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Effect of Diet on Sleeping Patterns and Energy Budgets of Two Mammalian Species, *Panthera tigris jacksoni* and *Giraffa camelopardalis tippelskirchi*

ABSTRACT

Sleep is often viewed as a vulnerable state of animal behavior as the animal becomes relatively unresponsive to the environment making them more susceptible to predation. Sleep must fulfill some universal function, however, as the behavior has survived species propagation and natural selection. This function is still unknown. The objective of this study was to investigate how diet can affect the sleeping patterns and energy budgets of two mammalian species, *Panthera tigris jacksoni* and *Giraffa camelopardalis tippelskirchi*. This was tested by conducting observations on the animals over several weeks at the Cincinnati Zoo and Botanical Garden (CZBG). Results show that the carnivore spent the most time resting (60% ± 0.4%), whereas the herbivore spent the most time feeding (68% ± 5.7%). Results are significant as they demonstrate diet contributes to an animal's sleeping pattern and overall activity. Diet is simply one piece to a bigger picture; several other ecological variables have been implicated in affecting sleeping patterns as well. It still remains to determine which of the proposed functions of sleep are universal across mammalian species and which functions may only be achieved during sleep, but scientists are well on their way to accomplishing just that.

INTRODUCTION

Many animals, ranging from insects like *Drosophila* to large mammals like the ever-swimming Indus dolphin and the polar bear, engage in some form of sleep or sleep-like behavior (Lima *et al*., 2005; Siegel, 2008; Zepelin *et al*., 2005). Sleep is most commonly defined as sustained stillness in a species specific posture, reduced responsiveness to external stimuli, characteristic changes in brain activity, homeostatic regulation, and is rapidly reversible. These criteria, however, exhibit notable interspecies variation. For example, an animal does not necessarily have to be immobile to sleep; some crustaceans have been reported to sleep while moving (Zepelin *et al*., 2005). Also, while we typically think of laying on the side or stomach with the eyes closed as the typical sleeping posture in mammals, some animals like the giraffe and elephant can sleep while standing and other animals can sleep with their eyes open.

Despite the prominence of sleep in the lives of animals, up to 20 hours a day in some species, sleep has received little attention from animal behaviorists throughout history and was often treated as a behavioral state that exists simply when the animal 'has nothing better to do'. Recently, however, as advances have been made in molecular biology and neuroscience, an explosion of sleep studies in animals have been published. Even still, the majority of studies have been performed on mammalian species and represent only about 3% of roughly 4260 extant species (Zepelin *et al*., 2005).

Sleep is often viewed as a vulnerable state of behavior as the animal becomes relatively unresponsive and alert to the environment making them more susceptible to predation. Sleep must fulfill some universal function, however, as the behavior has survived species propagation and the natural selection process and is so widespread across the phylogentic tree. Although it has been proposed that sleep has a universal function across all species, there has been no consensus to date as to what that function might be; neocortical maintenance, development, memory consolidation, system regulation, and energy conservation have been proposed, to name a few (Zepelin *et al*, 2005).

One might expect species in each mammalian order to have similar sleep patterns because of their genetic, behavioral, and anatomical similarities. This is not the case, however (Siegel, 2005). In fact, phylogenetic relations convey a confusing message about the function of REM sleep. Studies of placental and marsupial mammals indicate three major predictors of REM sleep duration: REM time is positively correlated with total sleep time, maturity at birth, and security of sleep site. These predictors, however, do not explain REM sleep durations in birds nor the nature of sleep in echidna, and it can be stated that REM sleep time is not strongly correlated with phylogenetic order (Siegel, 1995). Differences in order do not simply explain differences in sleep amounts. Primates as a group do not have sleep characteristics that distinguish them from Rodentia, Insectivora or other orders. More often, across mammals the amount and nature of sleep have been correlated with age, body size, and ecological variables, such as whether an animal lives in a terrestrial or an aquatic environment, predation and the safety of their sleeping sites, and their diet.

