

PHOTIC PREFERENCE OF THE SHORT-TAILED OPOSSUM (*MONDELPHIS DOMESTICA*)

A. M. H. SEELKE,^a J. C. DOOLEY^a AND
L. A. KRUBITZER^{a,b,*}

^a Center for Neuroscience, University of California, Davis,
1544 Newton Court, Davis, CA 95618, United States

^b Department of Psychology, University of California, Davis,
1544 Newton Court, Davis, CA 95618, United States

Abstract—The gray short-tailed opossum (*Monodelphis domestica*) is a nocturnal South American marsupial that has been gaining popularity as a laboratory animal. However, compared to traditional laboratory animals like rats, very little is known about its behavior, either in the wild or in a laboratory setting. Here we investigated the photic preference of the short-tailed opossum. Opossums were placed in a circular testing arena and allowed to move freely between dark (0 lux) and light (~1.4, 40, or 400 lux) sides of the arena. In each of these conditions opossums spent significantly more time in the dark than in the illuminated side and a greater proportion of time in the dark than would be expected by chance. In the high-contrast (~400 lux) illumination condition, the mean bout length (i.e., duration of one trip on the light or dark side) was significantly longer on the dark side than on the light side. When we examined the number of bouts greater than 30 and 60 s in duration, we found a significant difference between the light and dark sides in all light contrast conditions. These data indicate that the short-tailed opossum prefers the dark to the light, and can also detect very slight differences in light intensity. We conclude that although rats and opossums share many similar characteristics, including ecological niche, their divergent evolutionary heritage results in vastly different behavioral capabilities. Only by observing the behavioral capabilities and preferences of opossums will we be able to manipulate the experimental environment to best elicit and elucidate their behavior and alterations in behavior that can arise from experimental manipulations. © 2014 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: marsupial, behavior, evolution, vision, nocturnal, photic preference.

INTRODUCTION

One of the most fundamental behavioral characteristics of any living species is diel pattern. Yet, for mammals there is relatively little comparative data on basic aspects of

behaviors associated with the diel pattern such as photic preference. Diel pattern varies dramatically within orders, families, and genera, and can even vary within a species depending on climate and environmental context. For example, in the wild, a pig's (*Sus scrofa*) diel pattern can be dependent upon climate, such that in temperate regions pigs are diurnal while in tropical regions they are nocturnal. However, North American and European domestic pigs show a strong tendency toward diurnality, due to a temperate climate and the environmental constraints imposed through domesticity (Ruckebusch, 1972; Campbell and Tobler, 1984; Robert and Dallaire, 1986; Robert et al., 1987). Behavioral patterns can even vary within the same animal depending on the amount of illumination present, as in the case of nocturnal desert rodents (Lockard and Owings, 1974; Price et al., 1984; Wolfe and Summerlin, 1989; Daly et al., 1992; Longland, 1994). In the current study we examine the photic preference of what is becoming a more commonly used animal model, the gray short-tailed opossum (*Monodelphis domestica*).

The gray short-tailed opossum is a South American marsupial that has been gaining popularity as a laboratory animal. In the wild, these semi-arboreal opossums are found in the dry forest landscapes of Brazil, Bolivia, Argentina, and Paraguay where they consume insects and other invertebrates, fruits, and small vertebrates (Streilein, 1982; Wilson and Reeder, 1993; MacDonald, 2001). They are primarily nocturnal, with their most active period occurring within 1–3 h of sunset (Streilein, 1982). In the laboratory, these animals have proven to be useful for a wide range of research questions, particularly studies of development, due in no small part to the early stage at which their offspring are born and the lack of a pouch, which makes offspring accessible (Saunders et al., 1989; Karlen et al., 2006; Karlen and Krubitzer, 2009). Furthermore, the short-tailed opossum was the first marsupial to have its genome sequenced, opening the door to many evolutionary and genetic studies (Mikkelsen et al., 2007).

We recently assessed the visual acuity of opossums using the optokinetic test, which relies on the reflexive head movements that follow a moving stimulus (Dooley et al., 2012). On average, opossums exhibited a visual acuity of 0.58 cycles per degree, which is similar to the acuity of albino rats determined using the same methodology (Prusky et al., 2002). Recent analysis of the short-tailed opossum genome has indicated that their retinas contain two classes of cones in addition to rods (Hunt

*Correspondence to: L. A. Krubitzer, Center for Neuroscience, University of California, Davis, 1544 Newton Court, Davis, CA 95618, United States. Tel: +1-530-757-8868.
E-mail address: lakrubitzer@ucdavis.edu (L. A. Krubitzer).

et al., 2009), although this has yet to be anatomically verified. Likewise, the proportion of rods to cones has yet to be determined in this species. Thus, while there has been a great deal of recent progress in understanding their visual capabilities, much remains to be learned.

Although the behavior of opossums in the wild is qualitatively similar to that of eutherian mammals of a similar size that occupy a similar niche (Kimble, 1997), behavior of any animal in the laboratory is a different matter entirely. One challenge in working with opossums is that, contrary to what many might assume, they do not behave like more traditional laboratory animals, such as mice or rats (Kimble and Whishaw, 1994; Ivanco et al., 1996; Pisula et al., 2012). Differences in motivation, as well as memory capacity, may require researchers to devise opossum-specific behavioral tasks. Just as researchers developed novel behavioral tasks based on the ecological preferences of rats and mice, proper behavioral studies in opossums can only be conducted once their basic behavioral preferences have been identified. In this experiment, we tested the photic preference of opossums by placing them in a round testing arena and allowing them to freely move between the light and dark sides of the arena. The results from this experiment could inform the next generation of behavioral tests designed explicitly for opossums.

