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RETINAL STRUCTURE AND FORAGING MICROHABITAT USE OF THE GOLDEN SPINY MOUSE (*ACOMYS RUSSATUS*)

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The golden spiny mouse (*Acomys russatus*), an inhabitant of rocky deserts, exhibits adaptations to diurnal activity, but also some characteristics that appear evolutionarily constrained to a nocturnal mode of life. This species is probably driven into diurnality by its congener, the common spiny mouse (*A. cahirinus*). We carried out a comparative study of the retinal morphology of *A. russatus* and *A. cahirinus*, in search of possible anatomical adaptations for diurnal activity in the eyes of golden spiny mice. The observed photoreceptors of both species had rod-pattern properties that characterize nocturnal mammals. We also carried out a field study of the foraging microhabitat use of golden spiny mice and of illumination levels in those microhabitats. Throughout the year, golden spiny mice preferred to forage between and particularly under boulders, where light intensities were lower than in the open. Thus, the retinal structure of golden spiny mice has not evolved to meet with their needs as a diurnal species, but the combination of the biochemical properties of their eyes, coupled with their foraging microhabitat selection, may enable them to withstand diurnal activity with nocturnally adapted retinas.

Key words: *Acomys cahirinus, Acomys russatus,* cones, diurnal, foraging microhabitat use, nocturnal, photoreceptors, retina, spiny mice

The golden spiny mouse (*Acomys russatus*) is a diurnally active rodent that inhabits rocky deserts in southern Israel, where it coexists with its congener, the nocturnal common spiny mouse (*Acomys cahirinus*). Several phylogenetic studies using dental and chromosomal patterns (Denys et al. 1994), mitochondrial gene cytochrome-*b* (Barome et al. 1998), protein polymorphism (Janecek et al. 1991), and pericentric satellite DNA (Kunze et al. 1999), found that the golden spiny mouse lineage branched out quite early, but it has been left within the genus *Acomys.* Closely related species are generally active during the same part of the diel cycle, because diurnal and nocturnal activity patterns require major physiologic and morphologic adaptations (Daan 1981). Among those adaptations are a shift in circadian rhythms, physiologic adaptations to different climatic conditions (days are warmer than nights), skin pigmentation adapted to differences in solar radiation, and adaptations of the eye to different light intensities.

A key study carried out at Ein Gedi, near the Dead Sea, demonstrated that when the common spiny mouse was removed from shared habitat, the golden spiny mouse changed its activity time and became nocturnal (Shkolnik 1971). Shkolnik (1971) concluded that the common spiny mouse

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competitively excludes the golden spiny mouse to diurnal activity. Temporal partitioning may be an important mechanism of coexistence between these 2 species (Kronfeld-Schor and Dayan 1999).

Kronfeld-Schor et al. (2001) discovered that in spite of historical coexistence with the common spiny mouse, which forces it into diurnal activity, the golden spiny mouse retains the endogenous activity and body temperature rhythms of a nocturnal species (Elvert et al. 1999; Kronfeld-Schor 2001). Moreover, Kronfeld-Schor et al. (2000a) discovered that the potential for nonshivering thermogenesis is similar in both species, although the common spiny mouse is exposed to colder temperatures in winter and actually spends significantly more energy than its congener, probably on thermoregulation (Kronfeld-Schor et al. 2000b, 2001). Thus, endogenous circadian rhythmicity and the capacity for nonshivering thermogenesis may be constrained evolutionarily (Kronfeld-Schor et al. 2000a, 2000b). However, the dark skin pigmentation of the golden spiny mouse is presumably an adaptation for activity under intense solar radiation. The golden spiny mouse seems to be accumulating adaptations associated with a diurnal activity mode, and as it evolves, some traits are more constrained whereas others exhibit greater evolutionary plasticity. We asked whether the retinal morphology of golden spiny mice has evolved in accord with its diurnal activity pattern, or rather reflects its legacy as a nocturnal mammal.

