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Influence of moonlight on predator/prey interactions between short-eared owls Asio flammeus and deermice Peromyscus maniculatus

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THE INFLUENCE OF MOONLIGHT ON PREDATOR/PREY INTERACTIONS BETWEEN SHORT-EARED OWLS, ASIO FLAMMEUS, AND DEERMICE, PEROMYSCUS MANICULATUS

by

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ABSTRACT

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The Influence of Moonlight on the Predator/Prey Interactions between Short-eared Owls, Asio flammeus, and Deermice Peromyscus maniculatus (44pp.)

Director: Lee H. Metzgar

Deermouse, Peromyscus maniculatus, activity supression in bright moonlight is presumably due to increased pressures from nocturnal predators utilizing visual cues such as short-eared owls, Asio flammeus.

Three nocturnal light intensities, labeled new, quarter, and full moonlight, were simulated in a laboratory chamber. Deermouse activity was observed and measured in the three light intensities in the chamber. The mice were then exposed to predation by short-eared owls in each light regime. The predator/prey parameters of search time, chase time, capture time, and number of escapes per chase were observed and measured.

The deermice reduced their activity significantly ($p < 0.01$) in bright moonlight as expected. The hunting efficiency (defined as 1/capture time) of the owls increased with moonlight intensity. The owls required significantly less time to search for and capture the mice ($p < 0.01$ and $p < 0.05$ respectively) as illumination increased. Chase time and the number of escapes also decreased in bright moonlight.

Deermouse activity and owl hunting efficiency in total darkness was also measured and observed with the use of infra-red light sources and a scope. Deermouse activity in darkness did not differ significantly ($p > 0.5$) from activity in new and quarter moonlight intensities. However, the owls were unable to capture the mice in the total darkness tests.

Moonlight was an important factor influencing the predator/prey interactions between deermice and short-eared owls. Thus, it was illustrated that the supression of deermouse activity in bright moonlight is adaptive as an anti-predator response.

ACKNOWLEDGEMENTS

I wish to express sincere thanks to my major professor, Dr. Lee H. Metzgar, whose advice, enthusiasm and friendship were invaluable to me throughout this study. Dr. Metzgar's guidance enabled me to both streamline the design and expand the concepts associated with my study, in addition to making it all enjoyable.

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Chapter I

INTRODUCTION

The activity patterns of numerous small, nocturnal, mammalian, prey species are well known and many of these prey species suppress their activity in bright moonlight. Species such as kangaroo rats (Lockard and Owings 1974, O'Farrell 1974, Schwab 1966), voles (Doucet and Bider 1969, Getz 1968), shrews (Vickery and Bider 1978), fruit bats (Morrison 1978), and deermice (Blair 1943 and 1951, Falls 1953, Kavanau 1967, O'Farrell 1974, Owings and Lockard 1971, Schwab pers. comm.) decrease their activity with increased nocturnal illumination.

The etiology of this activity supression is lacking. Metzgar (1967) proposed that as a prey species increases its activity it is more exposed to predation. It has also been hypothesized and generally assumed that visually oriented, nocturnal predators are more efficient in bright moonlight. Thus, a prey species' suppression of activity in bright moonlight is presumably an adaptation for avoiding predation when vulnerability is high (Blair 1943, Falls 1968, Morrison 1978, Vickery and Bider 1981).

If this hypothesis is correct, prey species should minimize activity when predation costs are maximal, as in bright moonlight, and maximize activity when the costs are minimal, as in dim moonlight. Thereby, a prey species will minimize its cost to benefit ratio. The benefits associated with activity, such as locating food and mates, can be capitalized on in dim light when the costs associated with activity, namely vulnerability to predation, are minor.

These benefits of activity are then forfeited in bright light when they are exceeded by the costs of being active. Utilizing these strategies, a prey species averages an optimum level of activity throughout time.

A nocturnal prey species can optimize its activity in varying moonlight intensities in numerous ways. A generalized activity pattern of the deermouse (Peromyscus sp.), a ubiquitous, nocturnal, prey species, is illustrated in Figure 1A. I consider this curve to represent the benefit-light intensity relationship. Juxtaposed with this known trend of prey activity in moonlight is the presumed trend of predator efficiency (Fig. 1B). This theoretical trend of the increasing hunting efficiency of a nocturnal predator in bright moonlight also depicts the increasing vulnerability (costs) of a prey species.

However, it has not been confirmed that nocturnal prey species are more vulnerable in bright moonlight to predators using visual cues. Therefore, the purposes of this study are to:

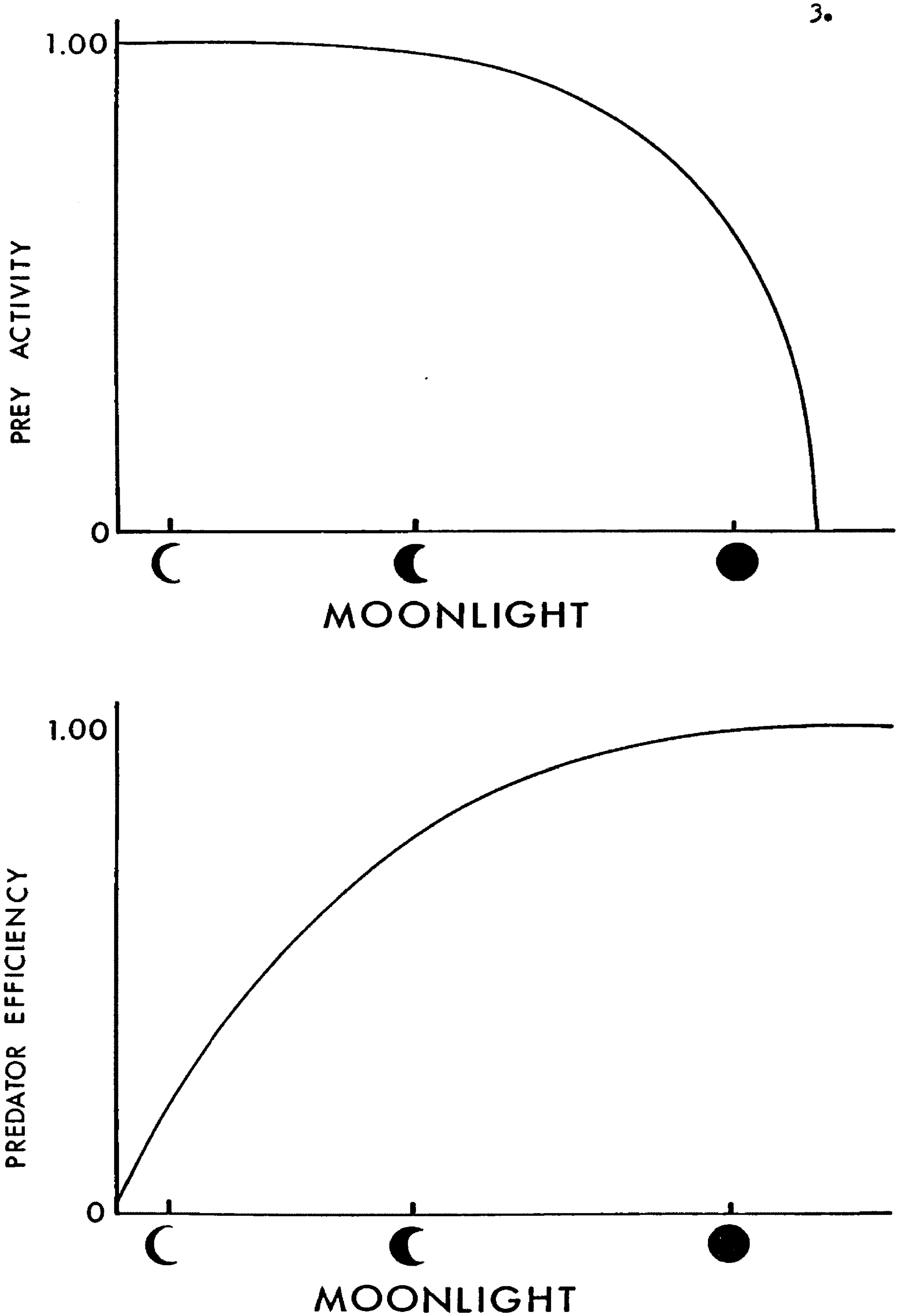
1. confirm the change in activity of a small, nocturnal, mammalian prey species in various nocturnal illuminations;
2. measure the hunting efficiency of a visually oriented, nocturnal predator in various nocturnal illuminations; and
3. evaluate the relationships between moonlight, predator efficiency, and prey activity to determine if the activity-light relationship is an adaptive response to predator pressure.

To accomplish these objectives I used deermice, Peromyscus maniculatus, whose nocturnal activity patterns are well documented.

Figure 1. The generalized trend of a nocturnal prey species activity in moonlight and the presumed trend of a nocturnal species hunting efficiency in moonlight.

A. This figure depicts the generalized trend of deermouse (*Peromyscus* sp.) activity in moonlight as determined in studies by Blair (1943) and Falls (1953).

B. This figure depicts the hypothesized trend of a nocturnal predatory species' hunting efficiency in moonlight.


1.00
0
PREY ACTIVITY
MOONLIGHT
1.00
0
PREDATOR EFFICIENCY
MOONLIGHT

Also, I used a predator of the deermouse, the short-eared owl, *Asio flammeus*. The short-eared owl is considered to be relatively visually oriented compared to the majority of nocturnal owls that rely more on auditory cues in hunting. This is demonstrated by the short-eared owl's habit of not confining its hunting strictly to nocturnal periods but occasionally hunting in diurnal and crepuscular periods as well (Walker 1974). I conducted this study in a laboratory enclosure in which I exposed the animals to simulated nocturnal illuminations. This laboratory situation allowed me to control for variation in other factors that may influence predator/prey interactions in the wild (i.e. temperature, precipitation, photoperiod, humidity).

