Tradeoffs of Food and Safety in Contrasting Environments:
From the Deserts of the Mojave and the Negev to the Coral Reefs of Eilat

Thesis submitted in partial fulfillment
of the requirements for the degree of
“DOCTOR OF PHILOSOPHY”

by

Austin K. Dixon

Submitted to the Senate of
Ben-Gurion University of the Negev

March 10, 2017

Beer-Sheva

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Approved by:

Burt P. Kotler
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March 10, 2017

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Research-Student's Affidavit for Submitting the Doctoral Thesis for Judgment

I Austin K. Dixon, whose signature appears below, hereby declare that
(Please mark the appropriate statements):

_X_ I have written this Thesis by myself, except for the help and guidance offered by my Thesis Advisors.

_X_ The scientific materials included in this Thesis are products of my own research, culled from the period during which I was a research student.

_X_ This Thesis incorporates research materials produced in cooperation with others, excluding the technical help commonly received during experimental work. Therefore, I am attaching another affidavit stating the contributions made by myself and the other participants in this research, which has been approved by them and submitted with their approval.

Date: _10-Mar-2017_ Student's name: _Austin K. Dixon_ Signature:_______________

Statement of Authorship:

This Dissertation incorporates research materials produced in cooperation with others. The following statements describe the contributions made by myself and the other participants in this research, which has been approved by them and submitted with their approval.

<u>Theoretical</u>*: Patch use as an indicator of habitat preference, predation risk, and competition across space and time*

I developed the theory and its predicted outcomes. Jorge F. S. Menezes and Burt P. Kotler provided guidance and assistance with how to perform theoretical modelling, including advanced derivatives and discussions on how best to describe nature through mathematics.

<u>Damselfish</u>*: A mechanistic approach to understanding the spatial structure of site attached planktivores*

I was the principle investigator for the study and was in charge of the design, implementation, analysis and writing of the study. Dimitry Churilov and Alexandra Khruzman were instrumental in developing the methods and getting this experiment up and running. Besides assisting with the physical work of running the zooplankton sonar and other systems, they helped analyze much of the preliminary analysis of current magnitudes and zooplankton abundances. Amatzia Genin was gracious enough to host me and open his lab and resources up to me. Additionally, he and Burt P. Kotler provided training and guidance through the various parts of the study.

<u>Gerbil Community</u>*: The importance of body size and constraint breaking adaptations in structuring communities*

I finalized the experimental design adding the aspects of lunar illuminance and its timing. Additionally, I ran the experiment and conducted the analysis. Burt P. Kotler created the initial experimental design and provided guidance throughout the experiment and its analysis.

<u>Intercontinental Comparisons</u>*: Effects of constraint breaking adaptations on two artificial intercontinental desert rodent communities*

I finalized the experimental design adding the aspects of lunar illuminance and its timing. Additionally, I ran the experiment and conducted the analysis. Burt P. Kotler created the initial experimental design and provided guidance throughout the experiment and its analysis.

<u>Personality</u>*: Variations in risk management between gerbils (Gerbillus andersoni allenbyi) with different exploratory/ boldness behaviors*

I finalized the design and led the vivarium work. Afterwards, I also analyzed the data. Jorge F. S. Menezes and Cinnamon Morrison assisted and provided input throughout the design, operation, and analysis of this study. Burt P. Kotler also provided guidance in the design and analysis of this study.

Acknowledgements

First, I would like to thank my advisor, Burt P. Kotler for the opportunity and experience to come to Israel and learn from him and the rest of the staff at BGU. He was always there with unlimited patience to teach, guide, and discuss the many difficulties that research presents. I also thank my committee members (Merav Seifan, Yaron Ziv, and Amatzia Genin) for their guidance throughout my Ph.D. studies. This is especially true for Amatzia who provided the opportunity for me to study with him in Eilat for several months, resulting in the work on damselfish foraging. Funding for this research was supported by grants from the Israel Science Foundation to B. P. Kotler (#976/14), the US-Israel Binational Science Foundation to A. Genin (HUJ) and J. Jaffe (Scripps, UCSD), and by a Grant-In-Aid of Research from Sigma Xi, The Scientific Research Society (#490587) to A. K. Dixon

I also thank my lab mates and friends who provided input, discussion, education, and encouragement during the 4 years arduous studies. At BGU, Keren Embar, Omri Shai, Jorge Menezes, Inbal Tiano, Ikram Salah, Jie Wan, and Stuart Summerfield were always there and in many cases provided the extra hands and brainpower to keep things running smoothly. In Eilat, Irina Kolesnikov was like a big sister always looking out for me as well as being a great friend in and out of the university. Yoav Lindemann, Dima Churilov, Alexandra Khruzman, and Yeala Reuben also provided help during my time in Eilat.

Besides the many people I had the privilege of working with during the past 4 years, I have to thank my friends and family back in the USA that put up with my absence for that time. Particularly for my wife Cinnamon, who loved me through my two-year absence and then came to Israel putting her career aspirations on hold for two years. Finally, I thank my Lord and Savior (Jesus or יֵשׁוּעַ in Hebrew) who gives me all I have and makes all things new!

For from Him and through Him and to Him are all things.
To Him be the glory forever. Amen.
— Romans 11:36 (NASB)

For since the creation of the world His invisible attributes, His eternal power and divine nature, have been clearly seen, being understood through what has been made, so that they are without excuse. For even though they knew God, they did not honor Him as God or give thanks, but they became futile in their speculations, and their foolish heart was darkened. Professing to be wise, they became fools, and exchanged the glory of the incorruptible God for an image in the form of corruptible man and of birds and four-footed animals and crawling creatures.

— Romans 1:20-23 (NASB)

For the scientist who has lived by his faith in the power of reason, the story ends like a bad dream. He has scaled the mountains of ignorance, he is about to conquer the highest peak; as he pulls himself over the final rock, he is greeted by a band of theologians who have been sitting there for centuries.

— Robert Jastrow in God and the Astronomers

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List of Abbreviations and Terms

ADCP	Acoustic Doppler Current Profiler
ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
Cp	*Chaetodipus penicillatus* (Desert Pocket Mouse)
Dm	*Dipodomys merriami* (Merriam's Kangaroo Rat)
Ga	*Gerbillus andersoni allenbyi* (Allenby's Gerbil)
GLM	Generalized Linear Model
GLS	Generalized Least Squares Model
Gp	*Gerbillus pyramidum* (Greater Egyptian Gerbil)
GUD	Giving-up Density
IR	Infrared
IUI	Interuniversity Institute of Marine Sciences in Eilat, Israel
SHV	Saharan Horned Viper
SWRS	Sidewinder Rattlesnake
ZOOPS	Zooplankton Sonar

Abstract

Coexistence can occur when a tradeoff exists between two species along an axis of heterogeneity. In many cases, the tradeoff incorporates a forager that is more efficient in the absence of risk and one that is more efficient in the presence of risk, thus hinging on tradeoffs of food and safety. Studying coexistence and tradeoffs of food and safety have helped in understanding the mechanisms operating within communities and addressing many of the questions relating to their structure. In this dissertation, I examine tradeoffs of food and safety in contrasting environments; this includes damselfish on Red Sea coral reefs and granivorous rodents from the Mojave and Negev Deserts. Examining these environments, I use tradeoffs of food and safety and foraging ecology to further the understanding of particular questions related to spatial structuring, community structure, and personalities. But I also discuss possible commonalities between such contrasting environments which may help ecologists to work towards more generalized theories of ecology.

The first part of this dissertation is a theoretical extension of Brown's (1988) optimal patch use model, which predicts that individuals should forage in a patch until their harvest rates become equal to their energetic, predation, and missed opportunity foraging costs. Its use, combined with the technique of giving-up densities, has been used extensively in many ecological disciplines, including foraging, behavioral, conservation, and community ecology. Despite this, the model ignores the spatial environment and direct interactions of foragers, which limits the understanding of animal distributions and patch use across time. We extend the original model to include a forager's spatial environment and interactions while maintaining the potential for spatial changes across time. Using this new model and planktivorous damselfishes as an example, we make predictions regarding mechanisms producing site attachment (e.g. *Dascyllus* sp., *Chromis* sp.) and pelagic (e.g. *Caesio* sp.) lifestyles observed in planktivorous fishes. The model suggests that site attachment occurs when energetic and/or predation costs are high and push foragers closer to refuge. When these costs are low, foragers should instead move higher into the water column and spread out horizontally. We also use the new model to predict group distributions, showing that when energetic gains from forager interactions are greater than their energetic costs and/or the cost of isolation increases, then fish form schools. When the opposite is true, individuals should be solitary. Further discussion of these results and the model's relevance for other systems (e.g. fission-fusion social dynamics) provide a simple, but more complete picture of patch use across a range of disciplines and environments.