EXPERIMENTAL PROCEDURES

Subjects

Ten adult South American short-tailed opossums (*M. domestica*) were used in these experiments. See Table 1 for age, weight, and sex. Animals were housed in standard laboratory cages with *ad libitum* access to food and water and were maintained on a 14:10-h light:dark cycle with the lights on at 7 am. All experiments were performed under National Institutes of Health guidelines for the care of animals in research and were approved by the Institutional Animal Care and Use Committee of the University of California, Davis.

Testing apparatus

The testing apparatus consisted of a 76-cm LCD monitor (LG, Seoul, South Korea) oriented parallel to the ground through which stimuli were presented (Fig. 1). One half of the monitor was obscured with an opaque panel of black Plexiglas, and the other half of the monitor was

covered with a clear panel of Plexiglas. One large sheet of clear Plexiglas was placed above those to create a smooth surface. A large cylinder (55.9 cm tall, 35.6 cm internal diameter) formed the walls of the testing arena and was positioned so that half the arena was over the dark stimulus and half was over the light stimulus.

The light intensity of both the light and dark sides of the arena was measured before each trial using a light meter (Digital Illuminance/Light Meter LX1330B; Dr. Meter, Union City, CA). The animals were exposed to three levels of light intensity: low intensity, which ranged from 1.2 to 1.7 lux (average 1.36 lux), medium intensity, which ranged from 36.0 to 46.0 lux (average 43.22 lux), and high intensity, which ranged from 327 to 443 lux (average 387.90 lux). The light intensity of the dark side always measured 0 lux.

Behavioral test

Behavioral testing was performed in a dark room illuminated by a dim red light. All testing occurred during the first half of the animal's light period. At the beginning of each test, animals were taken from their home cage and placed in the center of the testing arena, at the boundary between the light and dark sides. An infrared video camera (IR bullet camera; TelPix, Los Angeles, CA, USA) was suspended over the testing arena to capture the animals' behavior, and the video was recorded and digitized (Pinnacle Studio; Corel Inc., Mountain View, CA, USA). The animals were allowed to explore the testing arena for 10 min. At the end of the testing period they were removed, the arena was cleaned with ethanol, and the stimulus was changed. Each day the animal was tested on each of the three light intensities, and testing occurred on three consecutive days. Stimuli were presented in a semi-random order without replacement.

Data analysis

Behavior was scored using the open-access video coding program OpenSHAPA (datavyu.org). The 10-min exploration period began when the animal was first placed in the middle of the arena. The animal was considered to have crossed from one side of the arena to the other when the front half of its body moved over the center line. A single visit to the light or dark half of the arena was defined as a bout. The time of each crossing event was recorded. These times were exported into Excel (Microsoft Corp., Redmond, WA, USA), converted into milliseconds, and the duration of each bout spent in either the light or dark side was determined. From there, for each lighting condition we calculated: (1) the total amount of time spent on the light and dark sides, (2) the percentage of time spent on the light and dark sides, (3) the mean bout length within the light or dark side, (4) the number of times the animal crossed from the light to the dark side, and (5) the number of bouts in both light and dark that were longer than 10, 30, and 60 s.

Data analysis was performed using the JMP software package (SAS, Cary, NC, USA). Comparisons between

Table 1. Subject information

Animal #	Sex	Weight (g)	Age (d)
20633	M	110	230
10636	F	84	299
20628	M	100	238
10653	F	67	257
10639	F	69	293
20653	M	91	209
10649	F	102	538
10696	F	87	219
20656	M	104	245
20670	M	112	210

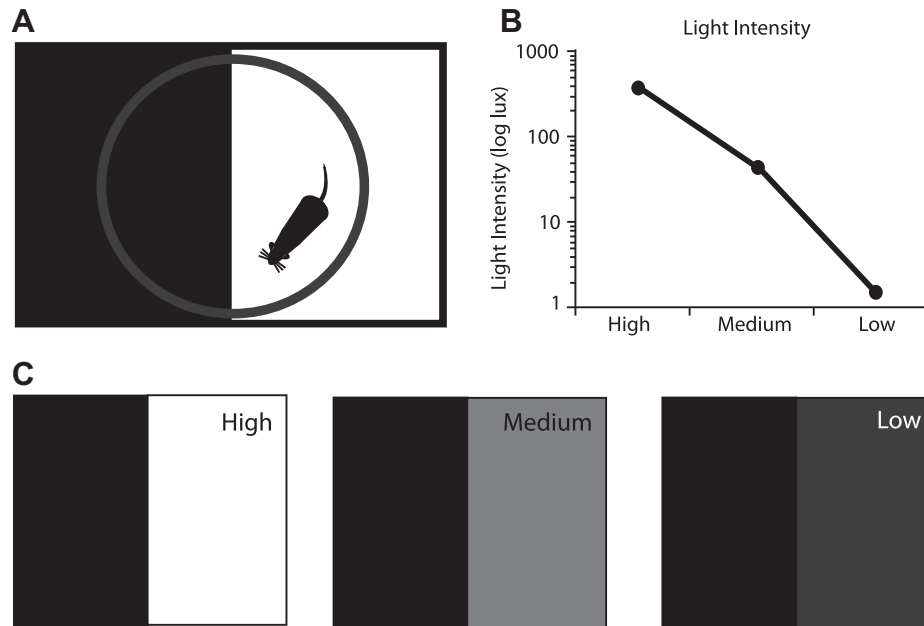


Fig. 1. Schematic of the testing apparatus and stimuli. (A) A top view of the testing arena. The floor consisted of an LCD monitor through which the visual stimuli were presented, and a large, gray, opaque cylinder formed the walls. (B) The logarithm of the light intensity in lux of the visual stimuli on the light side of the arena is represented on the X axis, and the illumination level is represented on the Y axis. The mean light intensity in the high-contrast condition was 388 lux, the mean light intensity in the medium-contrast condition was 43 lux, and the mean light intensity in the low-contrast condition was 1.4 lux. (C) Illustrations of the appearance of high-, medium-, and low-contrast visual stimuli.