Chapter II

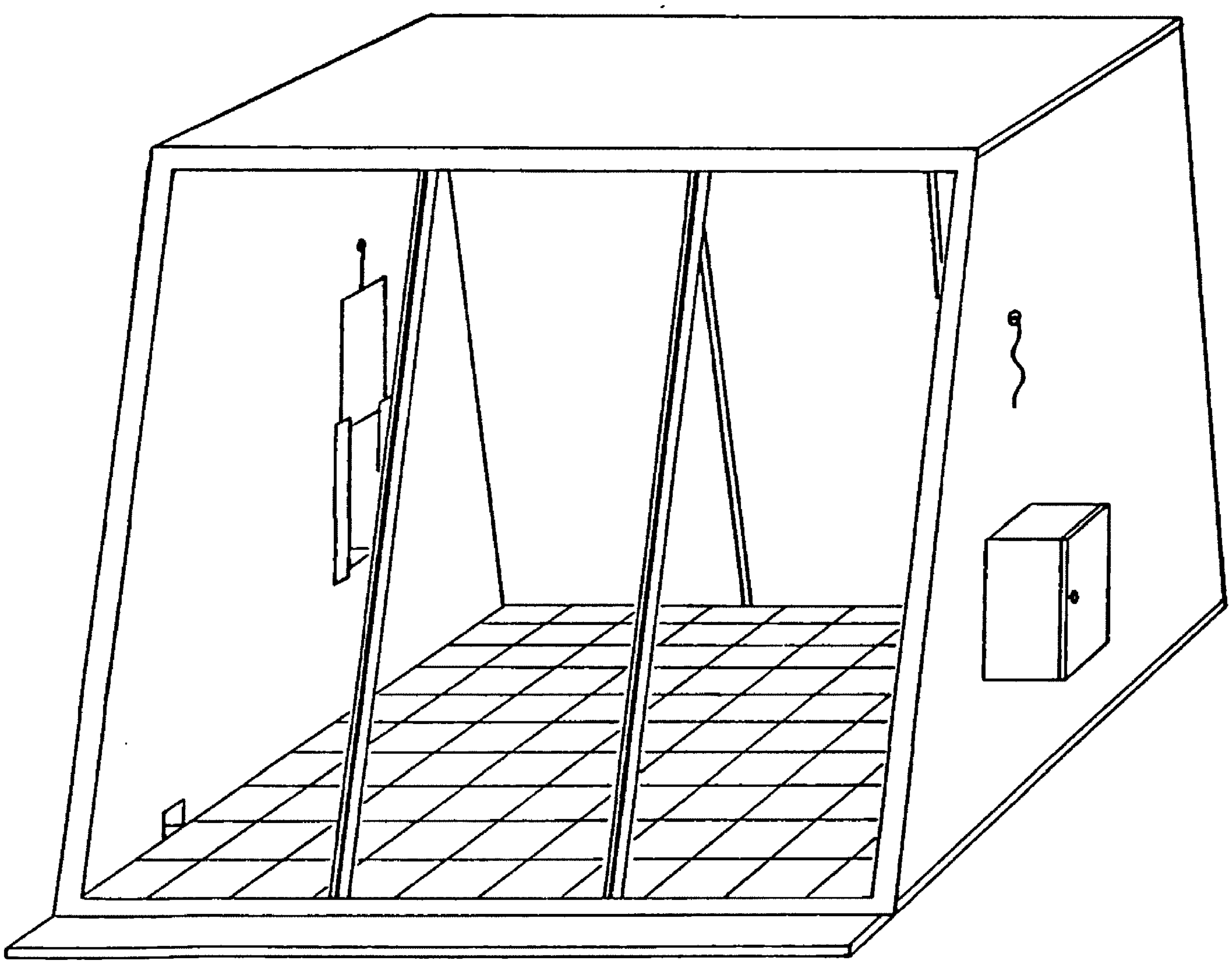
MATERIALS

I used female and male adult deermice (*Peromyscus maniculatus*) as the prey species. In the tests, I used laboratory born offspring of wild deermice caught approximately 16 km north of Missoula, Montana. I maintained the mice in box cages, 45 by 23 by 14 cm, provided with nesting material, Purina Lab Blox, and water *ad libitum*.

I used two wild, adult short-eared owls (*Asio flammeus*), a female and a male, as the predatory species. Both owls were caught approximately 8 km north of Missoula, Montana. The owls were maintained in the laboratory for 6 months prior to the tests. I provided them with 1 to 2 mice daily, Avitron liquid vitatmins twice weekly, and water *ad libitum*. The owls were housed in $1m^3$ cages constructed of light canvas material stretched over a wooden frame of 2.5 by 5 cm boards. On alternate days the owls were released to fly at liberty within the laboratory and exercised regularly thereby maintaining satisfactory flight condition and performance. Both the owls and the deermice were maintained in the light-proofed laboratory.

All tests were conducted in a large flight chamber in the light-proofed laboratory. The test chamber was constructed of plywood and clear plexiglas (Fig. 2). Two opposing walls were wooden and measured 2 by 2 by 1.6 m. The two remaining walls were comprised of 3 removable plexiglas panels each and measured 2 by 2 by 2 m. Two owl holding boxes, measuring 20 by 22 by 37 cm, were fitted to each of the wooden walls approximately 0.5 m. above the floor. These wooden boxes opened into the chamber through vertical sliding doors control-

Figure 2. The test chamber. This figure illustrates the indoor test chamber in which all tests were conducted. The chamber measured approximately 8 cubic meters, and was constructed of wood and plexiglas, with a gridded sand-covered floor and light sources in the ceiling.



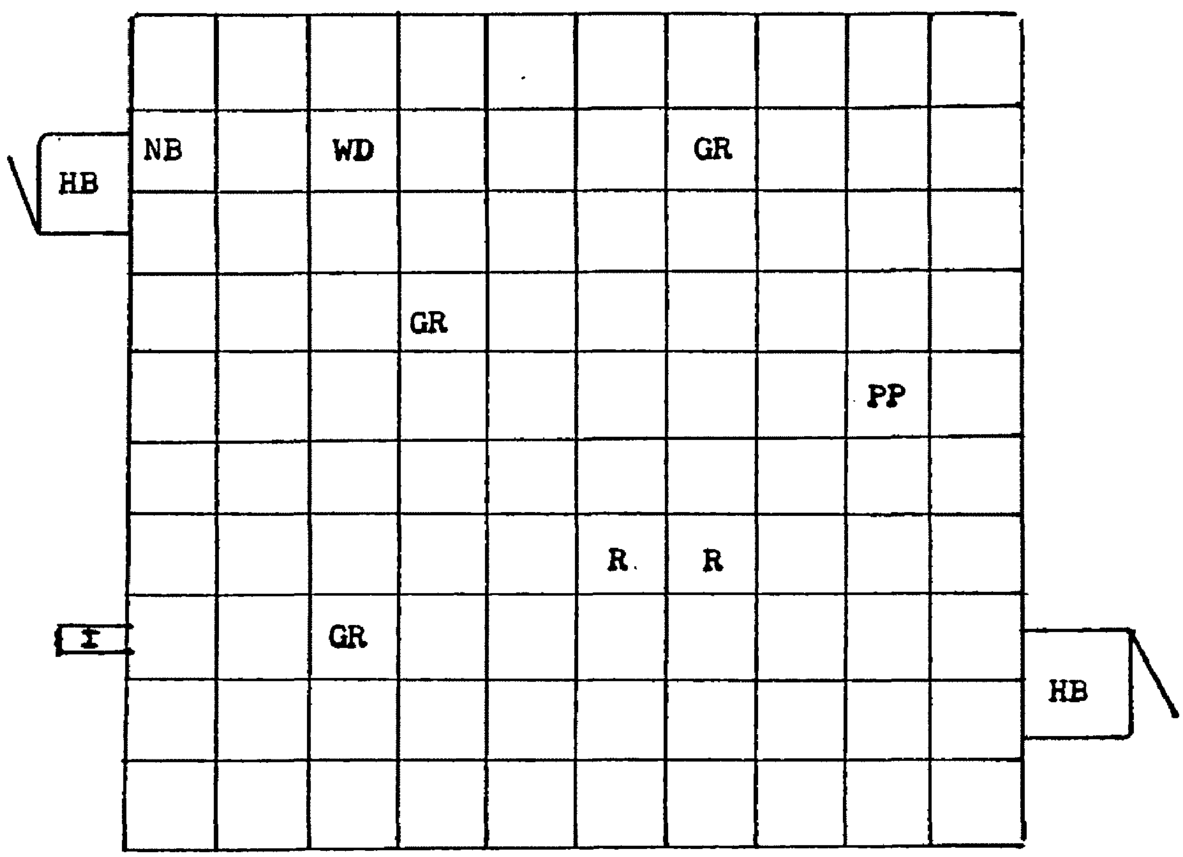
led by cords leading out of the chamber through a hole drilled above each box. A hinged door permitted outside access to each box. A mouse injector was fitted to the outside of one wooden wall at floor level. This wooden injector consisted of a channel, measuring 6.5 by 6.5 by 15 cm long, a sliding plunger block in the channel, measuring 6 by 6 by 15 cm long, and a horizontally sliding door covering the entrance into the chamber. Blinds were positioned in front of both plexiglas walls and were constructed of camouflage colored fabric fastened to a wooden frame measuring 2 by 1.5 m. Two small, rectangular openings in the blinds permitted observations of the chamber's interior.

The floor of the chamber was covered with fine-grain sand to a depth of 1 to 1.5 cm and gridded into 100 squares, each 20 by 20 cm, using narrow wooden slats. The uppermost edge of the slats projected slightly above the sand. Three clumps of bunch grass (Elymus cinereus), 4 groups of small rocks, a water dish, and a wooden perching post, measuring 9.5 by 12 by 85 cm tall, were arranged in the chamber (Fig. 3).