In the second part of the dissertation, the theoretical framework is used to begin building a mechanistic understanding of spatial structure on coral reefs. Space is a limiting resource on coral reefs that has resulted in many hypotheses for explaining the observed spatial structure. Despite these many hypotheses over decades of research, a mechanistic understanding explaining why these spatial structures develop is lacking. One of the most abundant spatial structures on coral reefs is the site-attachment of planktivorous fishes. Here we utilize acoustic and optical technology in a new method to study the foraging

behavior of a site-attached damselfish (*Dascyllus marginatus*) and its use of space. Acoustics measure of prey density, current magnitude, and overall prey flux, while optics in a stereo array provide the X, Y, and Z coordinates of each fish in a group. Combined with a theoretical spatial patch use equation, the positions of fish are compared with patch richness along different spatial dimensions to determine how foraging costs are mitigated. Results show that *D. marginatus* used its vertical dimension to control energy and predation costs and the horizontal plane to handle competition costs. These results suggest site-attachment occurs because 1) the optimal behavior is to move vertically above a refuge, thereby controlling energy and safety, and 2) prey must be replenished at a high enough rate to prevent starvation at the site of attachment. We also describe thresholds of foraging behavior and discuss the implications of the results on understanding group hierarchies. This study contributes to a mechanistic understanding of the spatial structure and use observed on coral reefs.

In the third part, the focus shifts from the oceans to terrestrial environments and tradeoffs of food and safety in granivorous desert rodent communities. Ecological studies of the 1960's and 1970's on up to the present often ended in the conclusion that each community is unique and there are no known general governing laws or mechanisms that function to produce their unique structure (Lawton 1999). Since then, progress has been made in areas of mechanisms of coexistence, tradeoffs of food and safety, and foraging games, which may allow us to better assess what makes otherwise similar communities in similar environments so different. Using a common garden vivarium experiment, we simulate a natural desert rodent community of two gerbils (*Gerbillus andersoni allenbyi* and *Gerbillus pyramidum*) in the presence of barn owls, Saharan horned vipers, and novel sidewinder rattlesnakes. This study builds on previous single-species experiments to show the effects of interspecific competition and body size on community attributes. Additionally, the effects of snake predators that possess sensory pits on the foraging costs of rodents are compared using the two species of vipers. Results are consistent with characteristics indicative of natural communities including centrifugal organization. Evidence supporting the aiding of coexistence was seen in tradeoffs in the timing of lunar illuminance during the lunar cycle, which may allow rodents to rebuild energy state during preferred portions. Additionally, body size contributed to winning interference competition, but also was beneficial in handling multiple levels of risk simultaneously, which likely was influence by larger auditory bullae. Finally, rodents modified their foraging behavior in the presence of pit vipers to avoid the waning crescent portion of the lunar cycle while avoiding true vipers during the waxing gibbous moon. These results set the foundation for future experiments to examine the formation of desert rodent communities and the effects that constraint-breaking adaptations have on them.

The fourth part builds from the third to make intercontinental comparisons in artificial communities. Over the past decades, ecologists have progressed in their understanding of species coexistence and community structure. However, I still do not fully understand what makes the mechanisms in one community different from mechanisms in a seemingly similar community. Here I build on previous studies to make intercontinental comparisons within artificial experimental communities to examine the effects of potential constraint breaking adaptations (external cheek pouches, bipedal locomotion, and sensory pits). Similarly sized desert rodents (*Chaetodipus penicillatus* with *Gerbillus andersoni allenbyi* and *Dipodomys merriami* with *G. pyramidum*) from North American and Middle Eastern deserts, respectively, foraged food trays under varying conditions including owl presence, microhabitat, viper species, and lunar cycle. The giving-up densities revealed little support for external cheek pouches and bipedal locomotion as constraint breaking adaptations. Instead, the similar body sizes produced characteristics indicative of competitive exclusion, giving support to the limiting similarity hypothesis. Nevertheless, constraint-breaking adaptations may still be important as the sensory pits in pit-vipers altered the foraging activities of all rodents except *D. merriami*. I suggest that constraint-breaking adaptations do play a lesser role in the mechanisms of coexistence compared to the competition for resources.

In the fifth part, the focus shifts to the population level to examine how differences in tradeoffs of food and safety may contribute to the creation and maintenance of individual behavioral differences. Reaction norms of behaviors, or personalities, are becoming better understood, but understanding their generation and maintenance through evolutionary processes is only starting to be examined. Several studies suggest that predation and resources are important components of this process. Here, we examine whether animal personality is related to how desert gerbils manage risk of predation and the tradeoff of food and safety. To do so, we sorted individuals of Allenby's gerbil (*Gerbillus andersoni allenbyi*) into four groups of different exploratory behaviors (strong bold being the most exploratory and strong shy the least) and exposed them in a vivarium environment to direct and indirect predation risk cues, including owl presence, bush and open microhabitats, and the lunar cycle . Foraging costs and patch use activities for each group were determined from giving-up densities (GUD) and husks left nightly in artificial resource patches (seed trays) Additionally, video recordings of patch exploitation, track data, and rodent mass allowed harvest rate curves, patch use, and state to be calculated and examined. Bolder individuals had lower GUDs, husked seeds less frequently in the patch, and used more time allocation, suggesting a grab and go strategy, while shyer individuals primarily utilized vigilance for managing the risk of predation. Such distinctions in risk management behavior between individuals that differ in their use of exploratory behaviors suggests that diverse personalities in a population may be generated and maintained through frequency dependence and/or traditional tradeoffs along axes of heterogeneity.

Together, these five components each make steps forward in addressing ecological questions involving tradeoffs of food and safety and foraging theory. Tradeoffs of food and safety were able to explain the site attachment of planktivorous damselfishes, allow intercontinental comparisons of artificial rodent communities, and suggest mechanisms for the maintenance of varying behaviors or personalities within rodent populations. While a generalized theory of ecological processes is still far from being concluded, the results presented here show the behavior of organisms that may maximize fitness can help explain many of the contrasting structures, communities, and personalities observed in nature.

Keywords: boldness, competition, constraint breaking adaptations, coral reef spatial structure, *Dascyllus marginatus*, desert rodents, exploratory behavior, foraging costs, foraging theory, *Gerbillus*, *Gerbillus andersoni allenbyi*, giving-up density, Gulf of Eilat/Aqaba, harvest rate curve, Heteromyids, husking, intercontinental community comparisons, marginate dascyllus, personality, pit-viper, predation risk, risk management, site attached planktivorous damselfish, spatial patch use, temporal patch use, time allocation, trade-offs of food and safety, vigilance

1.0.0. INTRODUCTION

1.0.1. General Introduction

Examinations of different communities over the past decades have sought to reveal the grand theme of community convergence. However, despite arduous efforts, researchers concluded that each community seemed to be a special case; different from all the rest (e.g. Barbour and Diaz 1973, Kelt et al. 1996, Brown et al. 2000). While the search to develop generalized, comprehensive, and predictive theories in ecology struggles on, it may be useful to step back and take a lesson from mathematicians studying chaos theory. Chaos theory shows complex and dynamic systems, similar to ecological communities, can produce seemingly independent and random outcomes. However, upon closer review, this appearance of independence and randomness are the result of the systems initial condition and the nonrandom mechanisms operating within. By approaching community ecology as a chaotic system, it may be possible to study the initial conditions (e.g. evolutionary adaptations, populations present, and resources available) present in communities as well as the mechanisms acting upon the various levels of ecological organization to better develop general principles of ecology.

One way to study mechanisms operating within populations and communities is using foraging ecology. Foraging ecology assumes an individual’s ability to gather and consume resources is directly related to its fitness (e.g. Hutchings 1991, Lemon 1991). For example, greater resource availability can increase an individual’s fitness by increased survival of offspring (Hutchings 1991). This relationship between foraging and fitness can then be used to model and understand coexistence between populations under a variety of conditions including, predation risk, resource abundance, and environmental conditions.

Early advances in understanding coexistence through the use of foraging theory focused phenomenologically on carrying capacities and intra- and inter-specific competition coefficients as seen in the Lotka-Volterra model (Volterra 1926, Lotka 1932). In this model, the population growth rate of species A over a given time ($\partial N_A/\partial t$) is determined by its own population dynamics in the absence of species B ($r_A N_A[1 - N_A/K_A]$), and through its interaction with species B ($\alpha_{A,B} N_B/K_B$): where r is the rate of increase, N is the population size, K is the carrying capacity, and α is the interaction coefficient. The same, but opposite, is true with calculating the population size of species two. Setting $\partial N/\partial t$ equal to 0 yields zero-growth isoclines for each species, which produce four different possible equilibrium conditions for such a community: 1,2) competitive exclusion of species A or B when the isocline for one species lies above the others for all combinations of species densities, 3) unstable coexistence and priority effects when isoclines intersect, but intraspecific competition is stronger than intraspecific competition, and 4) stable coexistence when isoclines again cross and intraspecific competition is greater than interspecific competition. This model took the first step to understand mechanisms of coexistence by concluding that coexistence within a stable community must have greater intraspecific competition than interspecific competition for each population within it.