(i.e., low, medium, and high-contrast conditions) and within light conditions (i.e., time spent in light vs. dark in the high-contrast condition) were performed using Analysis of Variance (ANOVA). The percentage of time spent on the light and dark sides was compared against chance using a two-sample *t*-test.

RESULTS

Each animal was tested over the course of three days. We examined the proportion of time spent in the light side and the dark side of the arena during each of the three days. The data collected from three days were averaged together for each animal. As part of our initial reanalysis of the data, we divided the animals by sex and compared the results using paired *t*-tests. We found no differences between males and females in any of the analyzed data. Thus, we analyzed the data from males and females together.

In order to gain an understanding of the overall behavior of these animals, we first calculated the total amount of time spent in the light side of the arena and compared it against the total amount of time spent in the dark side of the arena (Fig. 2A; Table 2). In the high-contrast light condition, opossums spent significantly more time on the dark side (437 s) than on the light side (194 s; Table 2). This was true for the medium- and low-contrast light conditions as well ($p < .0001$). Neither the time spent on the light side of the arena nor the time spent on the dark side of the arena significantly differed between the high-, medium-, and low-contrast conditions.

We next calculated the mean length of time the animal spent in either the light or the dark side of the arena before crossing to the other side of the arena (i.e., bout length; Fig. 2B; Table 2). In the high-intensity light condition, the mean bout length was significantly longer in the dark half of the arena (42.99 ± 6.36 s) than in the light half of the arena (13.71 ± 2.83 s; $F_{1,19} = 17.68$, $p < .0005$). In the medium-intensity light condition the mean amount of time spent in the dark side of the arena (13.91 ± 2.48 s) was not significantly longer than the light side of the arena (62.81 ± 24.31 s; $F_{1,19} = 4.00$, $p = .06$). Finally, in the low-intensity light condition, the mean bout length was significantly longer in the dark half of the arena (14.60 ± 4.45 s) than in the light half of the arena (39.87 ± 10.03 s; $F_{1,19} = 5.31$, $p < .05$).

We then calculated the proportion of time in each trial spent on the light and dark sides of the arena (Fig. 2C; Table 2). This calculation allowed us to determine whether opossums spent more time on a given side of the arena than would be expected by chance (50%). Across all contrast light conditions, opossums spent significantly less time on the light side (32.56%) than on the dark side of the arena (67.44%; see Table 2). Further, neither the time on the light side of the arena ($F_{2,29} = .797$, $p = \text{NS}$) nor the time on the dark side of the arena ($F_{2,29} = .797$, $p = \text{NS}$) significantly differed between the high-, medium-, and low-light intensity conditions. Thus, in all light conditions, animals spent significantly more time on the dark side and less time on the light side of the arena than would be expected by chance ($t_9 \geq 4.04$, $p < .005$).

We next calculated the number of times the opossums crossed from the light side to the dark side each minute

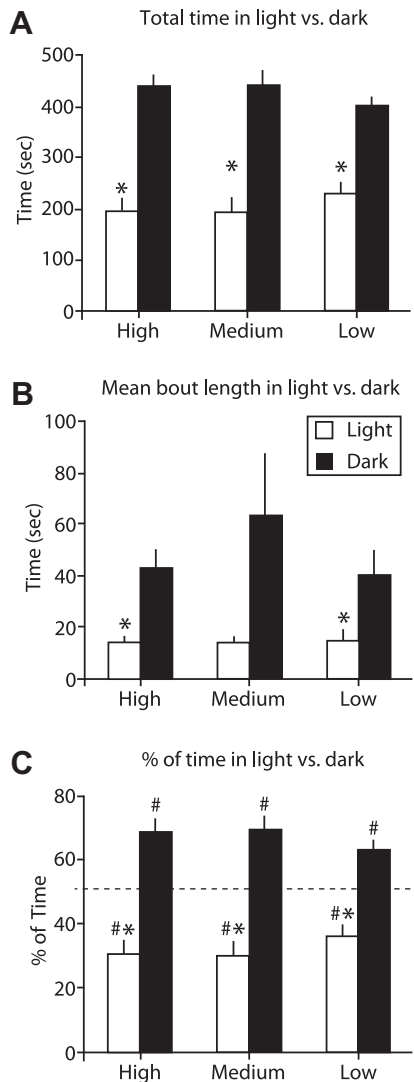


Fig. 2. Time spent in the light (white bars) and dark (black bars) halves of the arena. (A) The total amount of time spent in the light and dark halves of the arena in high-, medium-, and low-contrast light conditions. In all light conditions, opossums spent significantly more time on the dark side of the arena than the light side of the arena. (B) The mean bout length in the light and dark halves of the arena in high-, medium-, and low-contrast light conditions. The mean bout length on the dark side of the arena was significantly longer than on the light side in the high- and low-contrast conditions. There was a trend for mean bout length to be longer on the dark side of the arena in the medium-contrast condition. (C) The percentage of time spent in the light and dark halves of the arena in high-, medium-, and low-contrast light conditions. The dashed line indicates chance. In all light conditions, opossums spent a significantly larger proportion of their time on the dark side of the arena than on the light side of the arena, and a significantly greater proportion of their time on the dark side, and less on the light side than would be expected by chance. Mean + SE. * – differs from dark. # – differs from chance.

for each light intensity (Table 2; Fig. 3). This analysis was done to determine whether the overall activity level of the opossum changed in the different light intensities. There was no significant difference between the number of crossings per minute in the high-, medium-, or low-light intensity conditions ($F_{2,29} = 0.38$, $p = \text{NS}$).