It is likely that multiple factors influence mammalian sleeping patterns, however, the objective of this study was to investigate how diet alone can affect the sleeping patterns and energy budgets of two mammalian species, the carnivorous *Panthera tigris jacksoni* (Malayan Tiger) and the herbaceous *Giraffa camelopardalis tippelskirchi* (Maasai Giraffe). It was hypothesized that diet would have an effect on overall energy budget of the animals and it was predicted that the herbivore will spend less time asleep than the carnivore in order to accommodate its diet of low calorific density food items and increased need to feed.

METHODS

Identifying subjects

Observations were collected on two Malayan Tigers (male/male, carnivorous) and two Maasai Giraffe (male/female, herbaceous) at The Cincinnati Zoo and Botanical Garden (CZBG) in July 2012. Animals were selected initially based on diet alone. The tigers' daily diet included 7lbs of an assortment of ground beef (with bones and internal organs), rabbit, and horse neck divided between two feedings (AM/PM). The giraffes' daily diet included up to 75lbs of predominantly alfalfa, but also included rye crackers, fresh fruit and other plant-based material from grazing in the yard. Though selected initially based on dietary requirements, other similarities made subjects ideal study candidates: all animals studied were five years of age; both sets of animals were housed in outdoor exhibits and were the only the two animals that inhabited the space; the animals' native climates can reach temperatures recorded throughout the summer in Cincinnati, Ohio.

Categorizing activity

Animal behaviors were divided into four activity categories based on a preliminary ethogram as well as previous studies (du Toit & Yetman, 2005; Logan & Sanson, 2002; Mallapur & Chellam, 2002): resting, stationary alert, locomotion, and feeding (Table I). In the event that two or more categories co-occurred within a single time segment, the category recorded was determined on the basis of a rarity hierarchy (feeding—locomotion—stationary alert—resting*), where feeding was the rarest and given highest priority for the tigers and the reverse, resting, was the rarest and given highest priority for the giraffes.
*In this study, resting is used as a proxy for sleeping

Observations, data collection, and interpretations

Observations were collected in randomized blocks. Each block included two observational days, and on each day both animals were observed in multiple 1hr time segments. On the second day of observations, observations deliberately took place in the opposite order to ensure equal viewing that spanned the same time frame for each animal. A total of three observation blocks were completed, equating to 6.5hr of observation time per animal, by classifying the animal's behavior into one of the four pre-determined categories every minute. Observations were completed until deviation stabilized within sample sets.

Results were tabulated; each animal's daily activity budget was determined by dividing the time spent in each category by the total observation time and then converting to percent form. As two animals were observed per feeding group, means and standard error of the means were calculated for statistical comparison.

Table I Ethogram of Behaviors

Behavior Observed	**Description**
Feeding	The animal put food into mouth or chewed an edible substance. Includes foraging behavior and drinking. Ruminating behavior also included as suggested by du Toit and Yetman (2005).
Locomotion	Movement of the animal that resulted in change of location
Stationary Alert	The animal was motionless with eyes open and alert to surroundings
Resting	The animal was motionless with eyes closed

RESULTS

As predicted, diet and activity are directly related. Results show that the carnivore (Malayan Tiger) spent the most time resting (60% ± 0.4%), whereas the herbivore (Maasai Giraffe) spent the most time feeding (68% ± 5.7%). Both the carnivore (C) and the herbivore (H) spent similar amounts of time in the stationary alert and locomotion categories at 27.5% ± 0.9%(C) / 21.5% ± 4.5%(H) and 12.1% ± 0.9%(C) / 10.5% ± 1.2%(H) respectfully. Resting behavior was not observed in the herbivore throughout the course of study, and very little (<1%) time feeding was observed in the carnivore (Figure 1).