The next major step in understanding stable species coexistence was taken by MacArthur and Levins (1967) who examined limiting similarity in the frequency of traits or resources. Limiting similarity was founded on the conceptual framework that 1) there is a lower limit to species abundance that sets an upper limit to the number of species possible, 2) an upper limit to species abundance can be set by dangers (ie. predation or disease) which increases the number of species possible, and 3) environmental instability limits the degree of specialization, allowing for competition to limit similarities of coexisting species (MacArthur and Levins 1964, 1967, Schoener 1965, Paine 1966). In essence, limiting similarity states there is some maximum level of similarity (dependent upon the strength of predation, competition, etc.) between competing species short of complete overlap that allow for coexistence (Abrams 1983).

Tilman (1986) then used consumer-resource modelling and zero net growth isoclines plus consumption vectors in a state space of resource densities to indicate how coexistence occurs when more than one resource is partitioned between species. Zero net growth isoclines (ZNGI) can come in a variety of curves. For example, if resource A is substitutable with resource B, the ZNGI will be a straight line, whereas if the resources are essential then the ZNGI will be a right angle that does not intersect the axes (Tilman 1986). ZNGIs that intersect the resource axes and are curved represent complementary resources. The intersecting of two or more ZNGIs represents an equilibrium point of the intersecting species. From the points of equilibriums, resource ratios of R_2:R_1 can be used to plot resource supply lines. If a resource supply point falls into a region between the resource ratio lines, then the resource availabilities will be reduced down to its point of equilibrium. Scenarios using ZNGIs can also be shown where species do not exist or coexist. Mathematically, each species must have the lowest R* on a different resource for coexistence or else the species with the lowest standing crop (R*) wins in competition.

Building from these studies and others including Armstrong and McGehee (1976), Chesson (1985), and Brown (1989b), ecologists concluded that if species A can invade species B at its carrying capacity and species B can invade species A at its carrying capacity, then coexistence must exist because of two conditions: 1) environmental heterogeneity (ie. niche axis) and 2) a tradeoff where each species has a part of the axis that it dominates during competition. These two conditions allow for many different mechanisms of coexistence to be found in nature, depending upon the axis of heterogeneity and the tradeoff.

Such tradeoffs often incorporate an element of energy gain and the risk taken to obtain it (i.e. tradeoff of food and safety). To optimize a tradeoff of food and safety, a forager should continue to exploit a resource patch until its harvest rate falls equal to its foraging costs (MacArthur and Pianka 1966, Charnov 1976, Brown 1988). Foraging costs can include energetic, predation, or missed opportunity costs (Brown 1988). The point at which foraging ceases is an estimate of the quitting harvest rate and can be measured as the giving-up density (Brown 1988, Kotler and Brown 1990). Giving-up densities (GUDs) may be used to gauge a forager’s perception towards varying conditions in an experimental setup, including differences in environmental conditions, resource availability, predators, and competitors (Brown 1988).

The foraging models described above suggest that foragers with more similar functional traits and operating within similar functional groups under similar environments should result in more similarly structured communities (e.g., Chesson 1985, Tilman 1986). However, foraging experiments on communities from different continents with similar environmental characteristics and functional groups often display very different mechanisms of coexistence (Brown and Lieberman 1973, Kotler 1984a, Ziv et al. 1993). This difference may be the result of slight variances in the initial conditions (e.g. evolutionary adaptations) of the community. For example, sidewinder rattlesnakes and Saharan horned vipers are convergent and occupy similar functional groups. However, the sidewinder is a pit-viper which possess sensory pits that allow it to “see” in the dark. The possession of certain adaptations at the formation of communities, such as sensory pits, may be enough to alter the mechanisms of coexistence within seemingly convergent communities.

I describe such adaptations as constraint breaking adaptations. I define a constraint breaking adaptation as a physiological, morphological, or behavioral trait that produces a shift in its fitness function on a fitness landscape by producing a relaxation or elimination of tradeoffs. Constraint breaking adaptations differ from other adaptations in two ways: 1) they must have positive invasion potential in the species’ fitness landscape (i.e. invading species possesses a strategy value that would have been an evolutionary stable strategy within its donor community), and 2) the adaptation must occur within the invasion window (i.e. region of the invader’s adaptive landscape that lies above 0) of the species’ fitness landscape (Pintor et al. 2011).Without these two attributes, a species with a given adaptation may persist and even increase in fitness, but its presence will not break the constraints of the existing landscape. Thus, a constraint breaking adaptation affects a species’ fitness landscape and may aid it in invading or restructuring communities (Pintor et al. 2011).

To begin to address the causation behind the mechanistic differences of communities in similar environments and possessing similar functional groups, I compare and contrast tradeoffs of food and safety in contrasting communities including desert rodent communities of Middle Eastern and North American Deserts, and planktivorous fishes on coral reefs. In each of these, specific questions, unique to each system, are linked through their mechanistic origin of tradeoffs of food and safety and seek to advance our understanding of questions specific to larger scale ecological systems. By comparing these tradeoffs and the effects they can have within contrasting populations and communities, I hope to begin to identify commonalities within these ecological systems that may lead to more generalized, comprehensive, and predictive theories in ecology.

The following dissertation is a collection of works clumped into four distinct sections. These four major sections are arranged so that the introductions of each major section are combined into one introduction with subsections for each major section’s introduction. The same is true for the Methods, Results, and Discussion, allowing readers to more easily navigate within a single experiment or through the dissertation as a whole.

<u>1.1.0. Desert Rodent Communities Introduction</u>: Effects of constraint breaking adaptations on three experimental desert rodent communities

Research in desert rodent communities is unique for two main reasons. First, deserts are especially transparent (M.L. Rosenzweig, as cited by Kotler and Brown 1988). In all deserts, the limiting factor is water. This limits vegetation, seed production, and, ultimately, what organisms can survive there. Secondly, desert rodent communities across the world are well studied which provides abundant knowledge towards the differences and similarities of these environments and their communities across the world. Together these two factors provide a “simpler” community with abundant information for ecologists to examine for evidence of community convergence. However, studies comparing rodent communities of the Negev Desert (Middle East) and the Mojave Desert (North America) showed no evidence of convergence (Barbour and Diaz 1973, Kelt et al. 1996, Brown et al. 2000).

Desert rodent communities of the sand dune dwelling gerbils of the Negev Desert in the Middle East that coexist through interference and temporal variations in resource abundance (Kotler et al. 1993d, Ziv et al. 1993). The mechanism of species coexistence is based on a tradeoff between the gerbil species in foraging efficiency (ratio of energy gained to the total energy expended) at different resource availabilities. Larger rodents arrive to patches earlier when food is more abundant, handle and harvest food more quickly, and interfere with smaller rodents trying to forage (Ziv et al. 1993, Brown et al. 1994, Ziv and Kotler 2003). However, being large has its drawbacks; smaller rodents have lower total energetic costs, which allow them to harvest food profitably and with greater efficiency even at lower resource densities (Rosenzweig and Sterner 1970, Linder 1988, Ziv et al. 1993). This community utilizes a mechanism of coexistence that is driven by the pulse and depletion of resources, which differs from similar communities like those studied in the Mojave Desert of North America.

Despite possessing similar environmental and functional groups as the Negev Desert rodent communities, North American desert rodent communities differ in their mechanisms of coexistence. Heteromyids in the Mojave, Great Basin, and Sonoran Deserts often coexist through bush/open microhabitat partitioning (Brown and Lieberman 1973, Kotler 1984a, Brown 1989b). Here, the tradeoff is in competitive ability and foraging efficiency where risk is low (bush) versus lower foraging costs of predation relative to their competitors in areas more exposed to predators (open). Similarly, temporal variations in predation costs of foraging can be brought about by seasonal activity, migratory, and reproductive patterns of predators, leading to seasonal rotation of foraging efficiencies of different rodent species that differ in which predator they find riskiest, as documented in the Sonoran Desert community that includes kangaroo rats, pocket mice, and ground squirrels (Brown 1989b). Larger species like the desert kangaroo rat, *Dipodomys deserti,* forages in the most open microhabitats while smaller species with lesser anti-predator adaptations such as *Perognathus longimembris* forage in the bush microhabitats (Kotler 1984a). Tradeoffs hinging on anti-predator adaptations, such as bipedal locomotion, are seen between species including kangaroo rats (*Dipodomys* spp.) or kangaroo mice (*Microdipodops* spp.) that possess bipedal locomotion and species including deer mice (*Peromyscus* spp.) or pocket mice (*Chaetodipus* spp.) that do not. These mechanisms and tradeoffs characterize rodent communities in which partitioning is driven by predation.

