses regarding limited behavioral differentiation based on sex. Our observations are in agreement with previous studies of beavers (Sharpe and Rosell, 2003) and other socially monogamous mammals (Kleiman, 1977; Runcie, 2000) that suggest ethological differences between sexes are minimized when parental duties are similar and required by both sexes in rearing altricial young. Although previous studies indicate sex-biases in nest construction activities by beavers (Hodgdon, 1978; Busher, 1980), these results are inconsistent and, when compared with the current study, suggest a continuum exists wherein certain behaviors may be primarily conducted by males, females, or both sexes. Such a range in behavioral repertoires may reflect geographic or demographic variation attributed to such factors as: (1) availability and choice of den construction materials; (2) number of offspring assisting in den maintenance; (3) local climate effects on den integrity; or (4) time spent performing other behaviors.

We also observed ontogenetic behavioral shifts, with kits increasing time spent feeding and performing other behaviors in lieu of sleeping as individuals aged. These results are in agreement with our *a priori* hypotheses and highlight the importance of these activities to developing young. We note that nursing by kits was included under “Feeding”, such that ontogenetic increases in feeding do not solely represent increased ingestion of solid food, but rather increased ingestion of all food sources. As noted by Hodgdon and Lancia (1983), and confirmed by our observations, newborn kits are not restricted to nursing, as they are capable of self-feeding on vegetation within a few days following birth. Ontogenetic increases in self-feeding, play, and individual grooming are likely indicative of development of muscular strength, coordination, and sensory abilities, as our observations, in conjunction with prior studies, suggest kit behaviors are innate and not acquired. Lancia and Hodgdon (1983) observed that kits displayed almost all adult behaviors within weeks of birth, and in our colonies, all behaviors recorded among adults had been detected among kits within one month post-birth. As observed by Patenaude (1983), play behavior in our colonies was most common among kits, and they also displayed increased exploratory and locomotive behaviors 1–2 months following birth. Collectively, these observations support the hypothesis that kit behavior development may be most limited by physical development rather than by processes of acquiring adult behaviors through social learning, mimicry, or other mechanisms.

Adult beavers and kits also displayed diel rhythms of within-den behavior; overall, these findings are inconsistent with our hypotheses regarding the influence of external stimuli or other time-keeping cues present within the den. Among kits, diel patterns centered upon feeding and sleeping, which is consistent with the necessity of repeated bouts of rest and either nursing or self-feeding among newborn mammals (Green, 1986; Perry and Stenson, 1992). However, the periodicity of kit feeding activities, in which kits slept for 3–4 h between bouts, did not appear to correlate with either external photoperiod or activity cycles of parents, as feeding often occurs when adults are typically outside the lodge (Tevis, 1950) or predominantly sleeping. However, as stated previously, kit feeding activities were not limited to nursing, even among newborns; therefore, the ability of kits to feed themselves early in development may free them from a reliance on parental availability for nutrition. Contrary to the periodicity of kit behavior within dens, adults displayed a single diel sleep–wake cycle. Although beavers slept at times throughout the 24-h clock, if we characterize individuals as ‘active’ outside the intervals where sleeping was most

frequent (~80% or more of hourly behavior), beavers in our colonies exhibited an active period of ~13 h (1900–800 h), which is consistent with previous observations (Tevis, 1950; Hodgdon and Lancia, 1983; Buech, 1995). This estimate is consistent with observations that beavers were primarily active outside of dens at dawn and dusk. Adult activity periods were more closely aligned with ambient photoperiod than those of kits, though we could not quantify the intensity of external light cues within the den or their synchronicity with within-den activity. Regarding the influence of ambient light, it is interesting to note that beavers lack a tapetum lucidum and are thus unsuited for nocturnal vision (Richard, 1978), despite their largely crepuscular and nocturnal activity patterns. However, we could detect some changes in external light intensity within the den, so it is therefore possible that den conditions may not prohibit the influence of external photoperiod on within-den behavior.

Contrary to our initial hypotheses regarding the stability of den environments facilitating static seasonal behavior patterns, external conditions clearly influenced within-den behavior, as evidenced by seasonal shifts in adult activity patterns. Decreased sleeping, as well as increases in feeding and other behaviors observed in early spring, is likely associated with greater availability of aquatic habitats following spring melt, as well as increased abundance of vegetation utilized for lodge maintenance and direct consumption. Concomitant increases in grooming activities and feeding occurring through summer are likely also linked to increased habitat availability and use, which necessitate increased pelage care. Increased feeding throughout summer may also be associated with attempts to increase fat reserves or food caches (Jenkins, 1979; Richard, 1983) or maximize resource use prior to decreases in availability of open habitat or herbaceous vegetation in autumn or winter (Novakowski, 1967; Aleksiuk, 1970). Observed increases in lodge maintenance during autumn are consistent with previous observations (Hodgdon and Lancia, 1983) suggesting these activities are performed in preparation for winter condition of reduced resource availability. However, we also detected increased lodge maintenance immediately prior to parturition during early spring. These activities may reflect 'nesting' instincts described by Hodgdon (1978), as this period was also characterized by increased adult den exploration, which may represent increased sentinel behavior prior to and immediately following parturition similar to the 'protective triangle' formed by colony members around newborn kits (Patenaude, 1983). It could also be suggested that increased exploratory behavior within dens may be reflective of pre-dispersal restlessness of subadults within a colony; however, it should be noted that in our colonies, dispersal occurred prior to observing increased exploratory behavior (Bloomquist, 2007).

Based on our observations, within-den beaver behaviors are generally similar to those performed in the external environment, but certain activities are performed preferentially and with distinct periodicity. For example, Sharpe and Rosell (2003) observed that traveling, foraging, and 'being in the lodge' were the predominant activities of individuals observed outside of dens, and that grooming, sleeping, and social interaction represented a fraction of recorded behavior. While we observed a similar suite of activities, the increased prevalence of such behaviors as sleeping, individual- and allogrooming, and lodge maintenance suggest that certain behaviors are preferentially reserved for the confines of dens. These differences may reflect the relative security afforded by den structure, the propensity for related individuals to be aggregated, or other factors such as within-den light availability. Regardless of the mechanism by which individuals are influenced by within-den conditions, the lack of intra-colony aggression observed in our study suggests that certain behaviors, such as play and allogrooming, may contribute to social stability among colonial mammals.

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