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Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*)

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Summary. This study examines the effect of moonlight intensity on deermouse (*Peromyscus maniculatus*) vulnerability to predation by short-eared owls (*Asio flammeus*).

Three nocturnal light intensities, labeled new moon, quarter moon, and full moon, were simulated in a flight chamber. Deermouse activity was observed and measured by an index of tracking intensity in the chamber's sand floor. The mice were then exposed to predation by a short-eared owl in each light intensity and search time, chase time, capture time, and the number of escapes/chase were measured.

The results reveal the adaptive significance of deermouse activity suppression in full moon light as an anti-predator response. The deermice reduced activity significantly in bright moonlight during the activity phases. During the predation phases, the owls' hunting effectiveness increased as moonlight waxed. The owls required significantly less time to search for and capture the mice as illumination increased.

The costs and benefits to both species are discussed relative to the prey's variation of activity with moonlight intensity.

Introduction

Numerous small nocturnal mammals reduce their activity in bright moonlight. These include deermice (Blair 1943, 1951; Falls 1953; Kavanau 1967; O'Farrell 1974; Owings and Lockard 1971; Schwab personal communication), bats (Erkert 1974; Fenton et al. 1977; Morrison 1978), kangaroo rats (Lockard and Owings 1974; O'Farrell 1974; Schwab 1966), shrews (Vickery and Bider 1978) and voles (Doucet and Bider 1969; Getz 1968).

The etiology of this activity suppression is unknown. Metzgar (1967) proposed that increased activity increases a prey's exposure to predation. Also, it has been suggested that in bright moonlight prey species are more vulnerable to visual detection by nocturnal predators (Blair 1943; Falls 1978; Fenton et al. 1977; Morrison 1978; Vickery and Bider 1981). If these hypotheses are correct, the combined effect of high activity in bright moonlight would magnify a prey's susceptibility to predation.

It has not been confirmed that moonlight affects nocturnal predator/prey relationships. This study examines the relationships between nocturnal illumination and a prey's vulnerability to a visually oriented predator to determine if reduced activity in bright moonlight can be interpreted as an adaptive anti-predator response.

Deermice, *Peromyscus maniculatus*, whose noctural activity patterns are well documented, were used as the prey species. Short-eared owls, *Asio flammeus*, were used as the predatory species. They are natural predators of deermice and are considered relatively visually oriented because they hunt during day and night (Craighead and Craighead 1956).

Materials and methods

Animals and equipment. Adult female and male deermice (the first laboratory born offspring of wild deermice) were maintained in box cages and provided with nesting materials, Purina Lab Blox, and water ad libitum. Adult short-eared owls, a female and a male, were maintained in the laboratory for 6 months prior to testing. During this time and throughout test-

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ing, they were fed one to two mice daily, Avitron liquid vitamins twice weekly, and water ad libitum. The owls were housed in 1 m^3 canvas cages and on alternate days freed to exercise in the laboratory and halls to maintain satisfactory flight condition.

Tests were conducted in an 8 m^3 flight chamber constructed of plywood (roof, floor, and two sides) and, on two sides, clear Plexiglas. Two owl holding boxes and a mouse holding box opened into the chamber through the wooden walls. Blinds in front of the Plexiglas walls allowed observations to be made of the chamber's interior without disturbing the animals. The chamber floor was covered with fine-grain sand, gridded into 100, 20 x 20 cm squares using narrow wooden slats, and sparsely arranged with rocks, grasses, and a perching post. The chamber ceiling was equiped with 68, 0.5 W light bulbs, arranged to distribute light evenly throughout the chamber. These lights were rheostatically controlled and provided simultated nocturnal illuminations. Two infrared lights, centrally located in the chamber ceiling, permitted observations in all light intensities with a Varo Metascope Infrared Viewer. The infrared light did not appear to be detected by the owls since they were unable to capture mice in tests using infrared light alone (personal observation).

Procedures. The study was conducted in a light-proofed laboratory in which temperature, relative humidity, and photoperiod remained constant throughout the tests (20° C, 30%, and 11 L:13 D, respectively).