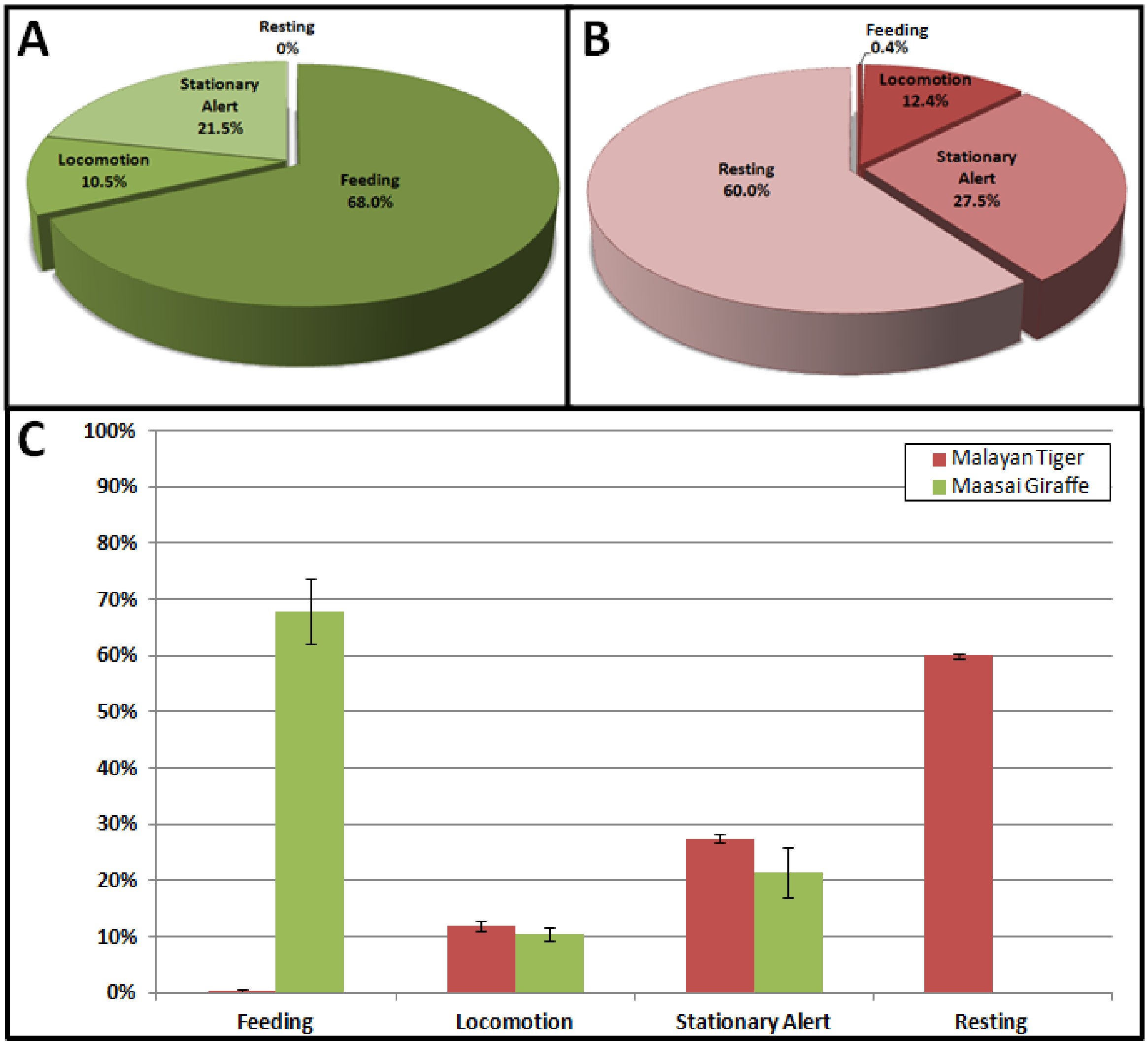

Figure 1. Activity distribution of the Malayan Tiger and Maasai Giraffe. Distribution of observed behaviors in herbivore **(A)**, and carnivore **(B)** relative to total observation time. Comparison of energy budgets **(C)** shows significantly different patterns for resting and feeding between the two feeding groups. The carnivore (Malayan Tiger) spent the most time resting (60% ± 0.4%), whereas the herbivore (Maasai Giraffe) spent the most time feeding (68% ± 5.7%). No statistical difference was observed in either locomotion or stationary alert behavior categories between the carnivore and herbivore. Error bars are the standard error of means.