The chamber ceiling was covered with black paper and equipped with 68 small light bulbs, each approximately ½ watt, which comprised the "moonlight" source. These lights were arranged in 4 even rows so as to illuminate all areas of the chamber equally, thereby reducing shadows. A rheostat located outside the chamber enabled me to vary the intensity of these lights thus simulating different moonlight intensities. Two infrared light sources were located centrally in the ceiling. These infrared lights permitted me to

Figure 3. Floorplan of the test chamber. The figure illustrates the arrangement of objects in the chamber and the locations of the owl holding boxes and mouse injector. The objects are defined as follows:

GR	bunch grass and rocks
HB	owl holding box
I	mouse injector
NB	nest box
PP	perching post
WD	water dish
R	rocks


NB
WD
GR
HB
GR
PP
R
R
I
GR
HB

make observations in extremely low light intensities when used in conjunction with a Varo Metascope Infrared Viewer. The infrared light was not detected by the owls (personal observation).

I recorded observations on a Panasonic cassette recorder and timed events with a digital stopwatch. I used a Gossen Luna-pro light meter to determine light intensities.

Chapter III

METHODS

Temperature, relative humidity, and photoperiod remained constant throughout the tests (20°C, 30%, and 11 L : 13 D, respectively). I conducted all tests when the mice were most active, approximately 1 hour after "sunset". I selected mouse sex and light intensity to be used in each test by a randomized schedule. I conducted the tests in either one of three light intensities or total darkness with the infrared lights on at all times. The three light intensities simulated natural illumination on clear nights in northwest Montana. I determined the light to be used in the tests by metering light reflected from a standard card in the field on nights of the new, quarter, and full moon and then reproduced these intensities in the laboratory. I defined the simulated intensities as new moonlight, quarter moonlight, full moonlight, and total darkness (approximately 0.0012 ft-c, 0.0057 ft-c, 0.023 ft-c, and 0 ft-c respectively).

I conducted 42 tests, 12 in each of the three moonlight intensities and 6 in total darkness. I used females and males of both species equally in the tests. I conducted the tests from May to August 1980.

Each test consisted of three phases: a Familiarization phase, an Activity phase, and a Predator/Prey phase.

A) Familiarization phase: I released a deermouse, via the injector, into the chamber which contained a nest box and scattered food. The mouse was free to explore and familiarize itself with the chamber for a period of 23 hours, afterwhich it was termed a resident of the chamber. Previous work indicated that this period was sufficient for a deermouse to become familiar with the area (Metzgar pers. comm.).

B) Activity phase: after the familiarization phase, I removed the mouse and the nest box from the chamber, swept the sand floor smooth, and adjusted the moonlight intensity. I then released the mouse, via the injector, to track the chamber for 5 minutes. I then recaptured it and indexed the track intensity. I assigned a score to each square in the grid based on the number of tracks per square (Table 1). The summation of the score of all the squares in the grid is the index of the activity for the mouse tested.

C) Predator/Prey phase: After evaluation tracks, I placed an owl in one of the holding boxes and released the mouse into the chamber. I observed, from the blind, when the mouse resumed typical foraging and grooming activities (approximately 30 seconds) and gradually raised the door of the holding box, releasing the owl. I tape-recorded my observations after the door was fully opened.

I observed and measured 4 major parameters in each test: capture time, search time, chase time, and the number of escapes per chase.

1.) Capture time: the summation of the owl's search and chase times.

2.) Search time: the amount of time the owl spent looking for the mouse.

Table 1. Scores and descriptions in the scoring of the Activity phase. Presented here are the descriptions and track scores associated with each category of tracking magnitude as determined by the number of tracks per square on the gridded chamber floor.

Tracks/square	Description	Track score
0 - 3	none	0
3 - 10	few	1
10 - 20	medium	2
> 20	heavy	3

3.) Chase time: the amount of time the owl spent in active pursuit of the mouse.

4.) Number of escapes per chase: the number of times the mouse eluded the owl's pursuit divided by the number of times the owl initiated a chase of the mouse.

I concluded each test with the owl's final prehension and capture of the deermouse or, in the case of the total darkness tests, after 10 minutes from the release of the owl. I then removed the owl and its prey from the chamber and performed the next test, using the other owl.

Statistical Methods

I used non-parametric statistical tests in analyzing the results because the data display non-normal distributions. I compare the measured parameters using median values and the significance values obtained from Mann-Whitney U tests for two sample comparisons and Kruskal-Wallis one-way analyses of variance for three or more sample comparisons. In analyzing the variability of parameters I employ range values and the computed confidence limits following the methods described in Campbell (1974).

Chapter IV

RESULTS

Moonlight Tests

I combined the data for the species' sexes because there were no statistically significant difference between females and males of either the deermice or the owls for any of the measured parameters within a light regime ($p > 0.05$, in all cases).

Deermouse activity decreased with increasing light intensity ($p < 0.01$, Table 2) as expected. Mouse activity is relatively hight in new moonlight (Median index value = M index = 144.0) and quarter moonlight (M index = 130.0) with no significant difference in activity between these two light regimes ($p > 0.10$). Activity decreases sharply in full moonlight (M index = 67.5) and differs significantly from activity in new and quarter moonlight ($p < 0.005$, both cases).

The measured predator/prey parameters also decrease in numerical value as light intensity increases. The owls require significantly more time to capture the mice with decreased moonlight intensity ($p < 0.05$, Table 2). The median capture time in new moonlight (M = 39.0 seconds) is nearly twice the median capture time observed in quarter moonlight (M = 23.8 seconds) and four times greater than in full moonlight (M= 9.0 seconds).

Search time shows the same trend as capture time, with the owls searching significantly longer for the mice in dim moonlight intensities ($p < 0.01$, Table 2). Median search time in new moonlight (M = 23.0 seconds) is twice as great as in quarter moonlight (M =

Table 2. Median parameter values and significance levels. The table presents the median values of deermouse activity indices and four predator/prey parameters in three simulated moonlight intensities and the level to which these parameters differ significantly between the three light intensities as determined by Kruskal-Wallis analyses.

Parameter	M parameter values			
	New moonlight	Quarter moonlight	Full moonlight	p
Activity index	144.0	130.0	67.5	**
Capture time(s)	39.0	23.8	9.0	*
Search time(s)	23.0	9.75	1.25	**
Chase time(s)	10.8	7.0	6.0	ns
Escapes/chase	0.66	0.66	0.58	ns

**: $p \leq 0.01$, *: $p \leq 0.05$, ns: $p > 0.05$

9.75 seconds) and 18 times greater than in full moonlight (M = 1.25 seconds).

The time spent by the owls actively chasing the mice also increases at lower moonlight intensities although this trend is not statistically significant ($p > 0.10$, Table 2). In new moonlight the median chase time (M = 10.8 seconds) is 1.5 times the median chase time observed in quarter moonlight (M = 6.0 seconds).

The percentage of capture time that is comprised of search time and chase time changes with light intensity (Table 3). In the dim intensities the owls spend the majority of their hunting time searching for the mice. Search time comprises an average of 78% of the total capture time in new moonlight and 65% of the capture time in quarter moonlight. The average percentage of capture time that is search time reduces to 40% in full moonlight with chase time as the major constituent of the total capture time.

No significant difference was noted in the number of escapes per chase between the three light intensities ($p > 0.10$, Table 2). The mice tend to escape about 66% of the owls' chases in both new and quarter moonlight and 58% in full moonlight. Mice escape owls' active pursuits in one of two ways: the mouse eludes the talons of the owl that is striking directly at it, or the mouse eludes the sight of the owl that is actively pursuing it. In new moonlight, 43% of the total number of escapes are due to the owls losing sight of their prey and consequently breaking off a chase without making a strike. Only 9% of the total number of escapes

Table 3. Mean percentages of search and chase times comprising total capture time. The table presents average percentages of hunting time that is spent by the owls in the two components of total capture time (searching and chasing), in the three moonlight intensities.

Light	Percentage of Parameter		
	% Search time +	% chase time =	% capture time
New moonlight	78	22	100
Quarter moonlight	65	35	100
Full moonlight	40	60	100

in quarter moonlight are attributed to the owls losing sight of the fleeing mice. In full moonlight, none of the escapes occur in this manner; all coincide with a strike.

The mean rankings computed in the Kruskal-Wallis one-way analyses of variance of deermouse activity and of predator prey parameters summarize the relationship between these behaviors and the moonlight intensities along a linear scale (Fig. 4). The first ordinal ranking scheme emphasizes the significant suppression of deermouse activity in full moonlight in contrast to the insignificant difference in activity between new and quarter moonlight. These ranking schemes also reiterate the significant reduction of capture time and search time in bright moonlight as well as the similar decreasing trend in all the measured predator/prey parameters as moonlight intensity waxes.