The above analyses revealed significant differences in the amount of time spent in the light and dark halves of

the arena, but they did not provide any insight into how individual bout lengths differed between conditions. In order to determine this, we examined the length of individual bouts to determine the number of bouts that were greater than 10, 30, and 60 s in both the light and dark sides of the arena in all light conditions. The number of bouts was counted for each 10-min session in the arena and the values for each condition were averaged across days. We found no difference between any conditions in bouts longer than 10 s (Fig. 4A; Table 3). However, when we examined bouts that were greater than 30 s we found significantly more long bouts on the dark side than on the light side in all light intensity conditions ($F_{1,19} > 11.76$, $p < .005$) (Fig. 4B; Table 3). Similarly, when we examined bouts greater than 60 s we found a significantly greater number of long bouts on the dark side than the light side in all light intensity conditions ($F_{1,19} > 5.19$, $p < .05$) (Fig. 4C; Table 3). Furthermore, a planned comparison revealed a significantly higher number of bouts greater than 60 s on the dark side in the high-intensity light condition than on the dark side in the low-intensity light condition ($p < .05$).

Together, these results indicate that in all light intensity conditions opossums spent approximately twice the amount of time on the dark side of the arena than on the light side of the arena, accounting for almost 70% of the total time that they spent in the arena. Furthermore, in the high-contrast light condition the mean bout length was longer on the dark side than the light side. Finally, in the medium- and high-contrast light conditions, the number of long bouts (i.e., greater than 30 or 60 s in duration) was higher on the dark side than the light side. Importantly, these differences were not due to a change in the frequency of crossings from light to dark, demonstrating that the overall amount of exploratory behavior did not change between the light conditions.

DISCUSSION

Summary of results

In this experiment we assessed the photic preference of short-tailed opossums by placing them in a testing arena, which was half dark and half illuminated, and determining how much time they spent on each side. The animals were tested under three illumination levels: high, which averaged around 388 lux, or about the same light level as indoor office lighting or sunrise on a clear day; medium, which averaged about 43 lux, or about the same light level as sunrise on a cloudy day; and low, which averaged around 1.4 lux, or about the same light level as the full moon on a clear night. In each of these conditions, the light side of the arena was bounded by a dark side that measured 0 lux. In all illumination conditions the opossums spent significantly more total time and a significantly greater percentage of time on the dark side of the arena than the illuminated side.

The results presented here demonstrate that short-tailed opossums exhibit a strong and significant preference for dark environments compared to light

Table 2. Results

	High contrast		Medium contrast		Low contrast	
	Light	Dark	Light	Dark	Light	Dark
Total time (s)	194.35 ± 23.19	436.94 ± 23.68	191.66 ± 29.27	439.64 ± 28.10	230.31 ± 21.41	398.00 ± 19.94
% Time	30.81 ± 3.71	69.19 ± 3.71	30.28 ± 4.61	69.72 ± 4.61	36.58 ± 3.32	63.42 ± 3.32
Bout Length (s)	13.71 ± 2.83	42.99 ± 6.36	13.91 ± 2.48	62.81 ± 24.31	14.60 ± 4.45	39.87 ± 10.03
# Crossings per minute	2.08 ± 0.67		1.90 ± 0.59		2.61 ± 0.53	

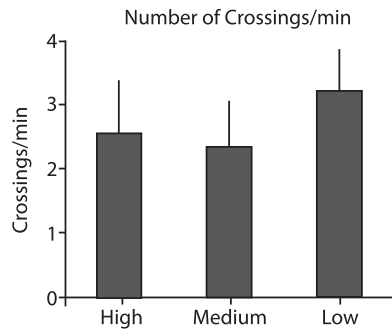


Fig. 3. The number of crossings from the light side to the dark side of the arena per minute did not differ between light intensity conditions, indicating that these results were not due to a change in the overall activity level of the animal. Mean + SE.

environments, defined as spending more time in the dark half than the light half of the testing arena. This preference is robust, existing in high, medium, and low illumination conditions. In each illumination condition, opossums spend a greater amount of time in the dark, a larger percentage of time in the dark, have longer mean bout durations in the dark, and a higher number of very long bout durations (greater than 30 or 60 s) in the dark. These differences in bout duration are not due to a change in overall activity level, as the number of times opossums crossed from the light side to the dark side of the arena did not differ between light conditions. Furthermore, the fact that opossums spent the majority of their time in the dark, even in the low illumination condition, indicates that they have the ability to discriminate between very low light conditions and complete darkness, an ability that could be exploited in the design of future behavioral tasks. To our knowledge, this is the first time the photic preference of short-tailed opossums has been experimentally determined.