Gerbilline rodent species in the Negev also differ in body but do not possess fur lined external cheek pouches (Morton et al. 1980) or bipedal locomotion (Thompson 1982, 1985, Longland and Price 1991) that some Heteromyids do. The absence of such anti-predator adaptations could allow Heteromyids to be superior to gerbils. For instance, external cheek pouches may allow Heteromyids to carry larger food loads while still being able to husk, process, and consume seeds. This ability could reduce the number of trips to burrows and caches as well as the attention needed to process seeds, which would ultimately reduce the risk of predation. Additionally, external cheek pouches also prevent salivary water loss to seeds, which is also advantageous in dry desert environments (Long 1976). Heteromyids such as kangaroo rats (*Dipodomys* spp.) and kangaroo mice (*Microdipodops* spp.) may further increase their ability to mitigate predation risk due to their bipedal locomotion and saltatorial leaping. Bipedal locomotion and saltatory leaping is advantagous when escaping avian predators or snakes by better allowing rodents with these adaptiations to hop out of the way of the attack (Webster 1962). Could it be that such specializations by Heteromyids in anti-predator adaptations compared to gerbils may be constraint-breaking adaptations and alter the way a community operates?

Desert rodents are not the only players in the community capable of possessing potential constraint-breaking adaptations. Rodent predators can also possess constraint-breaking adaptations, which alter their effectiveness in hunting prey. Increased effectiveness by the predator can lead to increased foraging costs and/or behavioral changes in the forager (Lima and Dill 1990, Brown et al. 1999, Brown and Kotler 2004). Such changes can include harvesting less (Kotler 1984b, Embar et al. 2011), visiting only safer patches or habitats (Kotler 1984c, Kotler et al. 1992), and reducing time spent in patches (Embar et al. 2011). In the Negev, true vipers (*Cerastes* sp.) hunt rodents via visual cues and ground-borne vibrations (Young and Morain 2002), making them more reliant on brighter lunar periods to detect prey. However, pit vipers in the Mojave Desert (*Crotalus* sp.) possess sensory pits allowing them to “see” in the infrared. This adaptation of pit vipers, may give them an advantage on dark nights over true vipers. From the rodent’s perspective, these adaptations may make pit vipers seem more fearsome than true vipers and alter behaviors to produce a different community structure.

One possible cause for the different community structures observed between these two deserts may be because of the different adaptations present in each community’s lineage. For instance, the presence of certain adaptations in one lineage may have produced one result, while the absence of these adaptations in a second lineage produced another. The presence or absence of adaptations could be particularly important if they are constraint breaking. By forming artificial communities in experimental settings, foragers can be placed in varying levels of risk and with predators and competitors possessing different combinations of potentially constraint-breaking adaptations. Responses by the foragers, predators, and competitors may then be examined to determine what mechanism of coexistence their interactions and responses are indicative of.

Recent studies attempting this have shown through "interview chambers" and "common garden" experiments that desert rodents can differentiate between and respond to viper predators and their differing adaptations (Bleicher et al. 2016, Kotler et al. 2016). In particular, the presence of pit-vipers from North American deserts produced higher foraging costs in gerbils during darker crescent portions of the lunar cycle while native true vipers produced higher foraging costs in gerbils during the brighter gibbous portions (Kotler et al. 2016). Because other predators (i.e. foxes, owls, cats, etc.) also give rise to higher foraging costs during brighter portions of the lunar cycle (Kotler 1984b, Kotler et al. 1992), the presence of only true vipers may produce a temporal refuge during darker portions of the lunar cycle and allows rodents to take advantage of lower foraging costs during the crescent moon. When pit-vipers are present, foraging costs remain high or even increase during the crescent moon, thus eliminating the temporal refuge and increasing the importance of microhabitats or predatory defenses. These previous studies focused on a single foraging population with under the risk of predators with differing potential constraint-breaking adaptations. However, they need to be expanded better represent communities by include interspecific competition between foraging populations.

To begin taking this step, I conduct three 'common garden' experiments to examine the effects the effects of potentially constraint-breaking adaptations on three experimental communities containing two foraging populations, two viper predators (one novel and one familiar), and an avian predator familiar to both foraging populations. These experiments are 1) *Gerbillus andersoni allenbyi* and *G. pyramidum*, 2) *Chaetodipus penicillatus* and *G. a. allenbyi*, and 3) *Dipodomys merriami* and *G. pyramidum*. The interactions between foragers, competitors, and predators will be examined to determine if the presence of certain adaptations within the artificial community alter the characteristics indicative of a natural Negev Desert rodent community; such adaptations would be constraint breaking and change the mechanism of coexistence operating in the community. Below are specific hypotheses for each of the three experiments.

The purpose of the *Gerbillus andersoni allenbyi* and *Gerbillus pyramidum* experiment is 1) to test if the two-species experiment based on a natural rodent community produces results consistent with the mechanisms of coexistence found in nature, and 2) to examine how competition between foragers changes the spatial and temporal foraging behavior in the presence of natural and novel predatory snake combinations. To do this, I create an experimental rodent community based upon a larger gerbilline species (*G. pyramidum*) and a smaller species (*G. andersoni allenbyi*) that naturally coexist in the Negev Desert. I hypothesize results to be consistent with coexistence based on the natural pulse and depletion occurring in nature. Here, *G. andersoni allenbyi* should be the more efficient forager (lower giving-up densities) showing consistency with natural mechanisms of coexistence. I expect *G. andersoni allenbyi* to also be more responsive to predators than *G. pyramidum*, fearing owls more than viper predators. Finally, I hypothesize *G. pyramidum* to visit a greater percentage of patches than *G. andersoni allenbyi* because of their larger size and greater mobility. Overall, I hypothesize the behaviors of experimental rodent communities in the vivarium to be consistent with those found naturally with the exception of where novel viper predators are located. Here, the sidewinder rattlesnake is expected to be feared more, especially by *G. andersoni allenbyi*.

The *Chaetodipus penicillatus* and *Gerbillus andersoni allenbyi* experiment builds from the previous experiment, by replacing *G. pyramidum* with *C. penicillatus*. In doing this, I control for body size by using two similarly sized small species, but can examine species that differ in evolutionary history and potential constraint breaking adaptations (external cheek pouches). This allows me to compare the results here with that of the *G. a. allenbyi* and *G. pyramidum* experiment to infer the affects external cheek pouches might have on a species' fitness and the community structure. Here I hypothesize findings to be consistent with coexistence through microhabitat (bush/open) selection. I hypothesize *C. penicillatus* to have a higher foraging efficiency (lower GUD) in the bush microhabitats while *G. andersoni allenbyi* is a more efficient forager in the open microhabitats. This is because heterogeneity in the abilities to deal with predators is great in the Heteromyids, but small in the gerbils, with *C. penicillatus* being especially poor and both gerbils being somewhat better. Both species are expected to visit similar numbers of patches and not to interfere with the other due to their similar size.

Similar to the premise in the *C. penicillatus* and *G. a. allenbyi* experiment; here I place *G. pyramidum* with *D. merriami* to control for body size by using two similarly sized large species with different evolutionary histories and potentially constraint breaking adaptations (bipedal locomotion and external cheek pouches). Again, these results can be compared with both previous experiments to allow inferences about bipedal locomotion and external cheek pouches. I hypothesize the results to be consistent with competitive exclusion of *G. pyramidum* by *D. merriami* due to the kangaroo rat's more efficient foraging (lower GUD) and ability to better cope with predators, thus maintaining a better foraging efficiency under all experimental conditions. Additionally, *D. merriami* has been shown to be involved in interference (Frye 1983, Kotler 1984a) and is expected to visit more patches and harvest more seed than *G. pyramidum*.

1.2.0. Personality Introduction: Variations in risk management between gerbils (*Gerbillus andersoni allenbyi*) with different exploratory/ boldness behaviors

The past several decades have seen substantial gains in our understanding of mechanisms for species coexistence, however, less is known regarding the coexistence of behavioral types (e.g. personalities, exploratory behavior, and aggressiveness) within populations. Animal personality traits, including exploratory behavior/ boldness, are behavioral tendencies that affect behavior in several different contexts, vary across individuals in a given population, and are consistent within individuals across time (Biro and Stamps 2008). While once considered infinitely plastic, behaviors are now viewed as being plastic only within certain limits, thus limiting an individual's ability to respond appropriately to specific situations (Sih et al. 2004). A challenge to behavioral ecologists is to better understand the generation and maintenance of animal personality traits including the relation to risk management and ultimately fitness within populations and communities.