Retinas of nocturnal and diurnal mammals differ in their photoreceptors. Cones are the receptors for day vision and rods are the receptors for night vision; day vision is colored and sharp, whereas night vision is colorless and blurred (Jacobs 1993). Strictly diurnal mammals have very high cone to rod ratios, whereas the retinas of strictly nocturnal animals show the reverse pattern (Jacobs 1993). Thus, the retina of the diurnal Mongolian gerbil (*Meriones unguiculatus*) contains about 12–14% cones (Govardovskii et al. 1992), retinas of diurnal ground squirrels (*Spermophilus beecheyi*) have <10% rods (Long and Fisher 1983), and retinas of nocturnal flying squirrels have <1% cones (Cohen 1972). Laboratory mice, which are nocturnal, have about 3% cones (Carter-Dawson and La Vail 1979).

These variations influence not only thresholds and dynamic ranges for rod- and cone-based vision but also impact accuracy of color-vision discrimination (Jacobs 1993). Presence of a single cone class extends the range of dynamic vision to higher light levels than those permitted by the operation of rods alone and affords other advantages that cone-based vision has over rod-based vision, such as heightened temporal resolution power (Jacobs 1993). Graded rod signals are often lost because of the saturation of rod receptor signals at higher light levels characteristic of good color vision, whereas, on the other hand, cones continue to operate efficiently (Baylor et al. 1984). Species possessing a retina composed almost exclusively of rods (>99%) probably have poor visual acuity but should be able to see better in low light conditions, enabling them to be active at night (Feldman and Phillips 1984).

Thus, if golden spiny mice retain the rod-based vision of nocturnal mammals, they may be expected to perform poorly during the day. Alternatively, they may be expected to seek sheltered microhabitats where levels of illumination are low even during the day. A field study conducted by trapping revealed that the golden spiny mouse showed a preference for being active among large boulders (Shargal et al. 2000). If golden spiny mice are active under boulders or in their shadow in the rocky desert, they may be exposed to relatively low levels of illumination.

We carried out the following studies: a comparative histologic study of the retinal structure of the golden spiny mouse and its strictly nocturnal congener, the common spiny mouse, in search of possible anatomical adaptations for diurnal activity in the

eyes of golden spiny mice; and a field study of the foraging microhabitat use of the golden spiny mouse and the illumination levels in those microhabitats. We asked whether the retina of golden spiny mice has evolved to fit with their diurnal activity pattern, or whether their foraging patterns reflected a preference to remain in conditions of low illumination.

Materials and Methods

Histologic study of the retina.—Six adult individuals of each species (*A. cahirinus* and *A. russatus*) were chosen for our study from a breeding colony at the Meir Segals Zoological Garden at Tel Aviv University. When kept separately under laboratory conditions, the 2 species are nocturnal (Kronfeld-Schor et al. 2001; Rubal et al. 1992). All animals were sacrificed and eyes were immediately enucleated. One-half of the eyes were fixed in Bouin fixative for light microscopy, and one-half were fixed with cold glutaraldehyde (2.5%) for toluidine blue–stained thin sections for light microscopy and electron microscopy sections. Hematoxylin and eosin–stained sections as well as thin sections (1–2 μm thick) stained with toluidine blue (1%) were prepared for light microscopy. For electron microscopy, the eyes were cut into anterior and posterior segments. Posterior segments of the eyes were then cut into 4 quadrants. In mice, the ratio of rods to cones remains essentially the same throughout the retina, and mice do not have a fovea or area with a higher proportion of 1 type of photoreceptors (Robison et al. 1982). Thus, no attempt was made to find a fovea or an area centralis in either species. Comparison of the ultrastructural morphologic details of the retinas was made using electron micrographic negatives and their corresponding prints.

All data were evaluated for normality with Shapiro–Wilks *W*-test. Normally distributed data were compared with Student's *t*-test and abnormally distributed data were compared with the Mann–Whitney *U*-test.

Field study.—We used artificial food patches to provide information on habitat and microhabitat use for foraging by golden spiny mice in relation to light intensities. The number of patches where mouse footprints or digging activity were recorded provided an indication of the extent of foraging in that microhabitat. Giving-up densities, represented by the weight of seed left in the tray, provided us with information about the foraging decisions of the mice after they had commenced foraging in a tray (Brown 1988).

