Influences of Light on Activity of the Small Mammals, *Peromyscus* spp., *Tamias striatus*, and *Mustela rixosa*

Given access to an activity wheel, confined small mammals spend almost all their active time running it[1–3]. Detailed studies of this running show that it depends sensitively on ambient light[2,3]. In fact, differences in running under various light conditions may reveal the state of adaptedness of the visual system for day and night activity and, accordingly, may have a bearing on the evolution of diurnality and nocturnality. For these reasons many small mammals are being studied. The general findings for white-footed mice, eastern chipmunks and least weasels are summarized briefly here together with a discussion of their implications.

White-footed mice (genus *Peromyscus*) usually run wheels in the same direction night after night. They get their bearings for this orientation from sightings of nearby objects, most frequently the artificial moon[2,3]. Time spent running, non-stop session lengths, speed and directional consistency all are influenced by light intensity, being greater the higher the illuminance level in dim light[3]. In an optimum range (0.0019–0.15 lux) the animals run the most time, at the highest speeds, in the longest sessions, and with the greatest directional consistency. In very dim light or darkness they run less, at lower speeds, in short haphazard sessions, and with poorer or no directional consistency.

Artificial twilights markedly affect running speed. Mice usually begin to run during dusk when the illuminance has dropped to 0.7–0.04 lux. At first running is at high speed, but it gradually slows down as the light dims further. During dawn, the animals gradually speed up as the light brightens, but cease running abruptly at 0.04–13 lux. Animals generally run longer and faster if night is initiated by a dusk than if by sudden dim light or darkness. They cease running no matter when a dawn is presented but often ignore bright light that comes on suddenly[3]. The mice are 99.5% nocturnal on regimes employing artificial twilights.

The running parameters of eastern chipmunks, *Tamias striatus*, and least weasels, *Mustela rixosa*, show the same light dependences as for mice, being greater the higher the illuminance at low levels. Like those of mice, the parameters for the chipmunks attained maxima at certain levels but the levels were much brighter than for mice. The running of the chipmunks and weasels proved to be highly unidirectional. Like mice, these animals use both light sources and enclosure features as reference points for orientation. The chipmunks were 98% diurnal but typically ceased running 2–5 h before dusk. They were stimulated to activity by dawn but only were slowed down by an early 'unexpected' dusk or sudden onset of dim light or darkness. The weasels were 99% nocturnal. They were stimulated to activity by dusk and inhibited by dawn but were not inhibited by sudden onset of bright light.

I refer to the activity type – diurnal, nocturnal etc. – of an animal in the wild as the 'ecological activity type' and that found in the laboratory, on light regimes that simulate natural conditions (including twilights), as the 'visual activity type'. I have adopted the working hypothesis that the visual activity type (a) primarily reflects adaptations of the visual system and, accordingly, is established genetically, and (b) either is identical with the most recent past ecological activity type or deviates from the current type in the direction of the past type. In other words, if the visual and ecological activity types differ, I postulate that evolution of the visual system is in progress from the former type toward the latter; if not, the ecological type is established genetically and I refer to the activity type as 'stabilized'.

According to the above hypothesis, the laboratory study of an animal's activity type may reveal the stabilized condition that existed an evolutionary step or two in its past. In the case of the least weasel, which has a nocturnal visual activity type and an arrhythmic (though primarily nocturnal) ecological one, I postulate a stabilized nocturnal recent ancestry with current transmutation of the retina toward the 24-h or arrhythmic type. On the other hand, I regard white-footed mice as stabilized nocturnals and eastern chipmunks as stabilized diurnals, since their activity types are the same in the laboratory and the field. The meadow vole, *Microtus pennsylvanicus*, is nocturnal in the laboratory but diurnal in the field[4]. This suggests to me that it had a stabilized nocturnal recent ancestor and currently is undergoing retinal evolution in the diurnal direction. Since the short-tailed vole, *M. agrestis*, is arrhythmic (though primarily nocturnal)[5], it may be less subject than meadow voles to selection pressure toward diurnality. The Alaskan tundra vole, *M. oeconomus*, may be the least modified of the 3 from the ancestral activity type, for it is nocturnal most of the year[6].

The illuminance-activity relationships found here differ from those expected by analogy with the circadian rule. According to this rule, in constant light (no imposed cycle) the ratio of active time to rest time and the amount of activity are greater the higher the illuminance for diurnal animals but lower for nocturnals[7]. But these experiments reveal opposite effects; in very bright light the running parameters of chipmunks decrease with increasing brightness, while in very dim light the parameters of mice increase as the light gets brighter. The reason for the discrepancy is that the circadian rule is based upon studies in light above the 'optimum' level for nocturnal rodents[3] and below it for diurnal ones[8]. A more accurate circadian rule, perhaps, would be that the ratio of active time to rest time and the amount of activity of many small animals in constant light are greater the higher the illuminance within certain ranges, but lower above these ranges.