Some theories for the existence of personalities come from knowledge of tradeoffs in food and safety. Bolder individuals are considered as taking more risk for more yield, while shyer individuals stay safer, but are rewarded less (Sih 1992, Werner and Anholt 1993, Lima 1998, Stamps 2007, Wolf et al. 2007). This favors shy individuals when risk is high and bold individuals when low (e.g. Riechert & Hedrick 1993, Sih et al. 2003, Brodin & Johansson 2004). Field studies have also shown support for the different advantages of boldness and shyness leading to increased fitness (Réale and Festa-Bianchet 2003, Dingemanse et al. 2004, Boon et al. 2007, Smith and Blumstein 2008). Despite these, studies have not examined potential differences in risk management and mitigation between the two personality extremes and their effects on foraging, which relates to fitness in many ways.

Risk management is commonly performed using time allocation, vigilance/apprehension, or a combination of the two (Lima 1987a, Kotler et al. 2002, 2004a, 2010). Time allocation mitigates risk by controlling the exposure to risks at a patch (Dierschke et al. 2003, Kotler et al. 2004b). Greater risks reduce or eliminate the time spent at the patch, thereby reducing the probability of encountering predators and the prey harvested (Kotler et al. 1992, 2010, Embar et al. 2014c). When present in a patch, foragers can use vigilance—which is the complete focus of attention on detecting risks—and apprehension—which splits this focus with other activities, including foraging (Brown 1999, Hochman and Kotler 2007). Here, greater risk increases apprehension/vigilance, thereby increasing the chances of detecting threats, but decreasing the ability to detect, handle, and harvest prey (Dall et al. 2001). Particular personalities may manifest through different strategies in managing risk, where bold individuals rush in and out using time allocation and shy individuals remain slow and vigilant while detecting threats.

Allenby's gerbil (*Gerbillus andersoni allenbyi*) of the Negev Desert provides an ideal species to examine the risk management strategies of differing animal personalities. Rodent personalities have long been measured and used (Dochtermann and Jenkins 2007). At the same time, much research has been conducted studying how gerbils mitigate different types and combinations of risk, including direct and indirect risk cues. Direct cues can include the presence of predators such as owls (Kotler et al. 2004b, St. Juliana et al. 2011), snakes (Kotler et al. 1993a, 2004b, 2016), and foxes (Kotler et al. 2004b). Gerbils also respond to indirect cues of risk including illuminance (Kotler 1984b, Kotler et al. 2010), the timing of illuminance (as demonstrated later in the rodent community section), and microhabitat (Brown et al. 1994) along with other more subtitle differences including patch substrate (Brown et al. 1992, Kotler et al. 2001), temperature (Kotler et al. 1993b), relative humidity (Kotler et al. 1993b), and the presence of parasites (Raveh et al. 2011). This knowledge makes gerbils excellent candidates for studying risk management in different personalities.

The objective of this study is to test for differences in risk management of individuals of *G. a. allenbyi* that differ in their personalities by comparing and contrasting foraging costs, time allocation, and vigilance / apprehension in response to different risk factors. We expect bolder individuals to take more risk, but harvest more seeds, while shyer individuals should forage in safer patches with less yield. Thus, we hypothesize strongly bold individuals to have lower giving-up densities, exploit more patches, and loose less mass during the experiment. Shyer individuals are expected to husk a higher proportion of seeds at the patch to reduce the attraction of risk by competitors and predators. By comparing the steepness of harvest rate curves and the position of the giving-up density on them, the use of time allocation and apprehension/vigilance can be compared between treatment groups. In this study, I hypothesize rodents of differing exploratory behaviors to show differences in their use of time allocation and apprehension/vigilant. Bold individuals should rush in using time allocation while shyer individuals use more apprehension/vigilance. I also expect each of these measures to show a sequential change across the spectrum of exploratory behavior to further support the analysis.

1.3.0. Theoretical Introduction: Patch use as an indicator of habitat preference, predation risk, and competition across space and time

1.3.1. Background

Coral reefs are about as contrasting an environment from desert rodent communities as one might get. But, is it possible that there is more in common than just the obvious differences in water abundance? One stark observation of coral reefs is their spatial structure. Each species seems to have its own position on the reef and in the water column where it can be found relative to other species or hierarchical dominance (Fricke 1977, Sale 1977, Schmitt and Holbrook 2002, Mellin and Ponton 2009). Various hypotheses have been formulated to explain this phenomenon, including the lottery hypothesis (Sale 1977, 1978, Chesson and Warner 1981), recruitment limitation hypothesis (Doherty 1981), and the storage effect (Warner and Chesson 1985). More recent studies still view space as a limiting resource for coral reef communities, but focus on species distributions (Brokovich et al. 2006) or recruitment (Levin 1993). Despite these attempts to explain coral reef spatial structuring, most hypotheses developed have been rejected, leaving the question of what mechanism(s) operate to produces coral reef spatial structuring.

One approach to understanding similar questions in terrestrial systems comes from the area of foraging ecology and mechanisms of coexistence. Optimal foraging theory's use in studying communities began in the 1960's (Emlen 1966, MacArthur and Pianka 1966) and has since yielded additional theories including the marginal value theorem (Charnov 1976), optimal diets (Pulliam 1974), optimal habitat selection (Fretwell and Lucas, Jr. 1969, Rosenzweig 1981, Rosenheim 2004), and even mechanisms of species coexistence for optimal foragers (e.g. Armstrong and McGehee 1976; Brown 1989; Richards et al. 2000), including consumer-resource models comprised of consumption vectors (Richards et al. 2000), resource supply points, and zero net growth isoclines (Tilman 1986). One of the most influential developments to foraging theory was the temporal patch use equation (Brown 1988), which combined theory with a simple and widely applicable measure known as the giving-up density (GUD). Since then, the GUD and temporal patch use equation have been used together in many variants and environments including giving-up bite diameters with nyala (Tadesse and Kotler 2013), rodents (Brown et al. 1997, Shaner et al. 2007, Embar et al. 2014b), birds (Brown et al. 1997, Nolet et al. 2006), and ibex (Tadesse and Kotler 2012). Aquatic ecologists also beginning to utilize foraging theories and methods (e.g. giving-up densities) in some studies (e.g. Stenberg and Persson 2005, 2006; Petty and Grossman 2010; Hedges and Abrahams 2015), but can be limited by the lack of spatial variables within the existing temporal patch use model (Brown 1988).

Brown's (1988) patch use model has provided a valuable foundation for foraging studies (Brown and Kotler 2004). In this model, a forager in a risky world and with various ways to spend its time maximizes its fitness through the allocation of limited time into gaining energy, seeking refuge, or performing alternative activities related to fitness (e.g. mating, grooming, territorial defense, etc.). In particular, Brown showed that a forager should exploit a resource patch until its harvest rate in that patch, H, falls to equal its energetic cost of foraging, E, its predation cost of foraging, P, and its missed opportunity cost of foraging, MOC (i.e., H = E + P + MOC). Although widely versatile and often used to compare foraging efficiencies at multiple locations during the same instance of time, this equation excludes spatial variables and the ability to harmonize temporal and spatial effects. For example, predation risk is not only a temporal attribute affected by the time spent exposed outside of a refuge, but is also a spatial attribute affected by the distance a predator is to the individual (Godin and Morgan 1985, Dill 1990, Kramer and Bonenfant 1997). Thus, the addition of spatial variable into Brown's model will allow researcher to further tease apart the complex mechanisms of species interactions and coexistence; this is especially useful for spatially structured environments such as coral reefs.

Such a model may allow researchers to more easily examine if coral reefs are spatially structured because of slight differences in each species' or individual's ability to mitigate foraging costs. For example, species A may be larger and more streamline, allowing it to efficiently forage higher portions of the water column where prey is more abundant but currents (energetic cost) and distance to shelter (predation cost) are higher. Species B may be less streamline and smaller, thus requiring less total energy, so it may forage closer to the reef floor where currents (energetic costs) and prey availability is below the GUD of species A (this means A would not forager where species B is found).

While many possible scenarios exist and likely occur on the reef, I take an initial step by extending Brown's (1988) temporal patch use equation to examine if tradeoffs in food and safety might explain differences in the lifestyles (i.e. site-attached or pelagic) and grouping (more clustered [e.g. tight school] or uniform [e.g. solitary or loosely schooled]). This should provide a foundation for studies more closely examining schooling behaviors and understand evolutionary differences between the lifestyles of *Caesio* sp. (pelagic planktivores) and species including *Dascyllus* sp., *Chromis* sp., *Amphiprion* sp., and *Pseudanthias* sp. (site attached planktivores). I also discuss this model's practicality with field measures and its possible application to other organisms and better understanding coral reef spatial structure. This extended model aims to provide added resolution to understanding foraging behavior and the mechanisms through which organisms coexist across space and time.