Our artificial food patches consisted of aluminum trays (30 by 20 by 4 cm, a size that fitted easily under boulders) containing 2 l of finely sifted local soil, which preserved clear mouse footprints, and 2 g of crushed and sieved sunflower seed (1- to 2-mm diameter) mixed thoroughly together. Frames constructed from heavy wire (40 by 60 by 30 cm for uncovered sites; 30 by 40 by 20 cm, necessarily smaller for under-boulder sites) and fine filament fish netting kept birds out of the trays. Mice easily reached the trays, by biting 1 strand in the net. Four weeks of preliminary trials and 3 days of prebaiting before each experiment ensured that mice were digging freely for sunflower seed in the trays and had discovered the location of each tray.

Trays were set out at dawn, and the remaining seed was collected at dusk. At the end of an experimental period, trays were sieved and remaining seed collected and weighed. We alternated starting the sieving at opposite ends of the study site on a 24-h basis.

We conducted experiments simultaneously at 2 sites, the Field School site and the Kibbutz Site, in the Ein Gedi Nature Reserve on the steeply sloping escarpment of the Judaen Desert near the Dead Sea in Israel (31°28′N, 35°23′E; 300–325 m below mean sea level). Both sites had an easterly aspect and received early morning sun. Steep escarpment and cliffs (500 m) to the west cast deep shade on the sites in the late afternoon. Mouse populations at the 2 sites were independent for the duration of the study because they were separated by 2 km and 2 deep canyons (Elvert et al. 1999; Shargal et al. 2000). We selected 2 linear sections of a discrete habitat boundary formed by the edge of a scree of large boulders (boulder habitat) at the foot of cliffs and the open slope or shelf below (open habitat) of small cobbles with isolated larger rocks. Two microhabitats were defined within each of the 2 main habitats.

The boulder habitat comprised jumbled rocks up to 2 m in diameter and provided continuous shelter for the mice in interstices under and between boulders. Seed trays in the under-boulder microhabitat were placed completely under

boulders in interstices large enough that a mouse could comfortably forage in the tray. Between-boulder sites were within 2 m of the continuous boulder field and had no overhead cover, but had some shade.

The open habitat comprised numerous small cobbles and isolated boulders, which were generally in full contact with the ground surface and offered no refuge. The 2 microhabitats used were defined by distance from the overhead shelter offered by the boulder field: open near was 2.5 m and open far was 5 m from the edge of the continuous boulder field.

Seed-tray stations consisted of 1 tray in each of the 4 microhabitats, providing a choice of foraging sites for the mice. The trays in the 2 microhabitats within each major habitat type (boulder or open) were placed 2.5 m apart, and the boulder and open-habitat trays were 10 m apart to account for the gradual rather than abrupt transition from continuous boulder field to truly open habitat. Stations within a site were situated 30 m apart, a distance based on daily movements known from trapping records (Shargal et al. 2000), which was designed to minimize the possibility of the same individuals feeding at >1 station. Ten stations were established, 5 at each site, with a total of 40 trays.

We conducted experiments lasting all day for 3 consecutive days in winter (December–February) and in summer (June–August) to compare foraging habitat preferences and efficiencies of golden spiny mice in relation to light intensity in the different microhabitats. If golden spiny mice have the visual morphology of a nocturnal mammal, they may be sensitive even to relatively low levels of light intensity during the day. The easterly aspect of the sites enabled us to compare the extent of open habitat foraging with and without deep shade during early morning and late afternoon, respectively, when light intensity was already comparatively low. We opened trays for just the first 2 h after dawn and the last 2 h before dusk.

Two types of data were derived from the study. The number of patches where mice foraged was analyzed with multiway frequency analyses and hierarchical log-linear modeling (SYSTAT 1997; Tabachnik and Fidell 1989). We tested for differences in giving-up densities with analysis of variance on rank-transformed means (Brown et al. 1994; Conover and Iman 1981). Before analyzing main effects, we tested for foraging differences among stations, sites, and dates with 1-way chi-squared tests (number of patches foraged in) and Mann–Whitney *U*-tests or Kruskal–Wallis *H*-tests (giving-up densities).