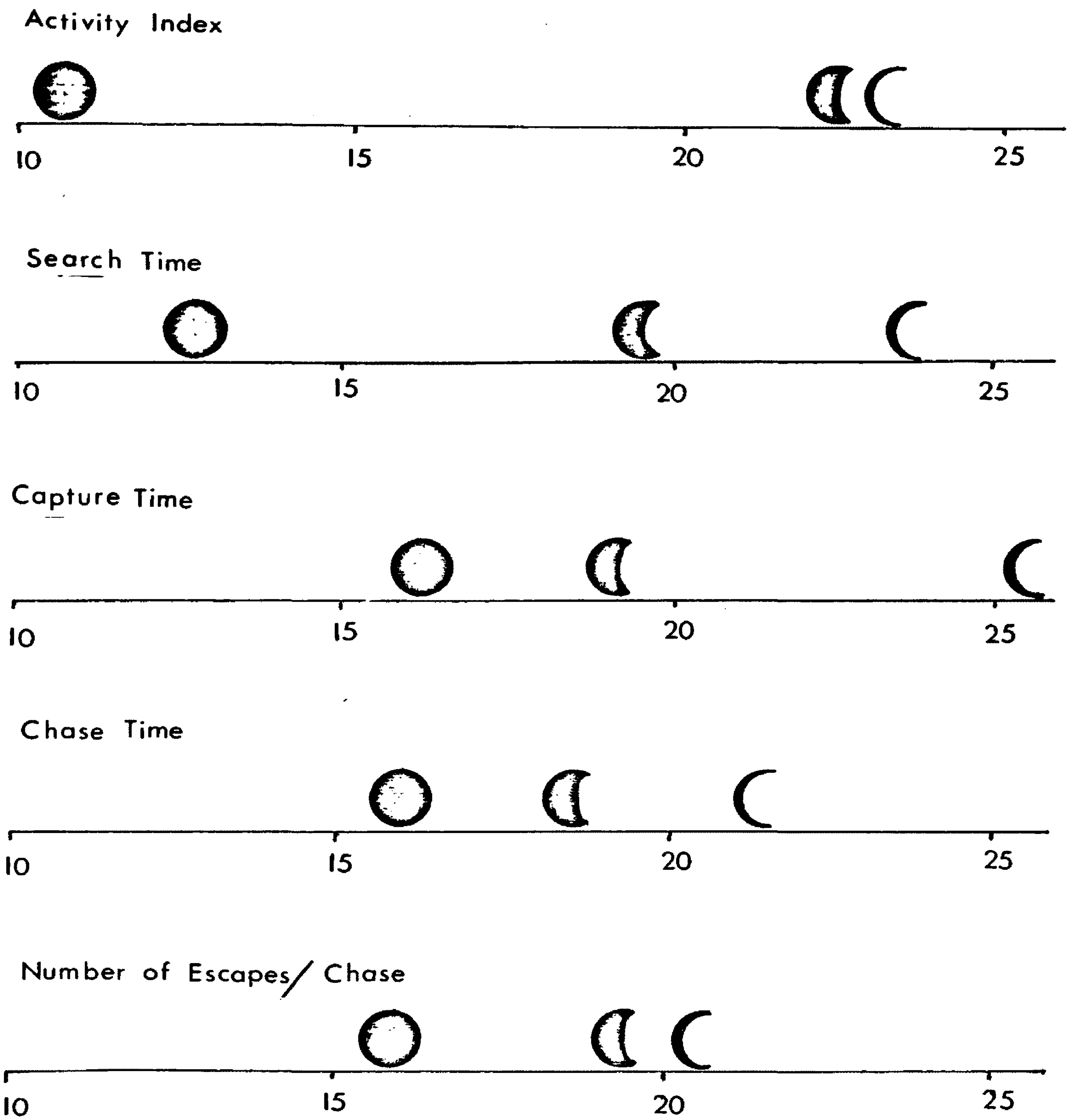
Differences in variation are evident between deermouse activity and the predator/prey parameters in the moonlight intensities. Deermouse activity is about equally variable in the three light intensities (Fig. 5). The ranges of the activity indices in new, quarter, and full moonlight are 135, 129, and 109, respectively. In contrast, the predator/prey parameters vary greatly between the three light regimes and in all cases the maximum variability occurs in new moonlight. Capture time ranges approximately 7 minutes in new moonlight, 0.5 minutes in quarter moonlight, and 0.3 minutes in full moonlight (Fig. 6). Search time reveals the same trend, ranging approximately 6 minutes in new moonlight, 0.5 minutes in quarter moonlight, and 0.3 minutes in full moonlight (Fig. 7).

Figure 4. Ordinations of the three moonlight intensities by the measured parameters. This figure presents the rankings obtained from Kruskal-Wallis one-way analyses of variance. These rankings graphically depict the relative magnitudes of the measured parameters in each moonlight intensity. The moonlight intensities are defined as follows:

 Full moonlight

 Quarter moonlight

 New moonlight



Activity Index
10
15
20
25
Search Time
10
15
20
25
Capture Time
10
15
20
25
Chase Time
10
15
20
25
Number of Escapes/ Chase
10
15
20
25

Figure 5. The medians, confidence limits, and ranges of Deermouse Activity Indices in three simulated moonlight intensities.

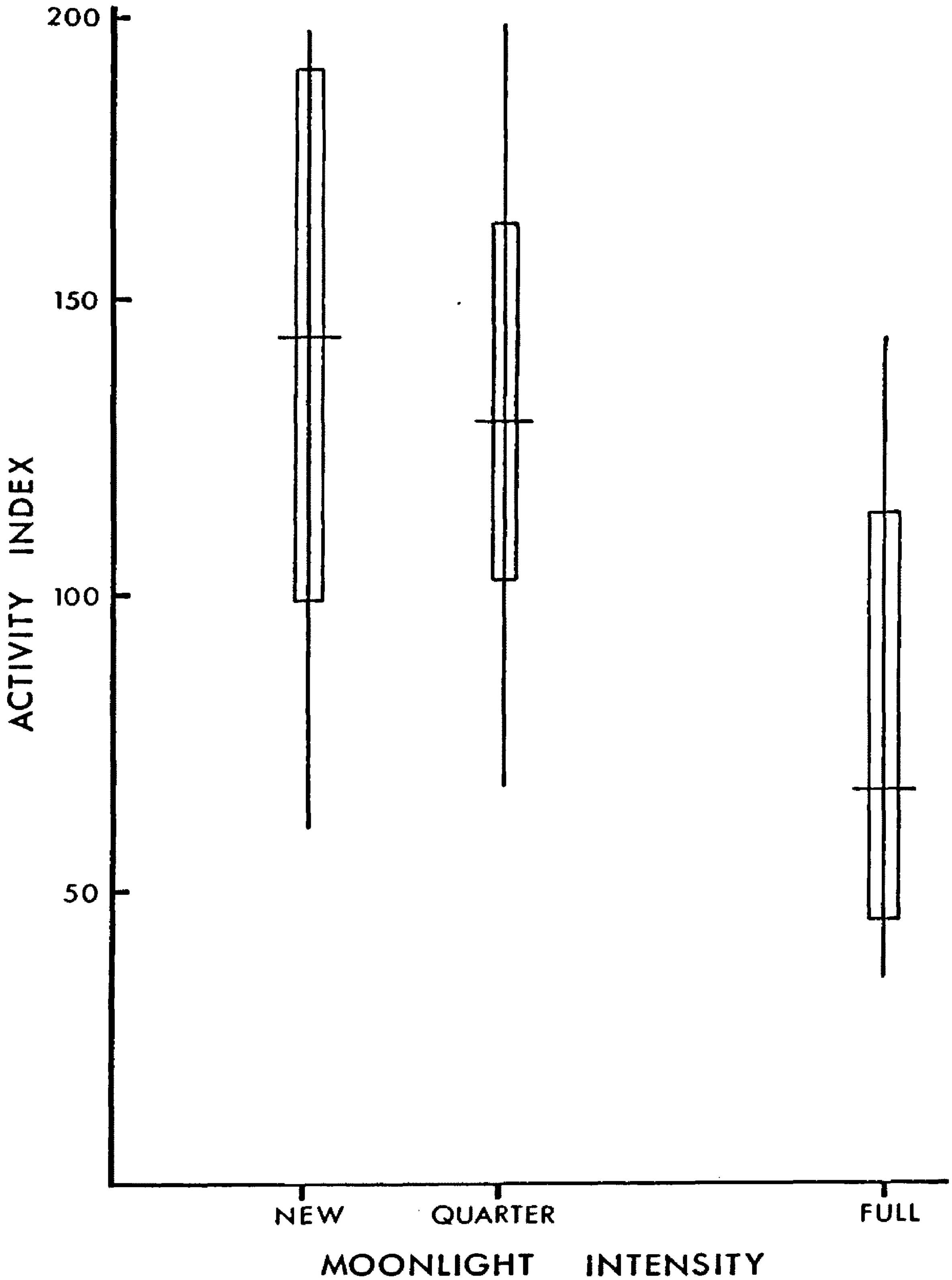

200
150
100
50
ACTIVITY INDEX
NEW
QUARTER
FULL
MOONLIGHT INTENSITY

Figure 6. The medians, confidence limits, and ranges of Capture Time (in seconds) in three simulated moonlight intensities.