Short-tailed opossum vision

Opossums are classified as nocturnal animals, although they are most active in the few hours following sunset and their activity is not decreased by the presence of lights (Streilein, 1982). This description of their natural behavior is consistent with our observations, in that the opossums distinctly preferred the dark side of the arena over the light side, but still ventured into the light. The opossums also showed evidence of sensitivity to small differences in low light levels, in that they spent more time in the dark side of the arena even in the lowest intensity

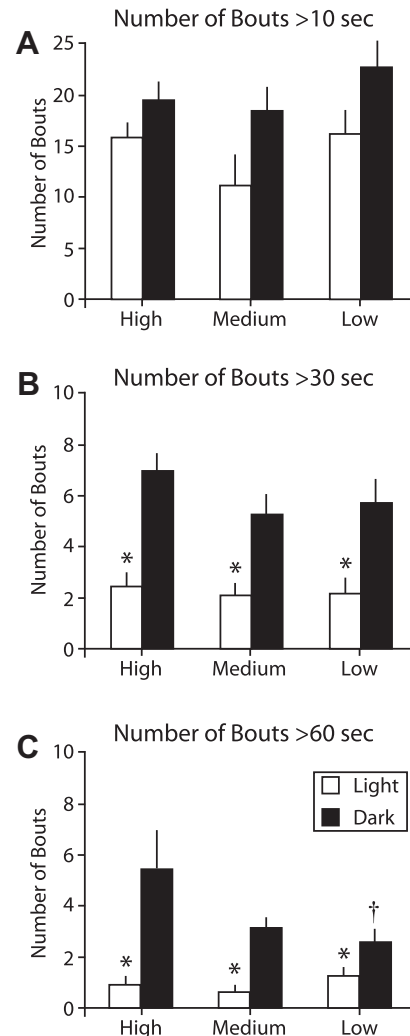


Fig. 4. The number of bout lengths that was greater than 10 (A), 30 (B), and 60 (C) s in duration in the light (white bars) and dark (black bars) halves of the arena in high-, medium-, and low-contrast light conditions. (A) There was no difference in the number of bouts longer than 10 s in the light and dark halves of the arena in any light contrast condition. In the high-, medium-, and low-contrast light conditions, there were significantly more bouts longer than 30 s (B) and 60 s (C) in the dark half of the arena than in the light half of the arena. Additionally, there were significantly more bout lengths that were greater than 60 s in duration on the dark side of the arena in the high-contrast condition compared to those in the low-contrast condition. Mean + SE. * – differs from dark. † – differs from high contrast.

light condition. This behavior, in part, may be due to their retinal composition, which includes rods and two sets of

Table 3. Number of bouts > 10, 30, or 60 s in each light condition

	High contrast		Medium contrast		Low contrast	
	Light	Dark	Light	Dark	Light	Dark
> 10 s	15.7 ± 1.6	19.4 ± 1.8	11.2 ± 2.9	18.3 ± 2.3	16.2 ± 2.2	22.6 ± 3.2
> 30 s	2.5 ± 0.5	7.0 ± 0.6	2.2 ± 0.4	5.3 ± 0.7	2.2 ± 0.6	5.8 ± 0.8
> 60 s	0.9 ± 0.3	5.4 ± 1.5	0.7 ± 0.2	3.1 ± 0.4	1.2 ± 0.4	2.6 ± 0.5

color-sensing cones, which respond to wavelengths within the UV (335–445 nm) and green (500–570 nm) light range (Hunt et al., 2009). While, to our knowledge, the ratio of rods to cones has yet to be characterized for the short-tailed opossum, other nocturnal marsupial species, such as the Virginia opossum (*Didelphis virginiana*) (Kolb and Wang, 1985) and Big-eared opossum (*Didelphis auritis*) (Ahnelt et al., 1995) have retinas with a high rod/cone ratio.

Comparison with rat vision

Rats (*Rattus norvegicus*) are commonly used in behavioral experiments, and in many cases behavioral tasks that have been designed for rats have been adapted for use in other species. Like short-tailed opossums, rats are nocturnal, prefer dark to light environments, and the proportion of time spent in illuminated areas is inversely proportional to the intensity of the illumination (Johnson, 1964a; Woodhouse and Greenfield, 1985). As in the short-tailed opossum, the retina of rats contains three photoreceptors: rods and two varieties of cones, which respond to UV and green wavelengths (Jacobs et al., 2001; Ortin-Martinez et al., 2010). And, like nocturnal marsupials that have been studied, albino rats have a high rod to cone ratio (approximately 1:100) (Walls, 1934; Szel and Rohlich, 1992).

While laboratory short-tailed opossums are an outbred population, rats have been selectively inbred to produce several distinct strains, including multiple albino strains. Because of this, it is important to consider the strain of rat when comparing them to different species. Albino and pigmented rats differ on many sensory measures, including vision. Like *Monodelphis*, albino strains have a stronger preference for dark areas over light areas (Matsuo and Tsuji, 1989) and relatively low visual acuity compared to pigmented strains (Prusky et al., 2002, report values of 0.536 cycles per degree vs 1.113 cycles per degree, respectively) (Birch and Jacobs, 1979; Prusky et al., 2002). However, albino rats have a number of anatomical anomalies, including a decreased number of rods and decreased cell density within the retina (Ilija and Jeffery, 2000), lower density and abnormal distribution of cone types within the retina (Ortin-Martinez et al., 2010), an incomplete decussation of the optic nerve (Lund et al., 1974), and increased collicular activity in response to light stimulation (Thomas et al., 2005). Thus, while some aspects of visual behavior are similar in albino rats and short-tailed opossums, ultimately, due to their normal pigmentation, short-tailed opossums likely share more common features of the

visual system with pigmented rats. However, even pigmented rats are far from an ideal comparison with *Monodelphis* due to many other factors, including their history of inbreeding, phylogeny, development, and differing natural habitats. This highlights the importance of carefully selecting species for comparisons, and the necessity of considering all aspects of the animal, including ecological niche, evolutionary history, and diel pattern, when making cross species comparisons.