We measured light intensity to assess the possible influence of illumination levels at different times of day and in different seasons on the behavioral selection of habitat by golden spiny mice. Light intensity was measured using a photometer (Li-Cor Quantum/Radiometer/Photometer Model LI-185A, Lincoln, Nebraska) in the early morning (in the first 2 h after dawn), in the middle of the day, and late in the afternoon (in the last 2 h before dark). We took readings with the sensor held upright near the ground at each tray location: under boulders, between boulders, and in the open habitat midway between the open near and open far tray sites.

Results

Histologic study of the retina.—The thickness of the neural retina of both mouse species did not differ significantly and was about 320 μm. The retinal pigment epithelium consisted of a monolayer of cuboidal cells containing pigment granules (Figs. 1a and 1b). Photoreceptor cells were uniform in shape and tightly packed, and they conformed mainly to the morphology of rods. We found no significant morphologic differences in photoreceptor structure among the 2 species; observed photoreceptors in both species had rod-pattern characteristics (Figs. 1a and 1b).

Some morphologic differences in the retinal ultrastructure were detected in the electron microscope photomicrographs (Table 1), including more pigment granules in the retinal pigment epithelial cells of *A. cahirinus*, more mitochondria in the photoreceptor outer segments of *A. cahirinus*, and mitochondria with a significantly smaller diameter than in *A. russatus*.

Field study.—In the initial tests among stations, sites, and dates, we found some differences in giving-up densities among stations in the between-boulders microhabitat in the winter experiments ($\chi^2_4 = 10.17$, $P = 0.038$, $n = 16$). Those differences may have related to natural variation in the

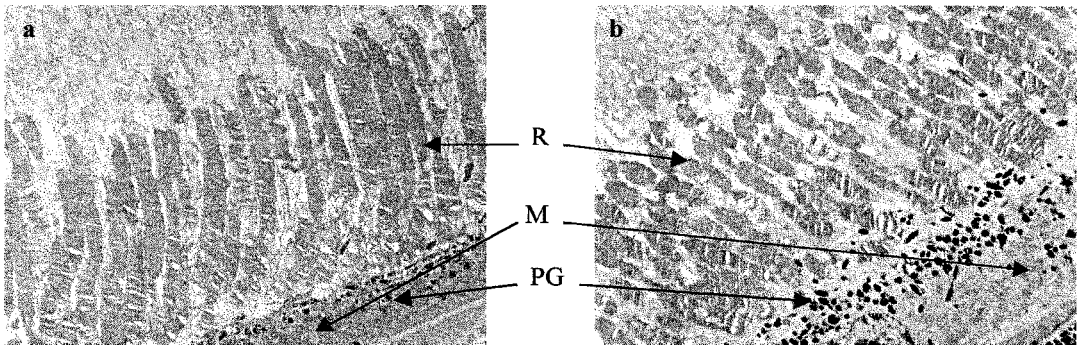

FIG. 1.—Electron photomicrographs of sections of retinal pigmented epithelium of a) golden spiny mouse and b) common spiny mouse (2,000×). R = rods outer segment; PG = pigmented granules; M = mitochondria.

amount of cover and connectedness to the continuous boulder field of the boulder habitat near its margin with the open habitat, despite our efforts to select places to put trays that satisfied a defined set of criteria. Because that variation represented the habitat as actually experienced by the mice, we pooled data for tray groups and those for sites and dates.

Golden spiny mice showed a strong gradient in foraging behavior in summer and winter, preferring microhabitats providing more overhead shelter and shading. Golden spiny mice foraged in the most trays (log-linear modeling, microhabitat by number of trays foraged term: $G = 160.01$, $d.f. = 6$, $P < 0.001$) to the lowest giving-up densities (analysis of variance on rank-transformed means, microhabitat term: $F = 65.797$, $d.f. = 1$, $P < 0.001$) under boulders, followed by the between-boulders microhabitat, the open near microhabitat, and with the least trays foraged to the highest giving-up density in the open far microhabitats in the open habitat (Fig. 2). The foraging microhabitats most important in determining the relative strength of the effects for the number of patches foraged were firstly under boulders, followed by the 2 open microhabitats (standardized log-linear parameter estimates: under boulders = 7.317, between boulders = 3.062, open near = −4.816, open far = −5.796 for yes; sign reversed for no; effects with the largest standardized parameters were the most important in influencing the frequency of a cell—Tabachnik and Fidell 1989).