DISCUSSION

The effect of diet, an ecological variable, on sleeping patterns of two mammals was examined by conducting behavior observations and constructing energy budgets. Results show that the carnivorous species, the Malayan Tiger, spent more time resting per day (60% ± 0.4%) than the herbaceous species, the Maasai Giraffe, (0%). This data supports the original hypothesis that diet would have an effect on overall energy budget of the animals. The original prediction, that the herbivore would spend less time asleep than the carnivore in order to accommodate its diet of low calorific density food items and increased need to feed, was also supported. The herbivore spent 68% ± 5.7% feeding, whereas the carnivore only spent 0.4% ± 0.4% feeding.

Similar studies have been conducted previously and have found comparable results. Sleep time in carnivores, omnivores, and herbivores has been demonstrated to be significantly different, with carnivore sleep amounts significantly greater than herbivores (Zepelin *et al*., 2005; Siegel, 2005). In herbivores, sleep time is inversely correlated with body mass; this in turn is associated with increased time budget allocations for feeding and moving (du Toit &Yetman, 2005). Other studies have produced energy budget data similar to those obtained in this study. One study conducted at the Harbin Zoo in Harbin, China, observed four Amur Tigers over the course of three years. It was found that all four individuals spent more time sleeping than any of the other behaviors, with time spent in this behavior category ranging from 47% to 60% (Li wei *et al*., 2002). A study completed across four zoos in India on another big cat and relative to the tiger, the leopard, found that resting behavior varied from 65% - 90% (Mallapur & Chellam, 2002). Other behaviors in both studies also showed similar trends to those here.

Though the resting behavior was not observed in the Maasai Giraffe in this study, it has been recorded in others. Tobler and Schwierin found that total sleep time in the giraffe was only 4.6hr of a 24hr sleep profile. Of this, only 4.7% of time was spent lying down in the paradoxical sleep position (Sup.Fig. 1A), which is the phase comparable to REM sleep in other mammals. Standing sleep, a characteristic of many ungulates, accounted for only 47 mins of the 24hr sleep profile. They continue by suggesting several factors that contribute to the amount sleep in ungulates: frequent disturbances by the public in zoos, night observations influence behavior simply by the presence of an observer, and their vegetarian diet which necessitates large amounts of food. Sleeping behaviors are fragmented, which could be a result of predator/prey behavior and standing sleep could have evolved as a means to avoid predation as the transition from lying down to standing posture is slow in giraffes (Tobler & Schwierin, 1996).

While the contribution of diet to sleeping patterns has been investigated before, a definitive link to why carnivores and herbivores have different behavior patterns is only speculation. Three hypotheses seem to be the most predominant in the literature: 1) the activity hypothesis, 2) the food quality hypothesis, and 3) the muscle performance hypothesis.

The activity hypothesis is based on the idea that correlation between basal metabolic rate (BMR) and diet would be the by-product of the relationship between activity and diet. Carnivores occupy a higher trophic level and their food is typically more widely dispersed than animals that eat only vegetable matter. Higher BMRs of carnivores could be a consequence of the fact that they expend more energy to pursue, kill, and handle their prey (Munoz-Garcia & Williams, 2005). These higher hunting costs along with high-speed chases call for an increase in resting time in the animal (Carbone *et al.*, 2007). A classic case of this scenario can be found in the cheetah's hunting habits; this predator is the fastest land animal, but expends so much energy when trying to catch its prey that it must immediately rest after hunting in order to recover, sometimes up to 30 minutes. In some cases, the cheetah may even be too tired to eat following a catch. Their body temperature can reach 105°F when sprinting, and after catching its prey, the animal is often seen dragging their kill to a shaded area which helps bring their body temperature back to normal levels (www.cheetah.org).