1.3.2. Model presuppositions

Interactions of space and time can be a complex concept, but for simplicity, this model views space as the environment during an instant in time (e.g. a photograph). Looking at an instant in space an organism perceives only its current environment. This may include food patches of differing densities, distances to predators or places of refuge, and variations in environmental conditions like temperature, irradiance, or turbidity. However, as space moves to the next instant of time (e.g. flip to the next photograph in the stack) the environment can change. Patches can be depleted or replenished, predators may become closer or farther away, the sun and moon can rise or set, etc. Thus, space is a representation of the present while temporal effects represents how the present environment is changing into the future.

Competition within space is viewed as a cost for that space. For example, a forager always has the choice to choose to occupy a certain space. An approaching competitor could result in the focal forager 1) ignoring it and continuing to forage, likely with reduced success, 2) fleeing to lesser-preferred space, or 3) aggressively chasing away the competitor to protect available resources. Both direct and indirect competition work in this manor but may affect different costs. For example, fleeing may prevent injury (i.e. an energetic cost), thereby being the most optimal use space. Alternately, if a forager were able to chase off a competitor without much risk or energy, then remaining and defending the most optimal space would be preferred. Thus, competition is not viewed as direct interactions between individuals, but how a competitor alters the spatial cost of a particular position.

By viewing space as an instant in time, we must address the scale of space and time. Minimally, Planck time (~10^{-44} s) or length (~10^{-35} m) would be the smallest unit, but ecologically these small scales are irrelevant. A more germane position in space should allow for limited movement of the forager within it while allowing enough space to represent the patch in a meaningful way (Sale 1998). For a foraging planktivorous fish, its spatial environment might refer to the fish and prey within its reactive distance (Kiflawi and Genin 1997). With time, an instant should exhibit a long enough period to allow the forager to interact with its environment while retaining relatively constant environmental conditions. In the case of planktivorous fish, this time may be the average time it takes a zooplankter to move through a fish's position. The scale of time and space is important to consider and can vary between organisms, study interests, and the capacities of the researcher to measure variables within them.

1.3.3. The model

Consider a forager whose fitness (G) is influenced by its net energy gain (e), probability of survival (p), and performance of alternative activities that affect fitness (a; e.g. mating, grooming, territorial defense, socializing, etc.). Let net energy gain be a function of the distance from refuge (d; i.e. resource gradients), nearest neighbor distance (n; i.e. resource competition), and the time spent foraging (t_f; i.e. depletion and renewal rates of resources). Similarly, let the probability of survival be a function of distance to refuge (d; i.e. decreased chance of fleeing to safety), nearest neighbor distance (n; i.e. dilution effect), and time spent foraging (t_f; i.e. being exposed to predators outside the refuge). Let alternative activities affecting fitness be a function of the time spent conducting these activities (t_a). Together these functions compose an individual's fitness, which is equal to a value (R; eq.1)

$$G\left(e_{(d,n,t_f)}, p_{(d,n,t_f)}, a_{(t_a)}\right) = R \qquad (eq.\ 1)$$

We can determine the values for d, n, t_f, *or* t_a that maximize fitness by taking the unconstrained derivatives of the equation with respect to each of those inputs (i.e. d, n, t_f, or t_a) and setting them equal to zero. In this manner, the strategy that maximizes fitness can be determined. We assume individuals will always "plan" to be alive in the next time step, therefore behaving without temporal constraints. The resulting derivative of the fitness function arranged with net energetic gain on the left side is:

$$\frac{\partial e}{\partial d}+\frac{\partial e}{\partial n}+\frac{\partial e}{\partial t_f}=\frac{-\frac{\partial G}{\partial p}}{\frac{\partial G}{\partial e}}\frac{\partial p}{\partial d}-\frac{\frac{\partial G}{\partial p}}{\frac{\partial G}{\partial e}}\frac{\partial p}{\partial n}-\frac{\frac{\partial G}{\partial p}}{\frac{\partial G}{\partial e}}\frac{\partial p}{\partial t_f}-\frac{\frac{\partial G}{\partial a}}{\frac{\partial G}{\partial e}}\frac{\partial a}{\partial t_a} \qquad (eq.\ 2)$$

The first term on the left, $\partial e/\partial d$, describes the change in the rate of net energy gained with distance from refuge. This term can be further split into the difference of the gross energetic gain (H_D) and the gross energetic cost (E_D) due to a forager's position in its environment (after Brown 1988). Gross energetic gain is the energy taken up by a forager. It can be estimated by measuring the energy of the amount of prey consumed in an instant of time. If direct measurements are unavailable, H_D may be estimated using prey density distributions of the environment and the species' functional response (Holling 1959). The gross energy cost is the energy it takes a forager to survive at and maintain a position in space (e.g. thermal regulation, respiration, swimming against a current). This value can be determined by measuring the metabolic rate of the individual under the environmental conditions of its spatial position. While metabolic rates are typically measured in laboratory settings, certain environmental parameters may be used to estimate E_D in the field. For example, if the water column has a uniform temperature, metabolic rates would be expected to be constant and can be estimated from laboratory studies. Alternatively, if thermoclines exist, the metabolic rate would be expected to differ between positions within the environment (Gillooly et al. 2001, Johansen and Jones 2011). Multiple parameters can exist and may vary between species and environments. Together, H_D and E_D represent the energy gained and expended due to the environmental characteristics at a position in space.

The second term, $\partial e/\partial n$, represents the change in the rate of net energy gained with nearest neighbor distance. As with the first term, this can be represented as the difference between the gross energy gain (H_C) and the gross energy cost (E_C) from inter- and intra-specific interactions. Gross energy gained from organismal interactions is energy made available to the forager through interacting with other foragers. This can include interference competition that provides the winner with more resources (Ziv et al. 1993, Ziv and Kotler 2003, McCormick and Weaver 2012), group foraging that overcome defended resources (Foster 1985), or drifting behind other fish in a school to conserve energetic costs (Johansen et al. 2010). The gross energetic cost of interactions is the energy lost due to interactions with other foragers. Examples include energy lost from losing at interference competition (Ziv et al. 1993, Ziv and Kotler 2003, McCormick and Weaver 2012), or energy expended to defend resources (Neat et al. 1998, Ros et al. 2006, Schacter et al. 2014). Together, H_C and E_C allow for both facilitative and competitive interactions depending upon the dominant term.

The third term, $\partial e/\partial t_f$, is the change in net energy gain with time spent foraging (i.e., rate of energy gained while foraging). It represents the energy gained by continuing to forage a position in space and can be split into the changes in gross energy gained (H_T) and gross energetic costs (E_T) of a position by moving to the next instant in time. Gross energy gains may include higher resource renewal rates from the birth, emergence, or immigration of prey as well as changes to environmental conditions affecting prey renewal and accessibility such as current magnitude (Kiflawi and Genin 1997) and lighting (Rickel and Genin 2005). Similarly, gross energy costs may include prey mortality, emigration, or retreating to refuge at the position. Energetic costs of the time spent foraging also include changes in environmental conditions (e.g., the environment warms or cools) and the effects of fatigue (e.g., energy required to cope with changing body temperature). For example, a forager in a cold environment cannot influence E_D, but it can alter metabolic costs by limiting the duration of exposure to the cold and foraging in several shorter bouts (E_T; Bozinovic et al. 2000). Together, H_T and E_T represent how a forager's energy budget will look in the next time step and help it decide whether to continue foraging or not.

The terms on the right side of the equation all contain two parts, the marginal rate of substitution $\frac{\partial G}{\partial p} / \frac{\partial G}{\partial e}$ or $\frac{\partial G}{\partial a} / \frac{\partial G}{\partial e}$ and the term of interest. Marginal rates of substitution (MRS) allow the terms of interest to be converted into a common currency (e.g. energy; Caraco 1979; Brown 1988). This can give the terms of interest a greater or lesser effect on fitness, depending upon the exchange rate. For example, individuals in a rich environment assume resources will still be available in the future causing them to put a greater importance on survival and making it to the future. This is the effect of devaluing energy within the marginal rate of substitution (Brown 1988). Marginal rates of substitution allow greater dynamics within the fitness function by adding varying weights to its components.

A forager's probability of surviving predation is managed across the spatial and time in the next three terms through a forager's distance from refuge ($\partial p/\partial d$), interactions with other foragers ($\partial p/\partial n$), and time spent foraging ($\partial p/\partial t_f$). These terms are all inversely proportional to energy gain as dictated by the negative sign before each term. This means a tradeoff of food and safety exists where foragers choose between rich but dangerous positions or depleted but safe positions (Brown and Kotler 2004, Hammerschlag et al. 2010). This first predation term, $\partial p/\partial d$, can be represented as the cost of predation from a forager's distance to refuge (P_D). A forager's ability to retreat to refuge and avoid predation weakens as its distance to refuge increases (Dill 1990, Kramer and Bonenfant 1997). Survival is also affected through interactions with other foragers as described in the fifth term ($\partial p/\partial n$). Isolated foragers bear a cost (I) due to the ability of a predator to more easily single them out while a forager with nearer neighbors dilutes the probability of predation on an individual (Foster and Treherne 1981). Lastly, the sixth term ($\partial p/\partial t_f$), is the change in the probability of survival to the time spent foraging, i.e., mortality risk. As a forager remains exposed for longer and longer periods of time, the chance a predator notices it increases, decreasing the forager's chance of survival (Brown 1988, Lima and Dill 1990). This term therefore represents the cost of exposure (P_T).