We found seasonal differences in foraging microhabitat choice and behavior. Golden spiny mice foraged more trays in all microhabitats in summer than in winter (log-linear modeling, season by number of trays foraged term: $G = 31.70$, $d.f. = 4$, $P < 0.001$; Fig. 2). In summer, foraging increased in the between-boulder microhabitat, with more trays foraged to a lower giving-up density, and decreased under boulders, with slightly fewer trays foraged to a higher giving-up density (Fig. 2). That seasonal inconsistency in foraging pattern across microhabitats resulted in significant season by microhabitat interaction terms for both the number of patches foraged (log-linear modeling: $G = 18.26$, $d.f. = 6$, $P = 0.006$) and the giving-up densities (analysis of variance on rank-transformed means, season by microhabitat term: $F = 26.006$, $d.f. = 1$, $P < 0.001$) and probably obscured differences in the seasonal main effect for giving-up densities (season term: $F = 0.020$, $d.f. = 1$, $P = 0.888$).

No significant differences were found in the number of trays foraged between early morning and late afternoon, although the number of trays foraged by time of activity was the last variable to be removed from

TABLE 1.—Comparison of selected aspects of the retinas of *Acomys russatus* and *A. cahirinus*.

Measurement[a]	*A. russatus*			*A. cahirinus*			*P*-value
	$\bar{X}$	*SD*	*n*[b]	$\bar{X}$	*SD*	*n*	
RPE[c] granules/6.25 cm^2	13.3	1.96	6	26.5	8.78	6	<0.01 (*t*-test)
Rod outer segments/6.25 cm^2	3.33	0.51	6	3.83	0.40	6	>0.05 (*U*-test)
No. of mitochondria in photoreceptor outer segments/25 cm^2	7.16	0.40	6	9.50	0.54	6	<0.01 (*U*-test)
Mitochondrial crista	5–6		6	5–6		6	
Maximum mitochondrial diameter (μm)	1.270	0.146	6	1.604	0.278	6	<0.05 (*t*-test)

[a] All measurements at 3,000×.
[b] Number of animals measured.
[c] Retinal pigment epithelial cells.

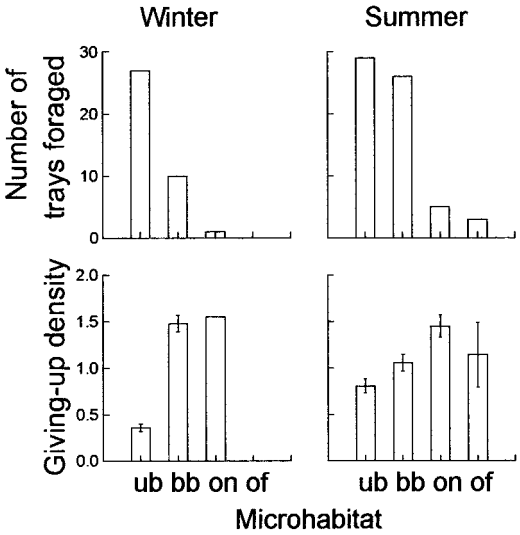

FIG. 2.—The number of trays foraged and giving-up densities (grams of seed remaining per tray) in trays foraged in by golden spiny mice across microhabitats in summer and winter. Ub = under boulders, bb = between boulders, on = open near, of = open far.

the model. A trend existed toward a greater foraging in the late afternoon shade than in the early morning, even in winter under the boulders (Fig. 2). The final log-linear model contained the same variables (microhabitat, season, and season by microhabitat interaction) as the analysis for trays open all day.