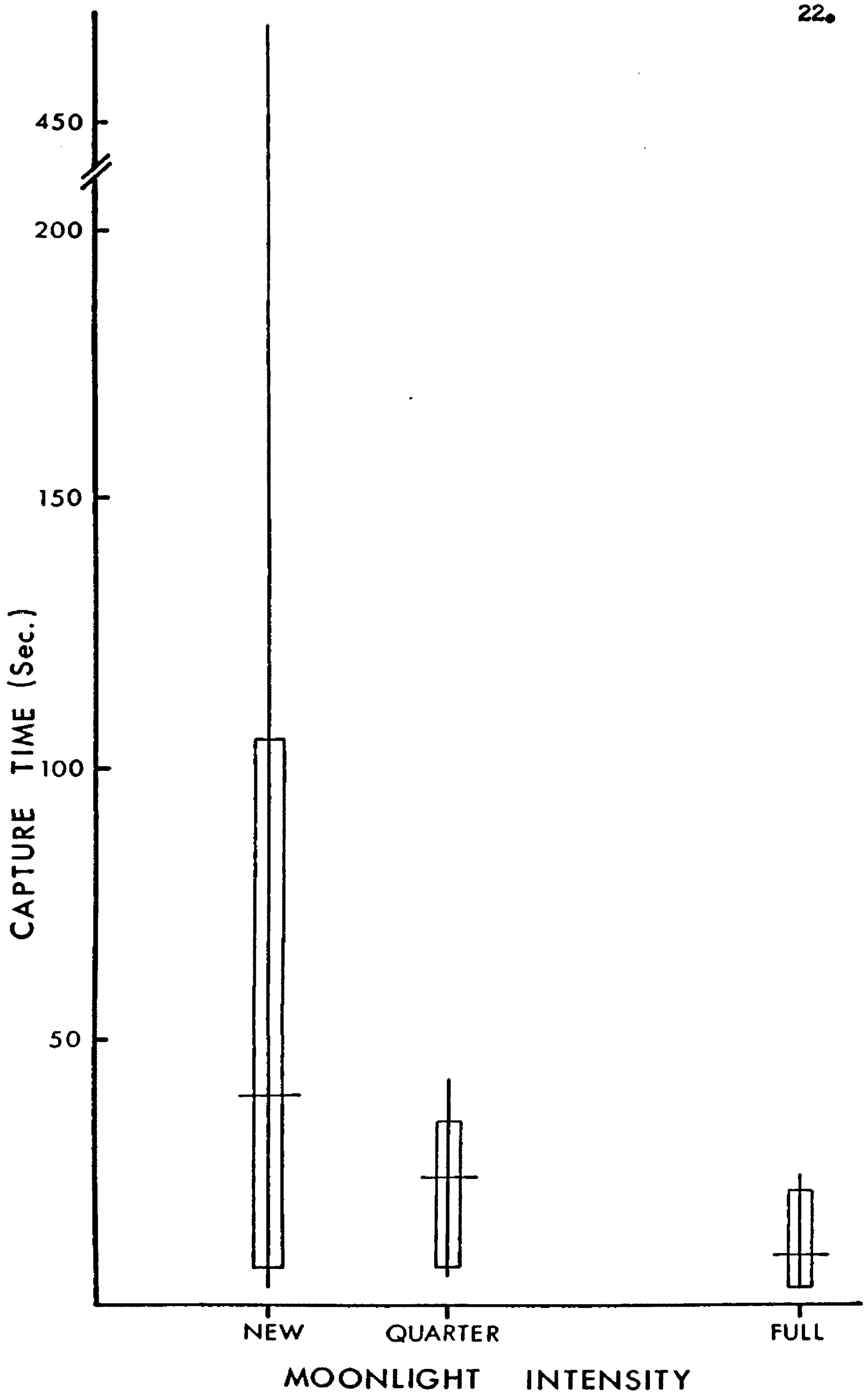
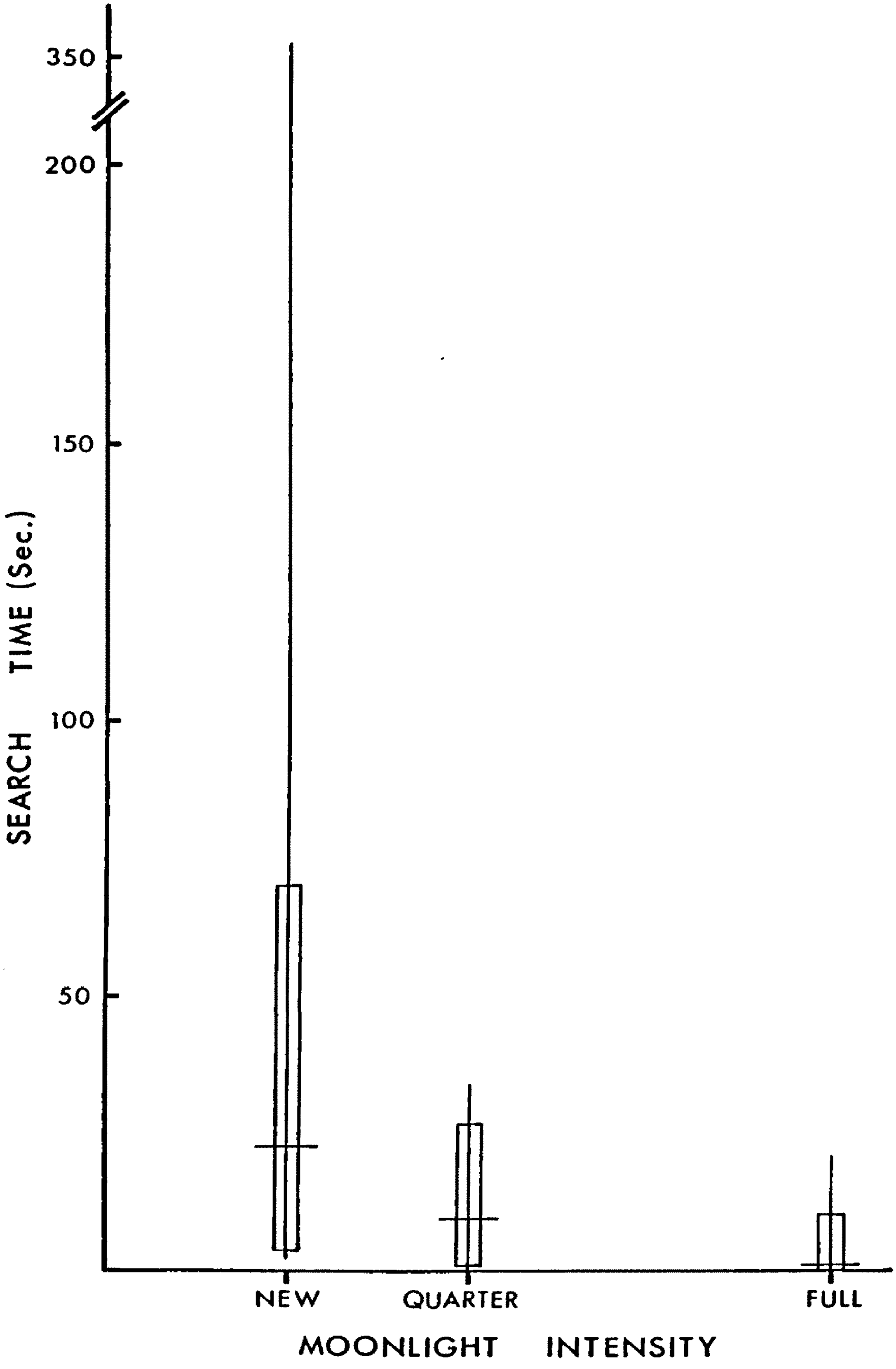

450
200
150
100
50
CAPTURE TIME (Sec.)
NEW
QUARTER
FULL
MOONLIGHT INTENSITY

Figure 7. The medians, confidence limits, and ranges of Search Time (in seconds) in three simulated moonlight intensities.


350
200
150
100
50
SEARCH TIME (Sec.)
NEW
QUARTER
FULL
MOONLIGHT INTENSITY

Again, most variation is in new moonlight. Variation in chase time and number of escapes per chase also shows this trend of increasing variability in waning moonlight, although less dramatically (Figs. 8 and 9).

Total Darkness Tests

I combined the data for the species' sexes in the following analyses because there were no statistically significant differences ($p > 0.50$) between females and males of either the deermice or the owls for the measured parameters in the total darkness tests.

Deermouse activity in total darkness (M index = 130, Table 4) is not significantly different from activity levels obsered in new moonlight (M index = 144, $p > 0.50$) and quarter moonlight (M index = 130, $p > 0.50$). Mouse activity in total darkness is significantly greater than in full moonlight (M index = 67.5, $p < 0.05$).

The measured predator/prey parameters in total darkness differ greatly from those in the moonlight intensities. The owls never capture the deermice in the allotted 10 minute period in the total darkness tests (Table 4). The owls appear to search for the mice continuously throughout the tests yet rarely orient in a mouse's direction (M = 1.5 orientations, Table 4). In these orientations, the owl's body is frontally facing a mouse yet if the mouse moves to another location the owl does not change its orientation to coincide with the prey's new position in the chamber.

Figure 8. The medians, confidence limits, and ranges of Chase Time (in seconds) in three simulated moonlight intensities.