Comparisons with other nocturnal animal models

As described above, short-tailed opossums are gaining popularity as a model species for many topics, including cortical development (Kahn and Krubitzer, 2002; Karlen et al., 2006; Seelke et al., 2013), motor development (Saunders et al., 1998; Cabana, 2000; Lavalley and Pflieger, 2009), and genetics (Goodstadt et al., 2007; Samollow, 2008). However, little is known about their behavior, especially in comparison to more traditional model species. There have been only a few studies that directly compared the spatial behavior of short-tailed opossums and other animals, specifically rats.

For example, comparisons of spatial memory using the Morris water maze and radial arm maze (Kimble and Whishaw, 1994) indicate that opossums exhibit different behavioral patterns than rats. While rats readily learned to find both visible and hidden platforms in the Morris water maze task, opossums took much longer to learn to find visible platforms and never successfully learned to find hidden platforms (Kimble and Whishaw, 1994). In the radial arm maze opossums required more attempts to find food rewards and were much more likely to reenter arms that had been previously searched (Kelly and Masterton, 1977). When compared in an open field maze (Wesierska et al., 2003) and elevated plus maze (Wesierska and Turlejski, 2000), opossums exhibited a higher amount of overall activity, and they switched from defensive to exploratory behavior more quickly than rats, which the researchers attributed to the hunting abilities of the opossum. Similar results were observed when opossums and rats were exposed to novel objects (Pisula et al., 2012).

Finally, comparisons of forelimb movements of the two species indicates that both rats and opossums could use a single limb to grasp the prey and bring it to their mouths (Ivanco et al., 1996), but rats displayed more complex movements of their forepaws and used their digits more than opossums. The authors concluded that the greater complexity of the rats' movements is related to the greater anatomical and functional complexity of their motor systems compared to that of opossums.

Photic preference in other nocturnal species

The phenomenon of how behavior changes in light and dark environments, especially in relation to circadian activity, has been very thoroughly studied, but only in a few animal models such as mice, rats, and fruit flies (e.g. Mendoza et al., 2005; Allada and Chung, 2010; Tapia-Osorio et al., 2013). However, there have been surprisingly few studies that examine a nocturnal animal's affinity for a given level of illumination. The studies that have been performed measure an animal's photic preference either indirectly, by using activity levels as a proxy for preference, or directly, by allowing the animal to choose between areas with different illumination levels, as in the present study.

Several studies have examined how the behavior of desert rodents (including *Peromyscus polionotus*, *Dipodomys merriami*, *Dipodomys nitratoides*, and *Chaetodipus baileyi*, to name a few) changes in response to the phases of the moon in their natural environments (Lockard and Owings, 1974; Price et al., 1984; Wolfe and Summerlin, 1989; Daly et al., 1992; Longland, 1994). The changing phases of the moon add another variable to nocturnal behavior, in that the amount of light available changes from night to night. It is brighter during a full moon (1 lux) than during a new moon (0.001 lux), and when the moon was full, animals spent less time in open spaces, preferring to stay under the cover of vegetation or within their burrows. On the other hand, when the moon was new, the animals spent more time foraging in the open. These studies demonstrate that these nocturnal species can differentiate between low light levels, and prefer the darker area. Such an ability would be useful for assessing the risk of predation during different illumination conditions.

Other studies have examined illumination preferences under more controlled conditions. In two studies rats were placed in an apparatus that allowed them to choose between different illumination levels. In both cases, rats preferred either complete darkness or the lowest illumination condition (~0.1 lux) over higher illumination conditions (Johnson, 1964b; Johnson, 1965). The behavior of non-rodent mammals has also been investigated. The slow loris (*Nycticebus coucang*), a nocturnal prosimian native to Southeast Asia and Indonesia, is more active during periods of low illumination (0.7–1.3 lux) and shows more behavioral quiescence during periods of higher illumination (4.1–43.1 lux) (Trent et al., 1977). Similarly, galagos (*Galago crassicaudatus*), another nocturnal prosimian, also show behavioral changes that are related to illumination levels (Randolph, 1971). Galagos exhibited significantly more locomotor activity during the lowest illumination conditions than during higher illumination conditions. Furthermore, galagos showed a strong preference for low levels of illumination, which is likely one way that these animals avoid predation.

Together, these studies demonstrate that the behavior of nocturnal animals can vary significantly based upon relatively small changes in illumination levels. Further, the description of an animal as “nocturnal” provides somewhat limited information about a particular species' behavioral patterns. It is clear that photic preference is

an important factor that contributes to specific behaviors that will be generated in a particular illumination context.

Acknowledgments—Thanks to Cindy Clayton, DVM, and the rest of the animal care staff at the UC Davis Psychology Department Vivarium. Additional thanks to Hoang Nguyen for assistance in building the behavioral arena. This work was supported by grants to Leah Krubitzer from NINDS (R21 NS071225) and NEI (R01 EY022987) and funding from the NEI (T32 EY015387) to James Dooley and Adele Seelke.