The final term, $\partial a/\partial t_a$, is the missed opportunity cost (MOC). In this model, as a forager moves forward in time, the MRS can change, making alternative activities more or less appealing in the next instant. Eventually, this cost can become high enough that a forager will cease foraging to perform other activities that promote its fitness (Brown 1988). For example, a female in estrus may enter the environment, giving the male a limited window for courting or mating. Additionally, the need for sleep, sociality, or refuge maintenance can also be MOCs. When a forager ceases foraging to perform other activities promoting its fitness, this model can become invalid as the individual no longer sees energy as its primary focus, but other potential resources including mates, nesting materials, etc.

Together, these terms build a temporally and spatially explicit patch use equation. The full equation, with foraging costs on the right side is:

$$H_D + H_T + H_C = E_D + E_T + E_C + P_D + I + P_T + MOC \qquad (\textit{eq. 3})$$

This equation can be manipulated to produce several variants depending upon a study's focus and focal organism. For example, if a study's focus is on the spatial environment at one instant in time, temporal terms can be excluded to produce:

$$H_D + H_C = E_D + E_C + P_D + I \qquad (\textit{eq. 4})$$

Gross gains and costs can also be combined into net variable (e.g. H_D [a gain] – E_D [a cost] = net energetic gain of a position). The alternative is also true where net variables can be split into gross gains and gross costs. For instance, when competition is costly ($H_C - E_C < 0$), competition terms can be combined and viewed as the foraging cost of competition (C):

$$H_D + H_T = E_D + E_T + C + P_D + I + P_T + MOC \qquad (\textit{eq. 5})$$

Related terms (i.e. net energy gain, probability of survival, or alternative activities) unable to be measured may be collapsed on themselves to produce a single term incorporating time, space, and interactions. The fully collapsed equation is the same reported by Brown (1988), but with broader definitions for the variables:

$$H = E + P + MOC \qquad (\textit{eq. 6})$$

Additionally, each spatial term can be further subdivided to incorporate dimensions of space. For example, H_D can be the sum of H_D along the vertical, forward, and sideways dimensions of a forager. This can be particularly useful for studies on coral reefs where plankton densities change along each axis differently (Lueck and Lu 1997, Holzman et al. 2005).

1.3.4. Model predictions

Using coral reef planktivorous fishes as an example, I apply the spatial components of our model (*eq. 4*) to examine whether manipulations of individual foraging costs may be enough to produce site attached (e.g. *Dascyllus* sp., *Chromis* sp.) and pelagic (e.g. *Caesio* sp.) lifestyles as well as more solitary or clumped groupings. In regards to site attachment, I expect site attachment to occur as energetic (E_D) and/or predation (P_D) costs increase, making conditions farther from refuge too costly to enter. Alternatively, reducing these costs, should allow foragers to more affordably reach the greater concentrations of resources higher in the water column and further away from refuge, producing a pelagic lifestyle. Similar to forager lifestyles, forager groupings should be influenced by the energetic costs of interactions (E_C) and the cost of isolation (I). An increase in E_C or a decrease in I should push fish further apart towards a solitary grouping. Schooling or tighter groupings should occur when competition is lax (E_C is low) and the cost of isolation is high. These predictions and the purpose of this manuscript is not to predict exact values for a single species, but rather to make generalities on potential mechanisms operating to produce coral reef spatial structuring. For example, do the shapes and distributions of optimal positions change when certain variables of the equation are manipulated? These theoretical predictions can then pave the way for further future studies and experiments. It is in these that a mechanistic understanding of coral reef spatial structure and their differences between species and individuals may become realized.

1.4.0. Damselfish Introduction: A mechanistic approach to understanding the spatial structure of site attached planktivores

The theoretical model presented in the previous section provides spatially explicit variables for studying foraging behaviors and interactions. Such variables may help explain the spatial structuring observed on coral reefs (Fricke 1977, Sale 1977, Schmitt and Holbrook 2002, Mellin and Ponton 2009). To begin unravelling such large scale structuring, researchers must first understand how individual foragers view and utilize their spatial environment. A variant of the patch use equation presented above can be used to help achieve these goals. First, because we are focusing on space, temporal terms can be dropped resulting in *eq. 4*. In planktivorous damselfish, schooling is not known to unlock additional troves of resources so we can assume the energetic costs of interactions (E_C) are greater than the gains (H_C; $H_C - E_C < 0$) and condense the equation into:

$$H_D = E_D + \mathrm{C} + P_D + I \qquad (eq.\ 7)$$

where H_D is the harvestable prey density at a position in space, E_D is the spatial energetic costs of the forager of keeping itself in that position, P_D is the spatial cost of predation at a position caused by the distance to refuge, C is the competition cost produced by having nearby neighbors, and I is the cost of isolation (i.e. dilution effect) on an individual’s survival. For simplicity, the subscripts can be removed and each term can be split along vertical (Z) and horizontal (XY) spatial axes to produce:

$$H_Z + H_{XY} = E_Z + E_{XY} + C_Z + C_{XY} + P_Z + P_{XY} + I_Z + I_{XY} \qquad (eq.\ 8)$$

To further simplify this equation, we can remove terms that are constant across its spatial axis. For example, because our focus is not on hierarchical differences of prey availability within a school of fish, we can assume relatively constant levels of prey horizontally across the reef (Holzman et al. 2005, Yahel et al. 2005, Heidelberg et al. 2010). Thus, H_{XY} would equal zero and can be removed from the equation. Similarly, horizontal differences in energetic costs of space should be constant since current magnitudes and thermoclines change primarily along vertical axes. The resultant equation becomes:

$$H_Z = E_Z + C_Z + C_{XY} + P_Z + P_{XY} + I_Z + I_{XY} \qquad (eq.\ 9)$$

Using the knowledge already known of planktivorous damselfish, including resource distributions, predation risks, and energetic demands, we can make predictions for how each variable will change with manipulations in space (Table 1). For example, prey for site attached planktivorous fishes, such as *Dascyllus marginatus,* consists primarily of strong-swimming zooplankton, including copepods (Popper and Fishelson 1973, Fishelson et al. 1974, Holzman et al. 2005), which are very abundant on reefs (Heidelberg et al. 2010). As zooplankton abundance is depleted from intense diurnal predation near the reef floor (Hamner et al. 1988, Motro et al. 2005, Yahel et al. 2005), an increasing gradient of zooplanktion abundance occurs vertically from the reef floor, extending 1.5 - 2 m above the reef floor (Holzman et al. 2005, Yahel et al. 2005, Heidelberg et al. 2010). Thus, if an individual, or school of site attached planktivorous fish, increase their vertical distance from refuge, we would expect more prey to be made

Table 1 *Predicted changes of spatially explicit foraging variables when manipulated along vertical (Z) or horizontal (XY) axes. Variables include the harvestable prey density (*H*), energetic cost of a position (*E*), energetic cost of forager interactions (*C*), predation costs of a position (*P*), and the cost of isolation (*I*). Arrows indicate the direction of change expected while "-" indicates no change.*

	H_Z	E_Z	C_Z	C_{XY}	P_Z	P_{XY}	I_Z	I_{XY}
Increase Vertical Distance to Refuge	↑	↑	-	-	↑	-	-	-
Increase Horizontal Distance to Refuge	-	-	-	-	-	↑	-	-
Increase Vertical Nearest Neighbor Distance	-	-	↓	-	-	-	↑	-
Increase Horizontal Nearest Neighbor Distance	-	-	-	↓	-	-	-	↑

available and consumed, increasing H_Z (Table 1).

An increase in vertical distance to refuge would also affect the energetic (E_Z) costs along that axis. Current magnitude is likely the most prominent energetic cost for planktivorous damselfish, which are known to differ in foraging behavior and habitat section depending upon their body shape and tolerability of strong currents (Hobson and Chess 1978, Bray 1981, McFarland and Levin 2002). For example, *Pseudanthias squamipinnis*, modify its foraging behavior in the presence of strong currents by producing feeding whorls to acclimate and conserve energy (Shapiro and Genin 1993). Because current increases logarithmically with vertical distance from the reef floor (Lueck and Lu 1997), an increase in vertical distance from refuge should also increase the energetic costs of a position (E_Z).