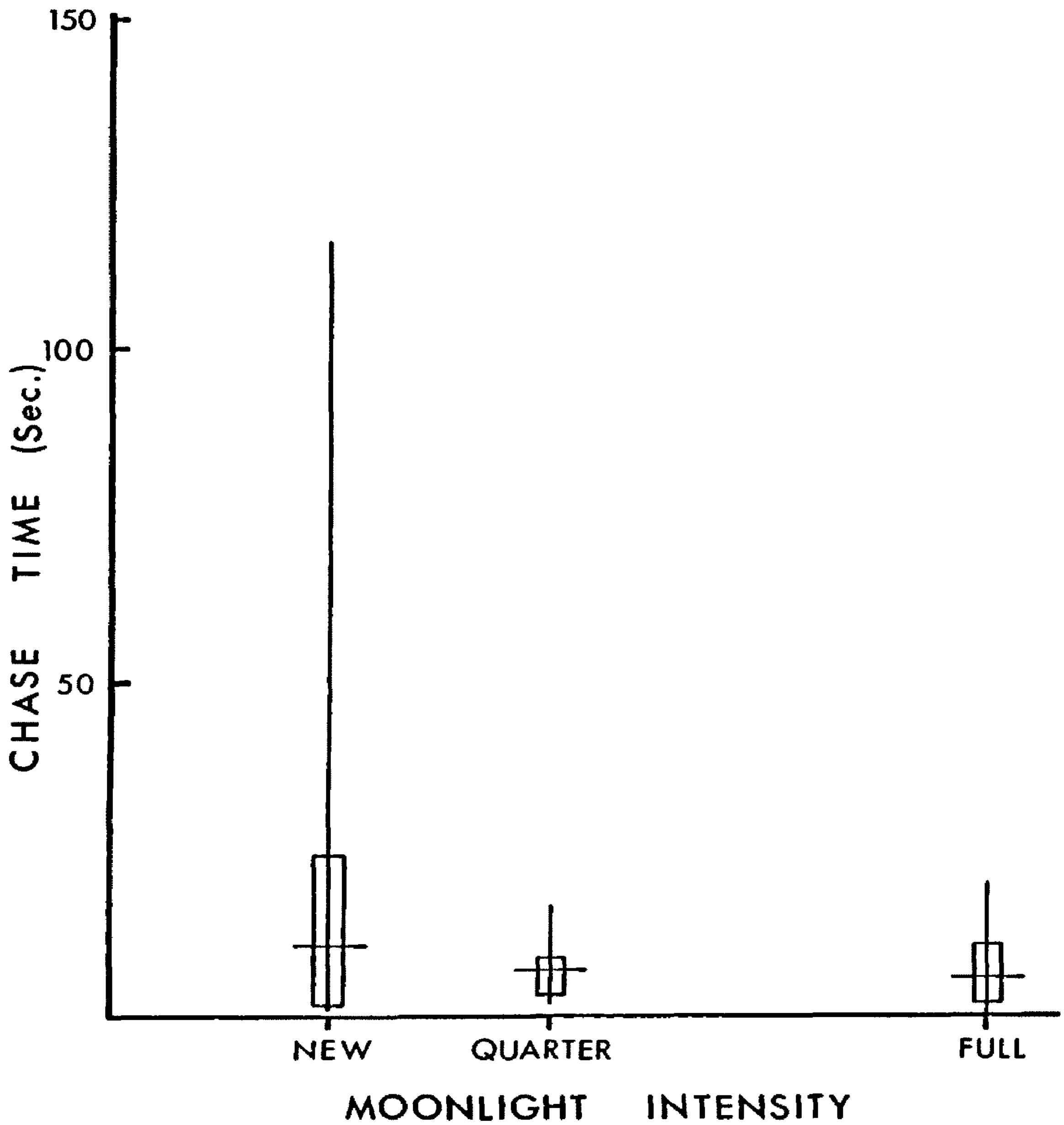

150
100
50
CHASE TIME (Sec.)
NEW
QUARTER
FULL
MOONLIGHT INTENSITY

Figure 9. The medians, confidence limits, and ranges of number of escapes per chase in three simulated moonlight intensities.

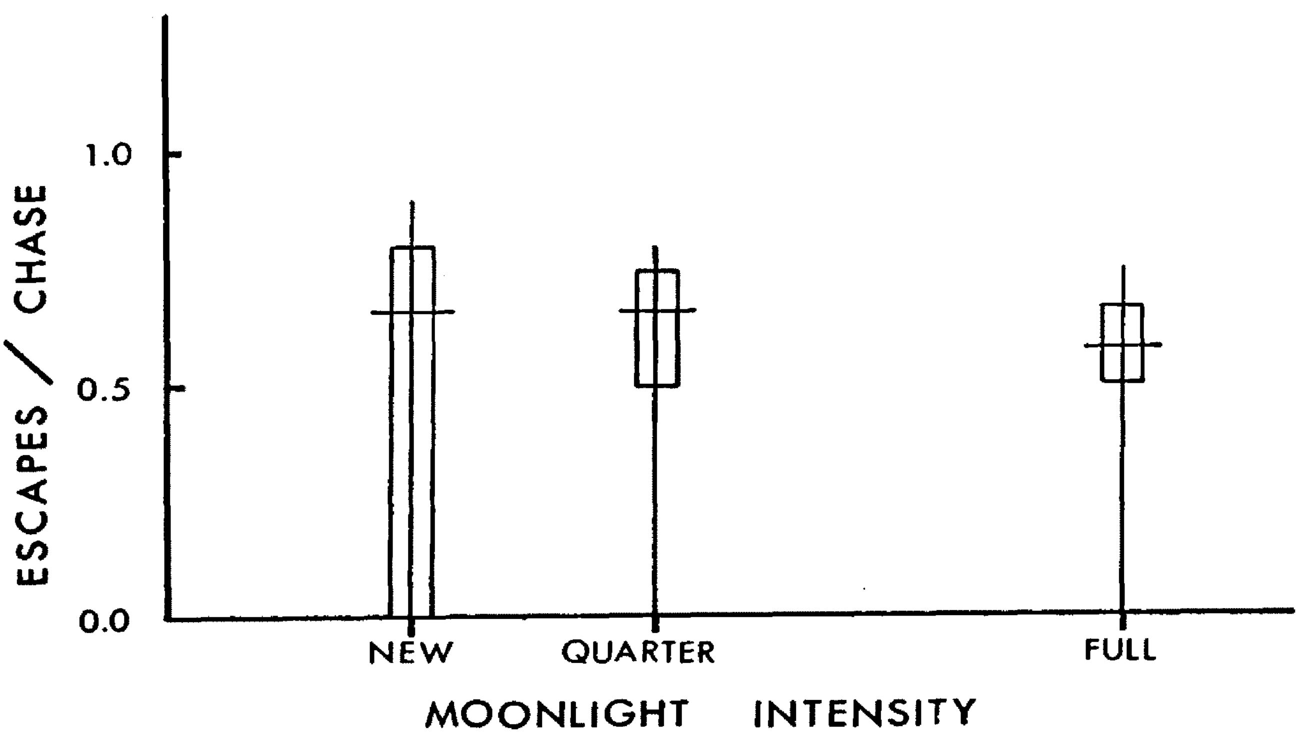

1.0
0.5
0.0
ESCAPES / CHASE
NEW
QUARTER
FULL
MOONLIGHT INTENSITY

Table 4. Median parameter values for total darkness tests. The table presents the median value for mouse activity in total darkness. In these tests no captures were observed in the 10 minute test periods, during which the owls appeared to search continuously, never chasing the mice.

Parameter	Median
Activity index	130
Capture time (minutes)	> 10
Search time (minutes)	> 10
Chase time (minutes)	0
Escapes/chase	0
Orientations	1.5

Thus, whether these orientations, seemingly toward a mouse, are actually in response to sensory stimuli or simply by chance is undetermined. Because the deermice appear to completely elude detection by the owls in the total darkness tests, chases or escapes per chase are not recorded (Table 4).

Chapter V

DISCUSSION

Moonlight is an important factor influencing the nocturnal predator/prey interactions between short-eared owls and deermice. As expected, the deermice suppressed their activity significantly in bright moonlight (Fig. 10A) and, as hypothesized, the short-eared owls' hunting efficiency improved significantly with increased moonlight intensity (Fig. 10B).