REFERENCES

- Ahnelt PK, Hokoc JN, Rohlich P (1995) Photoreceptors in a primitive mammal, the South American opossum, *Didelphis marsupialis aurita*: characterization with anti-opsin immunolabeling. *Visual Neurosci* 12(5):793–804.
- Allada R, Chung BY (2010) Circadian organization of behavior and physiology in *Drosophila*. *Annu Rev Physiol* 72:605–624.
- MacDonald D (2001) American Opossums. In: Macdonald D, Norris S, editors. *The new encyclopedia of mammals*. Oxford, UK: Oxford University Press. p. 808–814.
- Birch D, Jacobs GH (1979) Spatial contrast sensitivity in albino and pigmented rats. *Vision Res* 19(8):933–937.
- Cabana T (2000) The development of mammalian motor systems: the opossum *Monodelphis domestica* as a model. *Brain Res Bull* 53(5):615–626.
- Campbell SS, Tobler I (1984) Animal sleep: a review of sleep duration across phylogeny. *Neurosci Biobehav Rev* 8:269–300.
- Daly M, Behrens PR, Wilson MI, Jacobs LF (1992) Behavioral modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Anim Behav* 44(1):1–9.
- Dooley JC, Nguyen HM, Seelke AM, Krubitzer L (2012) Visual acuity in the short-tailed opossum (*Monodelphis domestica*). *Neuroscience* 223:124–130.
- Goodstadt L, Heger A, Webber C, Ponting CP (2007) An analysis of the gene complement of a marsupial, *Monodelphis domestica*: evolution of lineage-specific genes and giant chromosomes. *Genome Res* 17(7):969–981.
- Hunt DM, Chan J, Carvalho LS, Hokoc JN, Ferguson MC, Arrese CA, Beazley LD (2009) Cone visual pigments in two species of South American marsupials. *Gene* 433(1–2):50–55.
- Ilia M, Jeffery G (2000) Retinal cell addition and rod production depend on early stages of ocular melanin synthesis. *J Comp Neurol* 420(4):437–444.
- Ivanco TL, Pellis SM, Whishaw IQ (1996) Skilled forelimb movements in prey catching and in reaching by rats (*Rattus norvegicus*) and opossums (*Monodelphis domestica*): relations to anatomical differences in motor systems. *Behav Brain Res* 79(1–2):163–181.
- Jacobs GH, Fenwick JA, Williams GA (2001) Cone-based vision of rats for ultraviolet and visible lights. *J Exp Biol* 204(Pt 14):2439–2446.
- Johnson RN (1964a) Illumination preference of albino rats in a closed hexagonal maze. *Percept Motor Skills* 19:827–830.
- Johnson RN (1964b) Illumination preference of albino rats in a closed hexagonal maze. *Percept Motor Skills* 19(3):827–830.
- Johnson RN (1965) Illumination preference of albino rats in a tilt box as a function of age and illumination intensity. *Percept Motor Skills* 21(2):535–543.
- Kahn DM, Krubitzer L (2002) Massive cross-modal cortical plasticity and the emergence of a new cortical area in developmentally blind mammals. *Proc Natl Acad Sci U S A* 99(17):11429–11434.
- Karlen SJ, Krubitzer L (2009) Effects of bilateral enucleation on the size of visual and nonvisual areas of the brain. *Cereb Cortex* 19(6):1360–1371.
- Karlen SJ, Kahn DM, Krubitzer L (2006) Early blindness results in abnormal corticocortical and thalamocortical connections. *Neuroscience* 142(3):843–858.