The food quality hypothesis states that carnivorous species tend to have larger BMRs because food items they consume are more digestible, free of chemical deterrents, and are generally available throughout the year. Conversely, herbivores have lower BMRs because plant material is poorly digestible, more likely to have chemical deterrent, is less available during some seasons. It is the various properties of the foods the limit the rate in which energy is acquired by the mammal and therefore the rate at which the mammal can expend energy (McNab, 1986)

The muscle performance hypothesis recently put forth by Munoz-Garcia and Williams suggests that a carnivore's muscle structure is made for endurance as foraging for vertebrate prey typically requires movement over large distances. When a species incorporates vegetable material into their diet, home range size, thus activity, as well as muscle requirements can decrease (Munoz-Garcia & Williams, 2005). Protein synthesis in the brain has been shown to increase during slow-wave sleep (Siegel, 2005). Perhaps carnivores spend more time sleeping in order to synthesize additional muscle fiber that is not necessary in herbivores. Such an increase would help accommodate the higher demands for slow oxidative fibers in the muscles which yield high endurance and high efficiency (Munoz-Garcia & Williams, 2005).

There were multiple potential sources of error in the experiment that should be taken into account when interpreting data. First, the data collected on the Maasai Giraffe were from a male/female sample set, whereas the Malayan Tiger data were from a male/male sample set. While it was initially thought that this difference would not affect the sleeping behavior comparison to carnivores, it should be mentioned that it is likely to have affected the overall energy budget of the animal. A study conducted by Robin Pellew suggests that females and males have different feeding strategies; females have adopted the strategy of 'energy maximizers' and males have adopted the strategy of 'time minimizers'. This means that females increase their fitness by maximizing their net rate of energy intake in the allotted foraging time whereas males increase their fitness by minimizing foraging time, which leaves more time to seek out females and increase reproductive fitness (Pellew, 1984). This was directly observed in the present study. Tessa, the female Maasai Giraffe engaged in feeding behavior 73.7% of the study, and Kimba, the male giraffe only engaged in feeding behavior 62.2% of the study (Sup.Fig. 2A). This ‘time minimizing’ feeding behavior would conversely explain the increased stationary alert time observed in the male versus the female.

Another potential source of error comes from the inability to be able to accurately discern sleep in ungulates (Zepelin *et al.*, 2005). After the data for this study had been collected, it was determined that giraffes can be in a state of sleep with their eyes open or shut. It has been reported that giraffes sleep in the standing position, as well as in the recumbent position, described as lying on the brisket and the flank with the legs folded under and slightly displaced to the side and neck bent forward in a position less vertical than when awake (Tobler & Schwierin, 1996). Kimba, the male Maasai Giraffe, was observed in the recumbent position during this study (Sup.Fig. 3A); his eyes were open so this time was recorded as ‘stationary alert’, however, in hindsight, this posture potentially could have classified as sleep as well. Though data may have changed slightly with this revelation, again, trend that carnivores sleep more than herbivores would still hold true.

The contribution of diet to an animal’s sleeping pattern is only a piece of a very complex puzzle. Body mass, brain size, and developmental stage have also been implicated as factors of sleeping habits. Sleep likely has multiple functions for the brain and body. An important task for future research will be the identification of which of the hypothesized functions may only be achieved during sleep, and which may be executed during both waking and sleep, with sleep being a more efficient time for their accomplishment. It also remains to be determined which, if any, of the proposed functions are universal across mammalian species and across the lifespan, and which may be limited to particular phases of development. By combining the recent developments of neuroscience and molecular biology, scientists are well on their way to accomplishing just that.