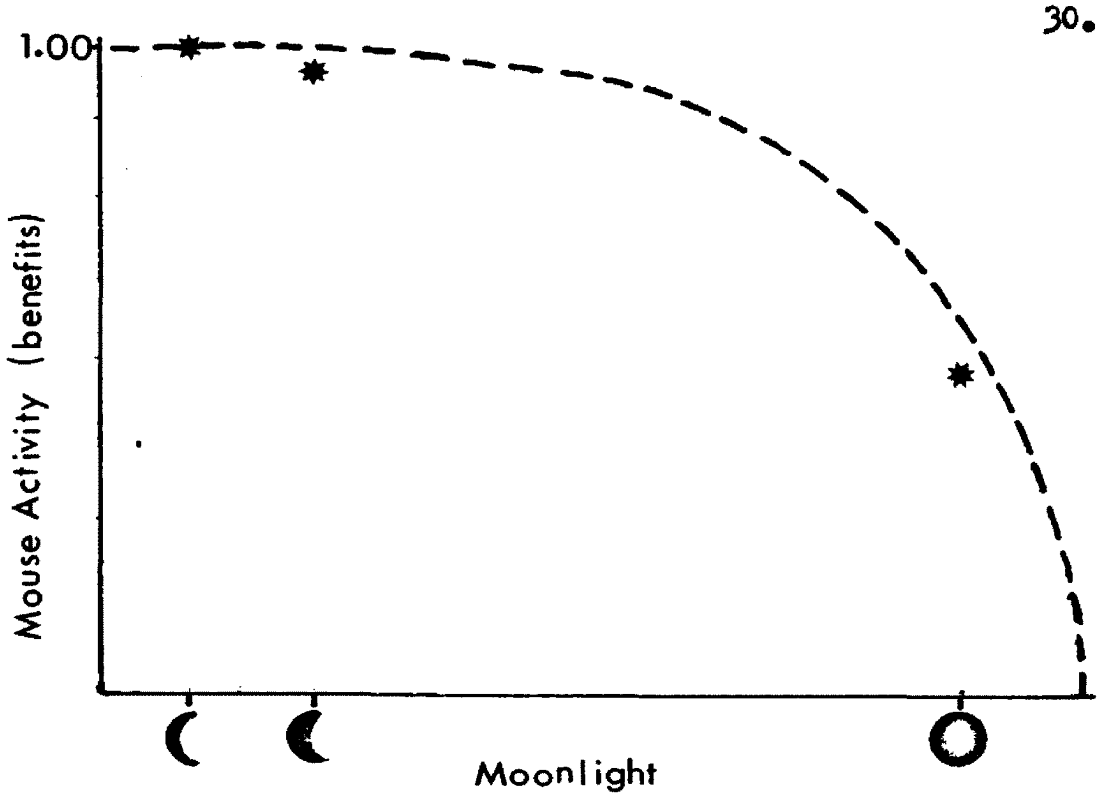
Deermouse Activity in Moonlight

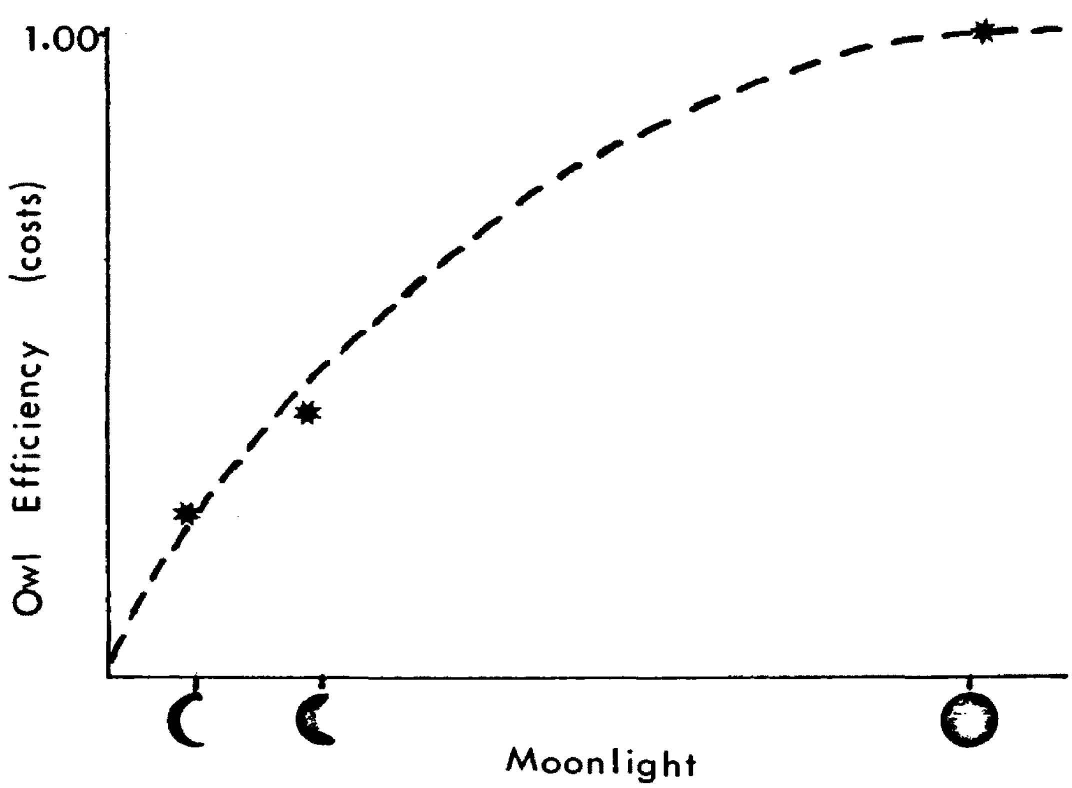
The deermice modified various behaviors with changes in moonlight intensity, accounting for differences in activity indices. In the dimmest light intensity, new moonlight, the mice engaged in typical foraging, exploring, and grooming behaviors (Eisenberg 1962 and 1968) throughout the activity phase. They utilized all areas of the chamber including the central portion which lacked rocks, grasses, or objects that could provide cover. The mice also rarely paused in their activities in response to sounds outside the chamber. This is intriguing as, in all probability, the mice were "aware" of the owls' presence in the area because the birds often flew about the laboratory. In quarter moonlight the mice slightly altered two facets of their behavior. They were less active in the exposed central area of the chamber in quarter moonlight and they occasionally paused in response to sounds outside the chamber, but immediately resumed typical foraging, exploring, and grooming activities. These modifications in behavior were minor and the slight reduction in activity indices from new to quar-

Figure 10. Trends of Deermouse Activity and Short-eared Owl Hunting Efficiency in Moonlight.

A. This figure depicts the three median predator efficiency values (costs) from this study and the hypothesized predator efficiency curve in moonlight (see Fig. 1B). The inverse of each median capture time is used because hunting efficiency is inversely proportional to capture time.

B. This figure depicts the three median prey activity indices (benefits) from this study and the generalized activity curve of deermice in moonlight (see Fig. 1A).


1.00
Mouse Activity (benefits)
Moonlight


1.00
Owl Efficiency (costs)
Moonlight

ter moonlight tests is insignificant.

The mice greatly modify their behavior in full moonlight. They often maintained tense, elongate posturing (Eisenberg 1962 and 1968) while initially circuiting the chamber, creeping closely to the walls. They eventually began foraging, exploring, and grooming activities (after approximately 2 to 3 minutes) but concentrated these activities in corners and near walls, rarely advancing toward the central area of the chamber. They responded to sounds outside the chamber by stiffening in a motionless upright posture or dashing for the nearest bunch grass or corner. These behavioral changes significantly reduced the activity indices in full moonlight.

The deermice are extremely active, foraging and exploring, in dim nocturnal illuminations when they are presumably less vulnerable to predation. Deermouse activity is restricted by alarm and predator avoidance behaviors (Eisenberg 1968) in full moonlight when vulnerability to predation is great.

Predator/Prey Behaviors in Moonlight

At the onset of each Predator/prey phase the owl immediately began searching for the prey scanning the floor of the chamber, turning its head from side to side while perched in the holding box, or on the post, or on the chamber floor. When the owl flew from the box the mouse altered its behavior, apparently sensing the predator's presence. I observed two stereotyped deermouse responses - the mice froze in position or fled to another location when they sensed the searching predator. Jamison (1975) noted similar behavior in deermice exposed to weasels. When the prey was located the owl oriented frontally toward the mouse, bobbed its head, tilted its body forward while shifting its footing, all in a fraction of a second, prior to taking flight in pursuit of the mouse. The owl would pursue the mouse for 1 to 5 seconds. I observed three stereotyped deermouse responses to the owls' active pursuits. The mice froze, fled in a straight line, or fled zig-zagging in the chamber. Falls (1968), Foster (1959), and Jamison (1975) also observed these behavior patterns in deermice. Pursuits were terminated when the owl lost sight of the fleeing mouse or when the owl struck at the mouse with its talons resulting in an escape or a capture.

Short-eared Owl Hunting Efficiency and Predator/Prey Interactions in Moonlight

Various components of the owls' hunting behaviors, namely searching and chasing, were affected by changes in moonlight intensity and account for differences in capture times in the tests.

Of the three moonlight intensities, the owls required the least time to detect, pursue, and capture the mice in full moonlight. The deermouse responses of fleeing or freezing in the presence of a searching predator did not hinder the owls in locating the prey. Unless a mouse froze behind an object that screened it briefly from the owl's view, the owls usually located the mice in 1 to 10 seconds. The owls never lost sight of their prey when pursuing a fleeing mouse in full moonlight, thus search time remained low. The deermouse behaviors while being chased slightly hindered the hunting owls. Mice that froze were immediately captured while those that fled were captured after one to three unsuccessful strikes. However, because the number of escapes was few, the chase time also remained low. No matter what tactics the prey used to elude the owls, they were quickly captured as evident in the lack of variability and low values of the measured predator/prey parameters in full moonlight.

In quarter moonlight, the owls' hunting efficiency appeared to wane with the light intensity. The owls required more time to initially locate the mouse, usually 1 to 25 seconds. This is probably due to the combined effects of low light, the mice concentrating activity near cover, and the mouse's behavior in the presence of the searching owl. Mice that froze, frequently behind objects, escaped the owl's sight longer than those that fled. Quarter moonlight Predator/prey phases were usually composed of rapid, sequential chases interupted by escapes and/or occasional searching bouts. The mouse's responses to the owl's pursuits generally hindered the owl's capture attempts. Mice that froze when pursued were quickly captured, as in full moonlight. Mice that fled were captured after escaping one to four strike attempts. On two occasions the owl lost sight of the pursued prey that was fleeing in a zigzag manner. In these cases, the owl broke off the chase, landed on the floor, and again searched for the temporarily-escaped mouse. This sequence of owl behaviors has also been observed in barn owls (*Tyto alba*) in similar situations (Konishi 1973). Searching from the floor appeared less effective in locating the mouse because these searching bouts were prolonged, and greatly contributed to total search time in quarter moonlight. In three additional cases, the owl lost sight of the prey following an unsuccessful strike and landed on the floor to again search for the mouse, thus increasing the total search time. The increased variability and numerical values of total search, chase, and capture times in quarter moonlight are consequences of the combined differing anti-predator behaviors of the deermice and the owl's efficiency in responding to these behaviors while hunting in decreased light intensities.

In new moonlight, the owls required significantly more time to capture the deermice. Interestingly, the owls initially located the mice in 2 to 5 seconds. This is in part because of mice extending their activities into the exposed central areas of the chamber. Additionally, the mice initially do not freeze in the searching owls' presence. Movement appears important to the owls in recognizing prey in dim light as has also been suggested in other studies (Craighead and Craighead 1956, Marler and Hamilton 1966); thus the owls quickly locate the moving prey. Predator/prey phases in new moonlight were similar to those in quarter moonlight, consisting of rapid, sequential chases interupted by escapes and/or prolonged searching bouts. When pursuing prey, the owls immediately captured mice that froze in open areas of the chamber but the zigzag and straight line fleeing responses of the mice effectively impeded the owls' capture attempts. In 12 chases, the owls entirely lost sight of the zigzagging mice before making a strike. In four cases the owls lost sight of the mouse immediately after an unsuccessful strike. In these situations, the owl's ability to relocate the temporarily-escaped mouse was poor, thus these prolong and frequent searching bouts inflated the total search time. A major factor contributing to the prolonged searches, in addition to dim light, was deermouse behavior. Mice that fled to cover following an escape and froze eluded discovery by the owl as long as the mouse remained motionless. Mice that fled into open areas were located and chasing again ensued. Each chase in new moonlight consumes approximately the same amount of time as those in the other light intensities, yet the total chase time increased due to the increased number of chases in new moonlight which in turn resulted from the numerous escapes in the dim light.

And finally, more variability was noted in the predator/prey parameters in new moonlight than in quarter moonlight. This indicates a continuum of increasing variability with decreasing light intensity due to the increased effectiveness of the prey's evasive behaviors in hindering the owls' hunting efficiency.

The ratio of escapes per chase remained relatively constant from new to full moonlight tests. This ratio indicates that the mice evade approximately the same percentage of chases in all light regimes, and it may also indicate that the owl does not attempt to chase a mouse unless it "senses" its chances are 33% or better of success. In view of the prolonged searching following unsuccessful chases and the probable energy expenditure in chasing, it is probably adaptive for the owl to pursue prey only when the probability of a successful prehension reaches and exceeds a threshold.