Natural nocturnal light intensities were recorded with a Gossen Luna-pro light meter near Missoula, MT, on clear nights of the new, quarter, and full moon. These three light intensities were reproduced in the test chamber and designated new moon light, quarter moon light, and full moon light (0.5 lx, 1.5 lx, and 3.0 lx, respectively, measured from a standard card).

Thirty-six tests, 12 in each of the three 'moonlight' intensities, were conducted using females and males of both species equally. One test was conducted per night from May to August 1980. Each test commenced 1 h after "sunset" using a moonlight intensity, one deermouse, and an owl selected from a randomized schedule.

Each test consisted of three phases:

1. Familiarization phase – a deermouse was released into the chamber which contained scattered food and a nest box. After 23 h, the mouse, now termed a resident of the chamber, was removed briefly while the sand floor was swept smooth.

2. Activity phase – the deermouse was released into the chamber and its activity was measured in a moonlight intensity using an index of its tracking intensity in the sand. A score (0, 1, 2, 3) was assigned to each square in the gridded floor based on the number of tracks per square (0–3 tracks, 3–10 tracks, 10–20 tracks, ≧20 tracks). The summation of the the scores for the grid was the index of activity for the mouse.

3. Predator/prey phase – under the same moonlight intensity the deermouse was exposed to predation by a short-eared owl released into the chamber from a holding box. During this phase the mouse could utilize only the rocks and vegetation for cover since the nest box had been removed.

Four parameters were measured in the Predator/prey phase: search time (the time spend by the owl in locating the mouse), chase time (the time spent by the owl in active pursuit of the mouse), capture time (the sum of search and chase time) and the number of escapes per chase (the number of times the mouse eluded the owl's pursuit). Each test concluded with the owl's successful prehension of the deermouse. The owl with its prey was then removed from the chamber and the next day's test commenced with the introduction of a deermouse into the chamber.

Statistical methods. The parameters were compared using Mann-Whitney *U*-tests and Kruskal Wallis one-way analyses of variance. The 95% confidence limits were computed following the methods described by Campbell (1974).

Results

The deermice significantly modified their activity with changes in nocturnal illumination. The mice actively foraged and explored all areas of the chamber in dim moonlight, rarely responding to any stimuli from outside the chamber. In contrast, under full moonlight the mice restricted activity to the immediate vicinity of rocks, grasses, and walls. This cover seeking behavior in full moonlight is similar to that of wild *P. maniculatus* (Falls 1953) and various bat species (Fenton et al. 1977) which concentrate activity near vegetation on bright nights, avoiding open areas. Furthermore, in full moonlight the deermice frequently froze and remained motionless for 2 or more seconds, apparently in response to sounds outside the chamber. These alterations in behavior contributed to the differences in activity indices between the three light regimes. In nature, deermice may further restrict activity on bright nights by remaining sheltered in a burrow or nest, an option unavailable to the prey in this study.

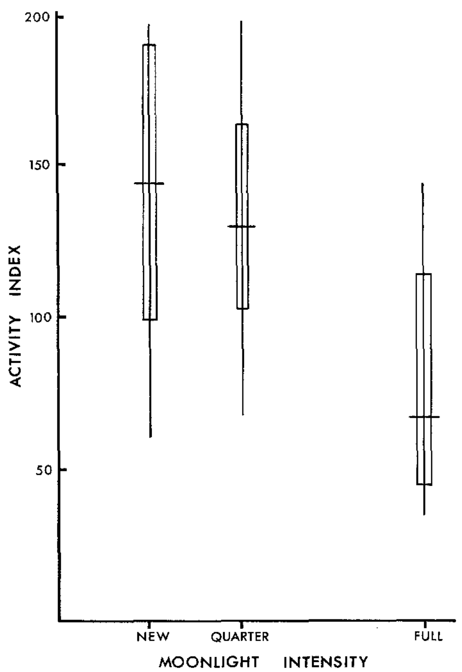

Fig. 1. The medians, 95% confidence limits, and ranges of deermouse activity, as measured by summing the scores of tracking intensity in simulated new, quarter, and full moon light (0.5, 1.5, 3.0 lx, respectively, reflected from a standard card). The activity medians decrease significantly ($P < 0.01$) as moonlight increases