In the middle of the day, light intensity (lux) was very high at the between-boulder and open-microhabitat stations (mean values ranged from 1,147 in between boulders in winter to 1,850 in the open in summer), but was very low under boulders (22–47 lux; Fig. 3). Midday light intensity was higher in summer (means of 1,845 lux in between boulders and 1,850 in the open) than in winter (means of 1,147 lux in between boulders and 1,260 in the open). Light intensity was very low in all microhabitats in the afternoon in both seasons (means range from 2 to 89 lux). Values were lower under boulders (winter, 8 lux; summer, 2 lux) than between boulders (winter, 68; summer, 48 lux) or in the open (win-

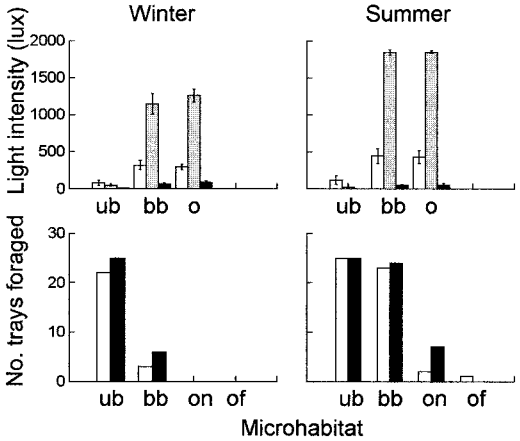

FIG. 3.—Light intensity (lux) and number of trays foraged in in each microhabitat in the early morning (white bar), midday (stippled bar; light intensity only), and late afternoon (black bar). Ub = under boulders; bb = between boulders; on = open near; of = open far.

ter, 89; summer, 56 lux). Winter values were marginally higher than summer values. In the early morning, light levels also were low but higher than they were in the afternoon. Mean values for the different microhabitats ranged from 79 lux in winter and 121 lux in summer under boulders to 320 lux and 446 lux between boulders and 295 lux in winter and 431 lux in summer in the open. In the early morning, summer values were always higher than winter values, but the difference was not as great as for the middle of the day (Fig. 3). The wide variability in values in the early morning and late afternoon was a consequence of sampling all the stations in the same 2-h early morning or late afternoon period. Light intensity at those times of day changed quite rapidly as the sun rose and set.

DISCUSSION

The observed photoreceptors in both species had rod-pattern properties that characterize nocturnal mammals. The golden spiny mouse turns nocturnal in absence of its congener, the common spiny mouse. This pattern suggests that the golden spiny mouse is competitively driven to diurnality (Shkolnik 1971). The golden spiny mouse has evolved dark skin pigmentation in response to the intense solar radiation in the desert, but its endogenous rhythms and capacity for nonshivering thermogenesis reflect its legacy as a nocturnal mammal (Kronfeld-Schor et al. 2000a, 2001). In its retinal anatomical features the golden spiny mouse does not differ from the common spiny mouse, and its rod-based vision is characteristic of nocturnal mammals. Thus, structure of the retina of the golden spiny mouse has not evolved morphologically to meet its expected needs as a diurnally active mammal.

Graded rod signals are often lost as a result of the saturation of rod receptor signals at those higher light levels characteristic of good color vision, where cones continue to operate efficiently (Baylor et al. 1984). A behavioral study examined the relative importance that olfaction, audition, and vision play in the common spiny mouse's localization of insect prey (Langly 1988), but a similar study was not carried out for golden spiny mice. However, spiny mice of both species were found to respond to visual cues (Greenberg 1986). How does the golden spiny mouse cope with the high levels of illumination in the desert during the day? How does it avoid saturation of rod receptor signals during daytime?

Koskela et al. (1989) found a 35-fold higher concentration of ascorbic acid in the eyes of the golden spiny mouse compared with eyes of the common spiny mouse. They suggested that this phenomenon is consistent with the hypothesis of Reiss et al. (1986) that a high concentration of ascorbic acid is a biochemical adaptation, similar to pigmentation of the skin, that permits the eye to withstand intense solar radiation (Koskela et al. 1989).

The retinal pigment epithelium develops from the outer layer of the optic cup and contains pigmented melanosomes at very early stages of embryogenesis (Rapaport et al. 1995). These pigmented intracellular

formations represent a barrier to prevent excess light coming through the sclera, which would decrease resolution of imagery. Melanin granules also are responsible for light energy absorption and cutting down light scatter. The retinal pigment epithelial cells contain enzymes (such as tyrosinase) for the synthesis and replacement of melanin granules (Zinn and Benjamin-Henkind 1979). Schraermeyer and Stieve (1994) recently showed that the melanin granules in the retinal pigment epithelia of mammals originate from photosensory membrane degradation.