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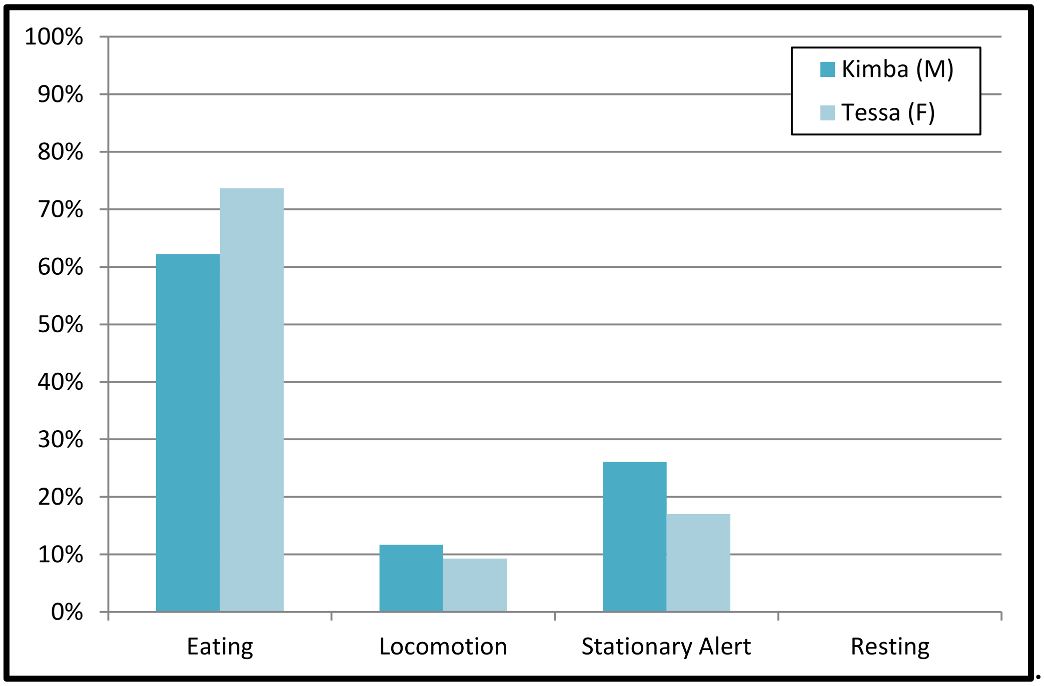
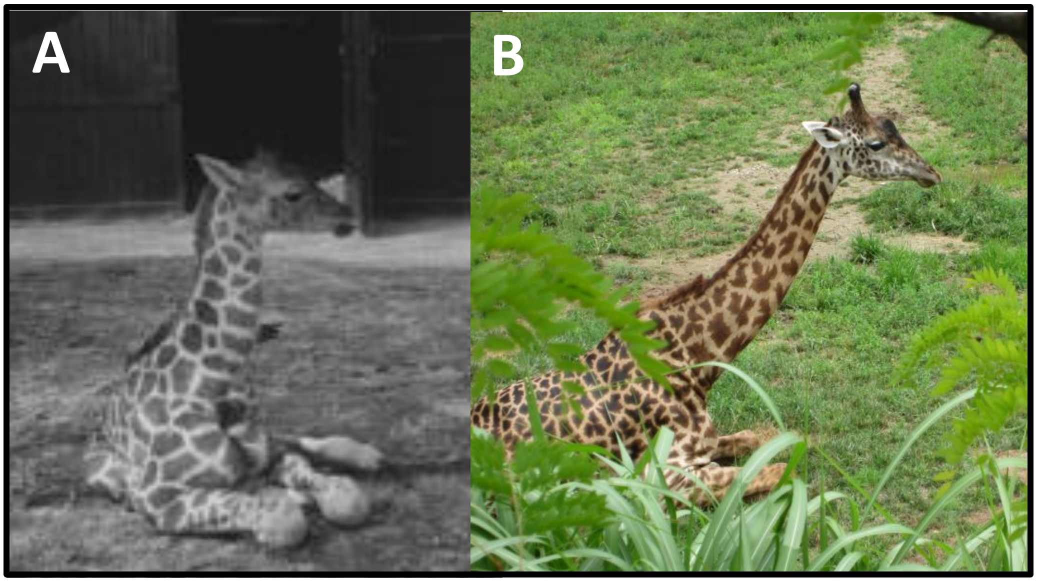
SUPPLEMENTAL FIGURES

Sup.Fig. 1A. Posture typical for paradoxical sleep in giraffe. (Tobler & Schwierin, 1996)



Sup.Fig. 2A . Activity distribution of the male and female Maasai Giraffe. Comparison of energy budgets show different feeding patterns between the male and female subjects. The female, Tessa, spent the more time feeding (73.7%) compared to the male, Kimba (62.2%). This result is consistent with the observation that females are 'energy maximizers' and males are 'time minimizers' put forth by Pellew.



Sup.Fig. 3A. Posture typical for recumbent sleep in giraffe. As defined in Tobler & Schwierin, 1996 (A) and behavior observed at CZBG (B).