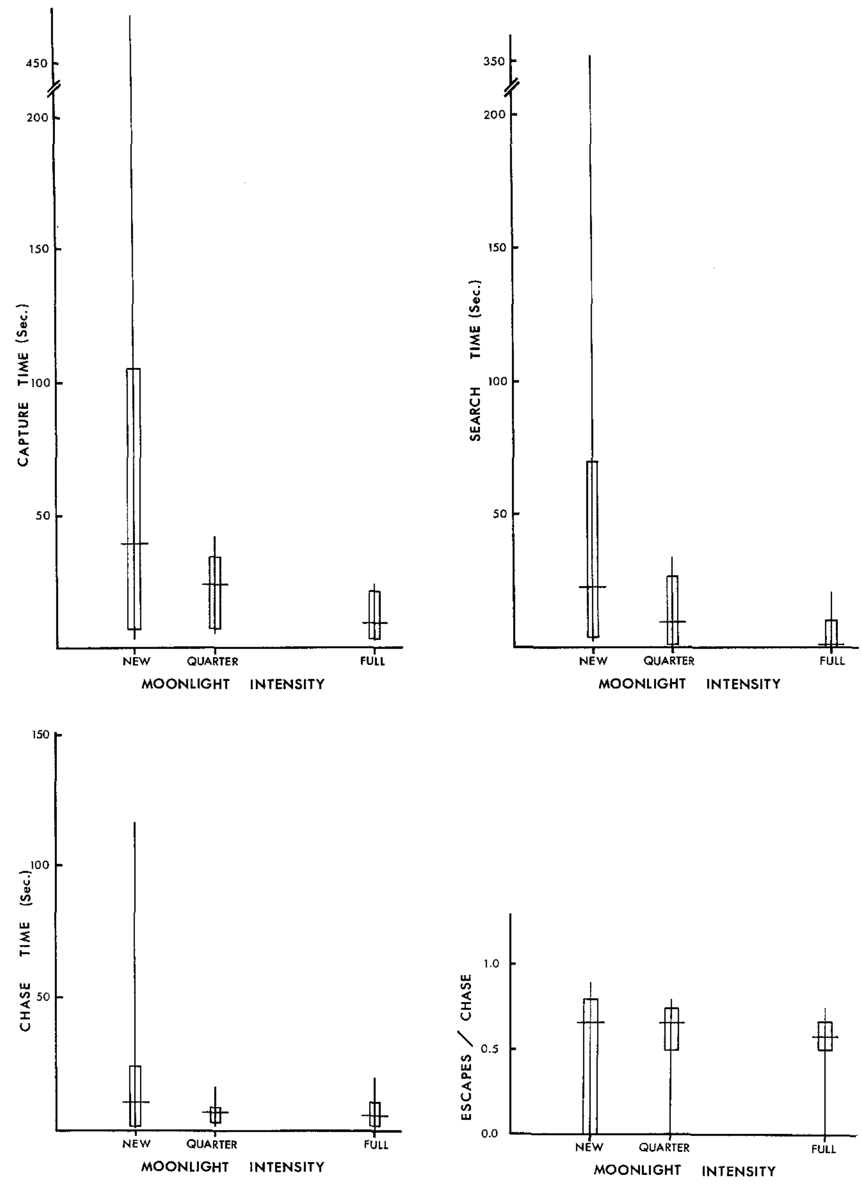

Fig. 2. The medians, 95% confidence limits, and ranges of capture time, search time, chase time, and the number of escapes/chase in simulated new, quarter, and full moon light (0.5, 1.5, 3.0 lx, respectively, reflected from a standard card). Capture time and search time medians decrease significantly as moonlight increases ($P < 0.01$ and 0.05, respectively)

Greater moonlight intensity significantly increased the short-eared owls' hunting efficiency and, consequently, deermouse vulnerability. At the onset of each predator/prey phase the owls immediately began scanning the chamber for prey. The mice either froze in position or fled to another location when exposed to the searching predator. Similar responses have been observed in *Peromyscus* spp. exposed to weasel predation (Jamison 1975) and hawk silhouette flyovers (Bildstein and Althoff 1979). The owls usually took flight in pursuit of a mouse within 1 s of locating the prey. In response to these pursuits the mice either froze, fled along a direct course, or fled zigzagging in the chamber. Falls (1968), Foster (1959), and Jamison (1975) observed similar escape behavior in deermice. Escapes occurred when the owl struck at a mouse and missed or when the pursuing owl lost sight of a fleeing mouse. Subsequent searching and chasing bouts ensued until the mouse was captured.