Schraermeyer (1993) postulated that all pigmented eye tissues (iris, retinal pigment epithelium, choroid) of adult vertebrates form melanin granules in vivo. Exposure to intense light triggered melanin synthesis and premelanosomes in adult Syrian golden hamsters (*Mesocricetus auratus*). However, the amount of degradation and synthesis turnover is not known. Ultraviolet B is known to increase melanocyte numbers and to stimulate pigmentation (Bessou et al. 1995). In response to light, melanin granules aggregate, and those are dispersed when placed in darkness (Moriya et al. 1996).

The retinal pigment epithelial cells of golden spiny mice had significantly more pigment granules than retinal pigment epithelial cells of common spiny mice (Table 1). This may result from the fact that eyes of golden spiny mice can withstand intense solar radiation (Koskela et al. 1989). Moreover, golden spiny mice used in our histologic study were kept separately from common spiny mice and consequently were active nocturnally (Kronfeld-Schor et al. 2001; Rubal et al. 1992). Variations in the number of melanosomes we found merely reflect a transitory adaptation to light intensity and probably not a fundamental structural pattern. The lower number of mitochondria present in the photoreceptor outer segment of golden spiny mice and the lower mitochondrial diameter of photoreceptors compared with common spiny mice may reflect the same phenomena. The existence of only a few differences between the retinas of the 2 species suggests that further electroretinogram studies should be carried out to more accurately establish possible different functional properties, which are not seen anatomically, between the 2 mice for a better understanding of the adaptation of golden spiny mice to diurnal vision. However, note that studies of birds demonstrate that physiologic responses in nocturnal and diurnal shorebirds and wading birds (measured by electroretinogram) were found to be in accordance with photoreceptor ratios and densities (Rojas et al. 1999a, 1999b).

We found the golden spiny mouse to be a habitat specialist that largely restricts its foraging activity to the boulder habitat and shows a strong preference for foraging under boulders within this habitat. Midday light intensity was low under boulders during winter and summer but was 50- and 25-fold higher in winter and summer, respectively, in the open habitat. Given that the golden spiny mouse forages mainly in covered microhabitats, it is exposed to relatively low light intensities most of the time. The combination of the biochemical properties of their eyes and their foraging microhabitat selection may enable golden spiny mice to withstand diurnal activity with nocturnally designed retinas.

Golden spiny mice seem to select times of day to forage that reduce their exposure to bright illumination. Light intensities in the between-boulder and open microhabitats were much lower in the early and late hours of the day than during midday. In summer, golden spiny mice prefer to forage during these cooler hours (Kronfeld-Schor et al. 2001; Shkolnik 1971), when solar radiation is lower. This phenomenon does not appear to occur in winter. Activity, as measured by trapping, peaks during the middle of the day (Kronfeld-Schor et al. 2001; Shkolnik 1971). A trend existed for more unsheltered (between-boulder and open microhabitat) foraging to occur in the afternoon when the sites were in deep shade

than in the morning when the easterly facing steep slopes caught the full rays of the rising sun. This trend was evident even under boulders. Steepness of slopes at the study sites meant that the rising sun illuminated even underneath boulders where trays were located.

Different ecological forces affect the foraging microhabitat choice of rodents, and multiple forces may operate. Trade-offs in foraging microhabitat use and efficiencies may be an additional mechanism of coexistence between common spiny mice and golden spiny mice (Jones et al., in press). Spiny mice also are affected by predation (A. Bouskila et al., in litt.; Eilam et al. 1999; Shargal et al. 1999), and their preference of the sheltered boulder microhabitat may reflect the structural complexity and partial overhead cover that protect them from avian and mammalian predators. Therefore, the foraging microhabitat choice of golden spiny mice (as well as common spiny mice) could reflect predator avoidance (Jones and Dayan 2000; Jones et al., in press; Y. Mandelik et al., in litt.). However, common spiny mice tend to use the between-boulder and open microhabitats to a greater degree than do golden spiny mice, although they are preyed upon by owls and foxes (Jones et al., in press). The strong tendency of golden spiny mice to forage more often and more thoroughly in the under-boulder microhabitat suggests that light intensity may be one of the factors that restrict them to the boulder habitat, and, in particular, to the under-boulder microhabitat.

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