Their high directional consistency of wheel running shows that these small mammals maintain continual 'awareness' of immediate surroundings and directions of movements. Taken together with the finding that bearings are obtained from sightings of discrete light sources and enclosure features, the possibility is raised that in the wild the animals (a) 'keep close track' of position relative to the nest and other points of retreat, and (b) can use celestial objects and landmarks as navigational aids.

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Since the mice and weasels are stimulated to activity by artificial dusk and inhibited by artificial dawn, natural twilights probably are the chief factor influencing onset and cessation of their activity. While artificial dawn stimulates chipmunk activity, artificial dusk merely slows it down. This suggests that natural dawn stimulates these animals to activity but that factors other than dusk inhibit them late in the day. The fact that dim light and darkness merely slow down chipmunk activity in the laboratory is consonant with adaptations of these rodents for living in and fleeing through dark burrows. A detailed report of these studies will appear elsewhere[8,9].

Zusammenfassung. Die Aktivität des Backenhörnchens (*Tamias striatus*) und des Wiesels (*Mustela rixosa*) wurde im Laufrad bei künstlicher Dämmerung und abruptem Tag-Nacht-Wechsel untersucht. Sowohl die Geschwindigkeit als auch die gesamte Laufzeit war bei diesen Tieren genau wie bei nachtaktiven Mäusen (Gattung *Peromyscus*) von der Beleuchtungsstärke abhängig. Die Bedeutung dieser Befunde für das zirkadische Gesetz und die Evolution von Tages- und Nachtaktivität wird diskutiert.

J. L. Kavanau

Department of Zoology, University of California,
Los Angeles (California 90024, USA), 29 July 1968.

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Hormonal Control of Colour Changes in Orange Peel

The recent years have broadened our concepts about substances which seem to play a hormonal role in plants and the list of processes which appear to be regulated by plant hormones has also grown considerably. Recent reports indicate that the colour changes associated with the ripening of fruits are also hormone controlled[1-4]. In the present communication we shall discuss some experiments conducted with Shamouti oranges (*Citrus sinensis* L.) harvested while still green. Growth regulators were applied to the fruits by dipping them into solutions consisting of 50% ethanol + 0.02% tween 80 and the desired growth substance. In a preliminary experiment we made sure that neither the ethanolic solution nor the detergent had apparent effects on the colour changes in orange peel. The changes in colour were detected by a Hunter Color Difference Meter (Gardner Laboratories Inc.) and the a/b ratio (a, a measure of redness; b, a measure of yellowness) served for the quantitative estimation of colour development[5].

Figure 1 shows the effects of several growth regulators, at concentrations of 8 and 80 ppm, on colour development of green harvested oranges, as compared with control. The auxin α-naphthalene-acetic acid (NAA) had almost no influence. Benzyl adenine (BA), which acts as a cytokinin, delayed the colour changes and this is no surprise since cytokinins act similarly in preserving the chlorophyll of detached leaves and delaying their senescence[6,7]. Gibberellic acid (GA$_3$) has already been known for several years to inhibit colour development in citrus fruits[4,8], and recently it became clear that it has the same effect also on tomatoes[1,3] and bananas[2]. Figure 1 shows the inhibitory effect of 80 ppm and 8 ppm GA$_3$. The Table shows that even much lower concentrations, down to 0.1 ppm GA$_3$, still have considerable inhibitory effect.

The effect of GA$_3$ might be easily obtained also when treatments are given to fruit attached to the tree[4] and in our experiments attached fruit remained green for more than 6 months after the time of colour break. Detached fruit treated with GA$_3$ attained satisfactory colour only after at least 2 months, whereas control fruit completed the process within 3 weeks. The inhibitory effect of GA$_3$ could be overcome by ethylene; GA$_3$-treated fruit held successively at 20 ppm ethylene needed 17 days to attain an almost satisfactory colour. Ethylene has been known for a long time to enhance colour changes and other ripening processes in fruits, and it appears that ethylene and GA$_3$ act antagonistically to each other in this case.

GA$_3$ is effective also when applied to a limited section of the peel. The fruits seen in Figure 2 have been harvested while still green and painted with GA$_3$ solution inside the marked circle. During a month of storage the fruit developed its typical orange colour, except for the treated zone, where the usual effect of GA$_3$ was obtained. Such local effects were obtained also by applying kinetin[9] and 2,4-dichlorophenoxyacetic acid[7] to restricted areas of detached leaves, thereby delaying the senescence in these areas. The results described in Figure 2 indicate that the process of colour development in peel may be controlled separately in each section of the peel or even in each individual cell. Since the effect of GA$_3$ is a local one it seems reasonable to relate the amounts of applied GA$_3$ to the surface unit of the peel. The oranges we treated had a surface of about 150 cm^2 and they adsorbed about 0.9 ml from the applied solution. Since 0.1 ppm GA$_3$ solution still had an effect (Table) it might be calculated that each cm^2 received not more than 6×10^{-4} µg GA$_3$ and actually only part of this amount penetrated the peel.

These very low amounts are not higher than the levels of endogenous gibberellins in plant tissues[10] and the sensitivity of the orange peel tissues to GA$_3$ might be

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