When released into the chamber in dim moonlight, the owls initially spotted their prey because the mice were active throughout the chamber, including the open areas. The few mice that froze in the open areas when detected were immediately captured, but mice that fled then froze behind cover evaded the hunting owls. The owls' abilities to relocate temporarily escaped deermice was poor in low moonlight. In these cases capture time was increased by numerous chases and prolonged searches. Individual difference in deermouse response to the owl's presence accounts for the variability in the predator/prey parameters in dim moonlight.

In comparison, deermouse responses of fleeing and/or freezing did not hinder the hunting owls in bright moonlight. The owls quickly captured their prey regardless of the escape tactics adopted by the mice. The lack of variability in search, chase, and capture times attests to the predators' greater precision in bright moonlight.

There were no statistically significant differences between females and males of either species for any measured parameter, thus the sexes' data were pooled.

Deermouse activity decreased significantly as light increased ($P<0.01$) and displayed approximately the same range of variation in each of the three illuminations (Fig. 1). There was an inverse relationship between illumination and search, chase, and capture times (Fig. 2). The significant decline in capture time in brighter moonlight ($P<0.05$) was mainly due to the significantly shorter search time ($P<0.01$) the owls required to locate their prey.

The percentage of capture time spent in searching activity averaged 78%, 65%, and 40% in new moon light, quarter moon light, and full moon light, respectively. The time spent by the owls actively chasing the mice did not change significantly with illumination level.

Although no statistically significant differences were noted in the number of escapes per chase between the three moonlight intensities, the manner in which escapes occurred varied with light. Mice escaped the owls' pursuits either by eluding the owls' striking talons or by eluding the pursuing owls' sight, hence causing the owl to resume searching. The percentages of escapes that are attributable to the owls losing sight of their prey were 43%, 9%, and 0% in new moon light, quarter moon light, and full moon light respectively.

Discussion

Nocturnal illumination is an important factor influencing the predator/prey interaction between *Asio flammeus* and *Peromyscus maniculatus*. Moonlight effects both prey behavior and predator effectiveness. The relationship among these factors provides insight into the selective forces acting on the prey.

Owing to the design of this study, the strategies of remaining inactive in a nest or burrow or concealed in shadows during bright nights were not available to the deermice. Hence, the mice were active throughout a range of nocturnal light intensities in a predator's presence. The adaptive importance of activity suppression in bright moonlight as an anti-predator response is evident in view of the deermouse's vulnerability to the owls' enhanced hunting efficiency.

The observations of this study illustrate the effect of moonlight on the cost/benefit relationships of predators and prey in nature. Deermice increase activity during nights when darkness is more abundant. It is reasonable to assume an increase in activity confers benefits to the deermice such as the increased probability of locating mates and/or food sources. However, this study shows that activity also increases the probability of predation to the deermice. On dimly lit nights the benefit of activity may substaintially exceed the cost of predation due to diminished capture efficiency in low light. Under bright conditions, lower activity reduces vulnerability to predators (by remaining in a nest or under cover). Costs incurred by temporary inactivity, such as reduced foraging and mating opportunities, would be exceeded by the benefit of avoiding owl predation. Thus, the deermouse strategy of varying activity directly with the availability of darkness minimizes the cost/benefit ratio that results from predator effectiveness and prey activity.

In natural situations the short-eared owl's cost/benefit ratio may remain constant regardless of flucuations in moonlight. This relatively visually oriented owl's efficiency is hindered on dark nights but the relatively high abundance of active prey provides more opportunities for a capture. Whereas on bright nights capture opportunities are rare due to prey inactivity, the individuals that are active are efficiently caught. In this manner the ratio of capture (predator benefit) to hunting effort (predator cost) may change little throughout variable nocturnal illuminations.

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