Predator/Prey Interactions in Total Darkness

The total darkness tests dramatically illustrate the importance of light to the predator/prey interactions between deermice and the owls. The deermice did not significantly alter their activity in total darkness. The only modification in mouse behavior that I observed was that the mice appeared to move more slowly, with a slightly flattened posture while engaged in foraging and exploring activities. This suggests that deermice utilize senses other than vision when engaged in these activities if light is not available, such as olfaction, audition, gustation, and possibly touch-pressure reception. Whether deermice perceive infrared light has not been confirmed, but in preliminary trials testing mouse activity in total darkness with and without infrared light, I determined no difference in mouse activity.

At the onset of the predator/prey phase, the owls hesitated for 5 to 10 seconds in the holding box then stepped directly onto the floor beneath the box entrance. The mouse responded to the owl's presence by pausing momentarily, facing in the owl's direction, then resuming normal activities. After approximately 1 minute the owl would begin to slowly stalk about the chamber, pausing frequently, and appearing to search for prey. Throughout these stalks the mouse remained active, often passing within a few inches of the owl. On these occasions the owl appeared not to detect the mouse's proximity. Often the mouse paused, crept slowly toward the owl with forward directed pinnae and vibrissae. When the owl moved the mouse darted away. In one case the mouse touched the owl's toe with its nose causing the owl to jump sharply away from the touch. Following these investigations, the mice either avoided the immediate vicinity of the owl but resumed foraging, exploring, and grooming activities, or they combined fleeing and freezing behaviors along the periphery of the chamber for the duration of the test. I observed the owl to occasionally turn, orienting directly toward the mouse, and stalk in the prey's direction. The owl appeared to perceive stimuli indicating the mouse's position. However, after the mouse moved, the owl continued toward the prey's original location without altering its orientation. After a few steps the owl would pause, terminate the stalk, and resume searching behaviors. Thus, the birds were unsuccessful in locating the mouse in the totally dark chamber.

In two instances I observed the male owl raising his wings and rotating them so the lower wing surfaces faced forward and the tips of the distal primaries touched over his head. In this posture he stalked around the chamber possibly utilizing this wing position to reflect sound in the manner of a parabolic reflector.

Evidently the short-eared owls did not perceive the infrared light, as has been demonstrated for other owl species (Konishi 1973, Matthews and Matthews 1939). In conclusion, the owls were unable to successfully hunt, utilizing audition or any other sensory stimuli, in the absence of light.

Costs and Benefits

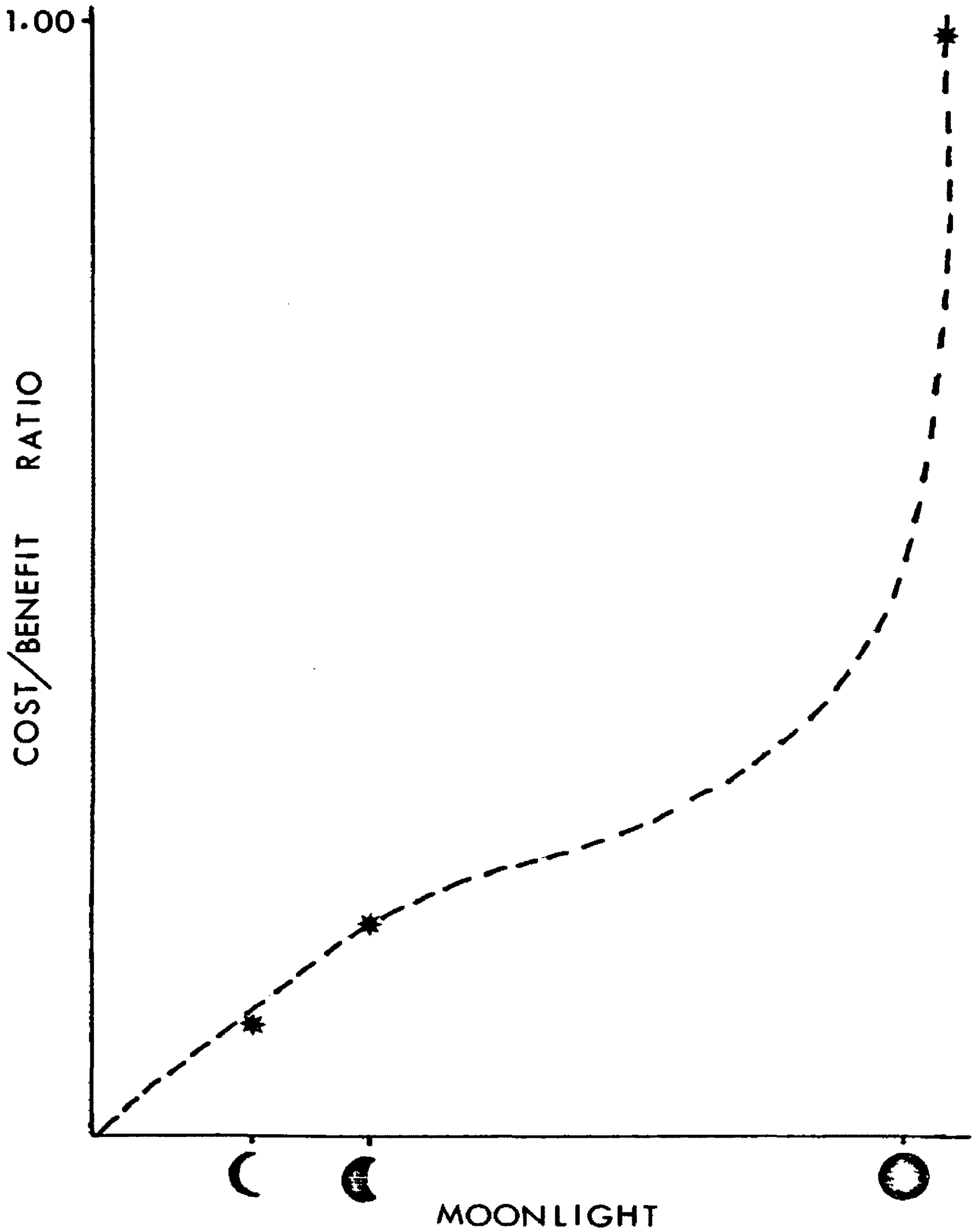
The etiology of activity suppression in bright moonlight of a prey species, such as the deermouse, can best be analyzed in terms of costs and benefits. Deermice benefit from increased activity in that the probability of finding food and mates increases. Deermice also incur costs as activity increases in that the probability of of being detected by predators and killed increases. Thus, I presume, due to the relative abundance and ubiquitousness of the deermouse, they have adapted an activity strategy in which the benefits of activity are not exceeded by the costs of activity.

In nature, deermice decrease activity in bright moonlight when the probability of predation is high. Although inactivity reduces the gain in benefits associated with activity, it concurrently reduces the high costs incurred by activity in bright moonlight; hence, benefits and costs balance. Yet, why are deermice active at all on brightly lit nights when costs to predation are so high? If deermice strictly confine activity to extremely dark nights they would often starve because of the relative scarcity of moonless or totally cloud-covered nights. Thus, sustained inactivity results in no gain in benefits and probable death.

Deermice increase activity (benefits) in dim moonlight when the probability of predation (costs) is low. Thus benefits are maximized when costs are minimal. Dim moonlight intensities are available for deermouse activity on moonless or cloudy nights and also in the dim light afforded by shadows cast on brightly lit nights (Falls 1968). Thus, deermice inhabiting dense forest and woodland areas have abundant darkness in which to be active relative to mice in alpine, desert, and grassland areas supporting less vegetation that could provide shadows. Yet, shadows are limited and extremely dark nights are few. What are the consequences if deermice are active regardless of moonlight and available shadows? My experimental design did not permit the deermice to utilize the strategy of decreasing activity with increasing moonlight as they do in nature. During the Predator/Prey phase the mice were not allowed to remain inactive, and sheltered in a burrow or nest as they would in the wild, nor were shadows available for cover. Thus, the mice were essentially forced to be active in bright moonlight. Consequently, due to the owls' increased hunting efficiency, the deermice were quickly detected and killed; in brief, costs greatly exceeded benefits (Fig. 11).

To conclude, as nocturnal illumination increases, deermice are vulnerable to the increasingly efficient hunting skills of the short-eared owls. These results and observations illustrate that the suppression of deermouse activity in bright moonlight is adaptive as an anti-predator strategy.

Figure 11. The Trend of the Deermouse Cost to Benefit Ratio. This figure depicts the increasing cost/benefit ratio of deermice active in three moonlight intensities. Costs equal predator efficiency (see Fig. 10B) and benefits equal prey activity (see Fig. 10A).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COST/BENEFIT RATIO
MOONLIGHT

Chapter VI

SUMMARY

1. To confirm previous observations of decreased deermous (*Peromyscus maniculatus*) activity in bright moonlight deermouse activity was measured in a laboratory chamber in three simulated moonlight intensities. The deermice suppressed their activity significantly ($p < 0.01$) in bright moonlight.
2. The hunting efficiency of a visually oriented predator, the short-eared owl (*Asio flammeus*), was measured in the three moonlight intensities in the chamber with deermice as prey. The owls required significantly less time to search for and capture the mice ($p < 0.05$ and $p < 0.01$ respectively) as moonlight intensity increased.
3. The activity of deermice and hunting efficiency of short-eared owls in capturing deermice was measured in total darkness. The mice showed no significant change in activity from that observed in dim moonlight ($p > 0.5$). The owls were unable to capture the mice in total darkness.
4. Moonlight was an important factor influencing the predator/prey interactions between deermice and short-eared owls. It was illustrated that the supression of deermouse activity in bright moonlight is adaptive as an anti-predator response.

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