- Kelly JB, Masterton B (1977) Auditory sensitivity of the albino rat. *J Comp Physiol Psychol* 91(4):930–936.
- Kimble DP (1997) Didelphid behavior. *Neurosci Biobehav Rev* 21(3):361–369.
- Kimble D, Whishaw IQ (1994) Spatial behavior in the Brazilian short-tailed opossum (*Monodelphis domestica*): comparison with the Norway rat (*Rattus norvegicus*) in the Morris water maze and radial arm maze. *J Comp Psychol* 108(2):148–155.
- Kolb H, Wang HH (1985) The distribution of photoreceptors, dopaminergic amacrine cells and ganglion cells in the retina of the North American opossum (*Didelphis virginiana*). *Vision Res* 25(9):1207–1221.
- Lavallee A, Pflieger J-F (2009) Developmental expression of spontaneous activity in the spinal cord of postnatal opossums, *Monodelphis domestica*: an anatomical study. *Brain Res* 1282:1–9.
- Lockard RB, Owings DH (1974) Moon-related surface activity of Bannertail (*Dipodomys spectabilis*) and Fresno (*D. nitratoides*) kangaroo rats. *Anim Behav* 22(February):262–273.
- Longland WS (1994) Effects of artificial bush canopies and illumination on seed patch selection by heteromyid rodents. *Am Midl Nat* 132(1):82–90.
- Lund RD, Lund JS, Wise RP (1974) The organization of the retinal projection to the dorsal lateral geniculate nucleus in pigmented and albino rats. *J Comp Neurol* 158(4):383–403.
- Matsuo M, Tsuji K (1989) Strain differences of the light-dark preference in inbred rats. *Behav Genet* 19(3):457–466.
- Mendoza J, Graff C, Dardente H, Pevet P, Challet E (2005) Feeding cues alter clock gene oscillations and photic responses in the suprachiasmatic nuclei of mice exposed to a light/dark cycle. *J Neurosci* 25(6):1514–1522.
- Mikkelsen TS, Wakefield MJ, Aken B, Amemiya CT, Chang JL, Duke S, Garber M, Gentles AJ, Goodstadt L, Heger A, Jurka J, Kamal M, Mauceli E, Searle SM, Sharpe T, Baker ML, Batzer MA, Benos PV, Belov K, Clamp M, Cook A, Cuff J, Das R, Davidow L, Deakin JE, Fazzari MJ, Glass JL, Grabherr M, Grealis JM, Gu W, Hore TA, Huttley GA, Kleber M, Jirtle RL, Koina E, Lee JT, Mahony S, Marra MA, Miller RD, Nicholls RD, Oda M, Papenfuss AT, Parra ZE, Pollock DD, Ray DA, Schein JE, Speed TP, Thompson K, VandeBerg JL, Wade CM, Walker JA, Waters PD, Webber C, Weidman JR, Xie X, Zody MC, Graves JA, Ponting CP, Breen M, Samollow PB, Lander ES, Lindblad-Toh K (2007) Genome of the marsupial *Monodelphis domestica* reveals innovation in non-coding sequences. *Nature* 447(7141):167–177.
- Ortin-Martinez A, Jimenez-Lopez M, Nadal-Nicolas FM, Salinas-Navarro M, Alarcon-Martinez L, Sauve Y, Villegas-Perez MP, Vidal-Sanz M, Agudo-Barriuso M (2010) Automated quantification and topographical distribution of the whole population of S- and L-cones in adult albino and pigmented rats. *Invest Ophthalmol Visual Sci* 51(6):3171–3183.
- Pisula W, Turlejski K, Stryjek R, Nalecz-Tolak A, Grabiec M, Djavadian RL (2012) Response to novelty in the laboratory Wistar rat, wild-captive WWCPs rat, and the gray short-tailed opossum (*Monodelphis domestica*). *Behav Process* 91(2):145–151.
- Price MV, Waser NM, Bass TA (1984) Effects of moonlight on microhabitat use by desert rodents. *J Mammal* 65(2):353–356.
- Prusky GT, Harker KT, Douglas RM, Whishaw IQ (2002) Variation in visual acuity within pigmented, and between pigmented and albino rat strains. *Behav Brain Res* 136(2):339–348.
- Randolph M (1971) Role of light and circadian rhythms in nocturnal behavior of Galago-Crassicaudatus. *J Comp Physiol Psychol* 74(1):115–120.
- Robert S, Dallaire A (1986) Polygraphic analysis of the sleep-wake states and the REM sleep periodicity in domesticated pigs (*Sus scrofa*). *Physiol Behav* 37(2):289–293.
- Robert S, Dancosse J, Dallaire A (1987) Some observations on the role of environment and genetics in behaviour of wild and domestic forms of *Sus scrofa* (European wild boars and domestic pigs). *Appl Anim Behav Sci* 17(3–4):253–262.
- Ruckebusch Y (1972) The relevance of drowsiness in the circadian cycle of farm animals. *Anim Behav* 20:637–643.
- Samollow PB (2008) The opossum genome: insights and opportunities from an alternative mammal. *Genome Res* 18(8):1199–1215.
- Saunders NR, Reader M, Mollgard K (1989) *Monodelphis domestica* (grey short-tailed opossum): an accessible model for studies of early neocortical development. *Anat Embryol* 180:227–236.
- Saunders NR, Kitchener P, Knott GW, Nicholls JG, Potter A, Smith TJ (1998) Development of walking, swimming and neuronal connections after complete spinal cord transection in the neonatal opossum, *Monodelphis domestica*. *J Neurosci* 18(1):339–355.
- Seelke AMH, Dooley JC, Krubitzer L (2013) Differential changes in the cellular composition of the developing marsupial brain. *J Comp Neurol* 52(11):2602–2620.
- Streilein KE (1982) Behavior, ecology, and distribution of South American marsupials. In: Mares MA, Genoways HH, editors. *Mammalian biology in South America*. Linesville, PA: The University of Pittsburgh. p. 231–250.
- Szel A, Rohlich P (1992) Two cone types of rat retina detected by anti-visual pigment antibodies. *Exp Eye Res* 55(1):47–52.
- Tapia-Osorio A, Salgado-Delgado R, Angeles-Castellanos M, Escobar C (2013) Disruption of circadian rhythms due to chronic constant light leads to depressive and anxiety-like behaviors in the rat. *Behav Brain Res* 252:1–9.
- Thomas BB, Aramant RB, Satta SR, Seiler MJ (2005) Light response differences in the superior colliculus of albino and pigmented rats. *Neurosci Lett* 385(2):143–147.
- Trent BK, Tucker ME, Lockard JS (1977) Activity changes with illumination in slow loris (*Nycticebus coucang*). *Appl Anim Ethol* 3(3):281–286.
- Walls GL (1934) The visual cells of the white rat. *Comp Psychol* 18(3):363–366.
- Wesierska M, Turlejski K (2000) Spontaneous behavior of the gray short-tailed opossum (*Monodelphis domestica*) in the elevated plus-maze: comparison with Long-Evans rats. *Acta Neurobiol Exp (Wars)* 60(4):479–487.
- Wesierska M, Walasek G, Kilijanek J, Djavadian RL, Turlejski K (2003) Behavior of the gray short-tailed opossum (*Monodelphis domestica*) in the open field and in response to a new object, in comparison with the rat. *Behav Brain Res* 143(1):31–40.
- Wilson D, Reeder D (1993) *Mammalian species of the world: a taxonomic and geographic reference*. Washington, DC: Smithsonian Institution Press.
- Wolfe JL, Summerlin CT (1989) The influence of lunar light on nocturnal activity of the old-field mouse. *Anim Behav* 37:410–414.
- Woodhouse R, Greenfield N (1985) Responses of albino and hooded rats to various illumination choices in a six-chambered alleyway. *Percept Motor Skills* 61(2):343–354.