Increasing a forager's vertical or horizontal distance to refuge will also affect its predation cost (P_Z or P_{XY}). When predators are encountered, fish can reduce their foraging distance from shelter, thereby decreasing the time to reach safety (Sackley and Kaufman 1996) or retreat to the refuge of their coral and cease foraging (Helfman 1989). Inability to find suitable refuge often results in mortality from predators (Holbrook and Schmitt 2002). Although energetic costs of site-attached planktivores only change along the vertical axis, predation risk increases with distance to refuge along all three spatial dimensions. Thus, both P_Z and P_{XY} should increase with respective increases from refuge (Table 1).

Because we assume changes in the environment will shift whole schools rather than just one individual, we can assume that competition (C) and isolation (I) costs do not change with changes in distance to refuge, but rather nearest neighbor distance. Intraspecific competition costs can reduce the energy gain of an individual (Booth 1995, Martinez and Marschall 1999, Webster and Hixon 2000). The ability for an individual to compete for a shared prey item (i.e. the competition cost) can vary between individuals due to body size, hierarchical ranking, and nearest neighbor distance. As individuals move closer to one another, competition for a single prey item would increase. However, being farther apart from individuals increases an individual's probability of depredation (i.e. the dilution effect; Foster & Treherne 1981). Thus, as nearest neighbor distance increases the cost of competition should decrease while isolation costs increase, regardless of the axis where they occur (Table 1).

By comparing environmental variables (e.g. prey density) with changes in a forager's vertical, horizontal, and 3-dimensional distance to refuge and nearest neighbor distance, we may better understand how a planktivorous damselfish utilizes its special environment. For example, as prey availability (patch richness) increases, it becomes less valuable towards fitness, devaluing the marginal value of energy and inflating the marginal value of safety and alternative activities (eq. 2; Brown 1988, Kotler et al. 2010). Planktivorous damselfish can achieve this within their spatial environment by reducing P_D and/or I, which affect their survival. A decrease in P_D could be achieved by moving closer to refuge along any dimension. Decreasing I can similarly be achieved by decreasing a forager's nearest neighbor distance along any dimension. However, such a decrease of I will simultaneously produce an increase in C since the two are inversely related. By observing such changes in spatial use, and the dimensions they occur along, a foraging planktivorous damselfish's perception of space may be better understood and set a foundation for understanding coral reef spatial structure.

In this study, I analyze the foraging behavior of *Dascyllus marginatus*, a planktivorous site-attached damselfish, by observing their distance to refuge and nearest neighbor distance along 3-dimensions, the vertical dimension, and horizontal dimensions as prey density increases. I hypothesize that fish will behave optimally and decrease risk in one of three ways: 1) reduce only the distance to refuge (P_Z and P_{XY}), 2) reduce only nearest neighbor distance (I_Z and I_{XY}), or 3) reduce both distance to refuge and nearest neighbor distances. Additional insights may be made if certain dimensions are solely utilized to mitigate certain costs.

2.0.0. METHODS

<u>2.1.0. Desert Rodent Communities Methods</u>: Effects of constraint breaking adaptations on three experimental desert rodent communities

2.1.1. Study Organisms

These experiments utilize a combination of foragers and predators from granivorous desert rodent communities of the Negev (Middle East) and Mojave (North America) Deserts including Allenby's gerbil (*Gerbillus andersoni allenbyi*; GA), greater Egyptian gerbil (*G. pyramidum*; GP), desert pocket mouse (*Chaetodipus penicillatus*; CP), Merriam's kangaroo rat (*Dipodomys merriami*; DM), Saharan horned vipers (*Cerastes cerastes*; SHV), sidewinder rattlesnakes (*Crotalus cerastes*; SWRS), and barn owls (*Tyto alba*; Table 2). Our foragers are similar in functional grouping, but differ in several traits including body size, possession of external cheek pouches, bipedal or quadrupedal locomotion, and their continent of

Table 2 *List of all the predators and foragers used in 'common garden' community experiments, their natural continent where they are found, and characteristics relevant to the experiments focusing on constraint breaking adaptations*

Species	Location	Relevant Species Characteristics
Barn Owl (*Tyto alba*)	Middle East & North America	• Sound localization • Silent flight • Low light vision
Saharan Horned Viper (*Cerastes cerastes*)	Middle East	• No sensory pits - hunting relies on visual and vibration cues
Sidewinder Rattlesnake (*Crotellus cerastes*)	North America	• Possess sensory pits allowing them to see in the infrared which can be advantageous on dark nights
Allenbyi's Gerbil (*Gerbillus andersoni allenbyi*)	Middle East	• 26.2 g mean mass • No cheek pouches • Quadripedal locomotion
Greater Egyptian Gerbil (*Gerbillus pyramidum*)	Middle East	• 39.9 g mean mass • No cheek pouches • Quadripedal locomotion
Desert Pocket Mouse (*Chaetodipus penicillatus*)	North America	• 13-20 g mass • External cheek pouches • Quadripedal locomotion
Merriam's Kangaroo Rat (*Dipodomys merriami*)	North America	• 33-53 g mass • External cheek pouches • Bipedal and quadripedal locomotion

origin. The two viper predators also share similar functional grouping and body size while differing in the presence of sensory pits and their continent of origin. Barn owls were included because they are a common avian predator for all rodent species used here, but owls also add an additional, and different, element of risk to the study. By using both vipers and owls, a forager's ability and strategy in mitigating varying levels and types of risk can better be assessed. Details of each species used in the study are detailed below.

Chaetodipus penicillatus – Desert Pocket Mouse

Desert pocket mice (family Heteromyidae) are found across the Mojave and Sonoran Deserts of North America (Jezkova et al. 2009). They are 155-185 mm in length, with a mass ranging between 13-20 g (Smithsonian, url: http://www.mnh.si.edu/mna/). As heteromyids, they possess external fur-lined cheek pouches used to hold and carry seeds. Some studies show pocket mice have lower GUDs than kangaroo rats (Brown et al. 1988), while studies in our vivarium produced giving-up densities of 2.612 ± 0.034 g that are higher than kangaroo rats (Bleicher 2015). The latter also showed *C. penicillatus* was very responsive to both owl and snake predators (Bleicher 2015). During winter months, they can enter a state of torpor where they lower their body temperatures and become inactive (Smithsonian, url: http://www.mnh.si.edu/mna/).

Dipodomys merriami – Merriam's Kangaroo Rat

Merriam's kangaroo rat (family Heteromyidae) is found across the Great Basin, Mojave and Sonoran Deserts of North America. Adults range from 33.2-53.1 g mass and 195-282 mm in length (Behrends et al. 1986; Smithsonian, url: http://www.mnh.si.edu/mna/). As heteromyids, they possess external fur-lined cheek pouches used to hold and carry seeds, green vegetation, and insects. Kangaroo rats are saltatorial and possess bipedal locomotion and inflated auditory bullae of 1859 mm^3 (Webster 1961, 1962, Kotler 1984a) that are important anti-predator defenses. In experiments similar to this current study, *D. merriami* had a mean giving-up density of 0.999 ± 0.034 g with a slight increase to owl presence and a greater increase to snake presence especially on new moon nights (Bleicher 2015). They have a slight preference for foraging open microhabitats, but show slight flexibility for changing (Kotler 1984a, Bleicher 2015).

Gerbillus andersoni allenbyi – Allenby's Gerbil

Allenby's gerbils (subfamily Gerbillinae) are found across the Negev Desert and Mediterranean coasts of North Africa (Abramsky et al. 1985). Their mean mass is 26.2 g (Abramsky et al. 1985). Diets consist of seeds (46.3%), green plant matter (45.5%), and insects (7.3%), but fluctuate between plant matter being dominant in the winter (81.8%) and seeds the rest of the year (Bar et al. 1984). Previous studies show their giving-up density around 2.004 ± 0.032 g and respond most to the presence of owls, followed by both SWRS and SHV, just SWRS, and finally just SHV (Bleicher 2015). They also perceive new moon nights as less risky than full, even in the presence of sidewinder rattlesnakes, suggesting that they either avoided rattlesnake altogether or failed to pick up on the snakes' extraordinary ability conferred by their sensory pits (Bleicher 2015).

Gerbillus pyramidum – Greater Egyptian Gerbil

Greater Egyptian gerbils (subfamily Gerbillinae) inhabit the Negev Desert and central areas of North Africa (Abramsky et al. 1985). Their mean mass is 39.9 g (Abramsky et al. 1985), allowing them to interfere with the smaller *G. andersoni allenbyi*. Diets consist of seeds (63.2%), green plant matter (29.7%), and insects (7.1%) and fluctuate between plant matter being dominant in the winter (55.0%) and seeds the rest of the year (Bar et al. 1984). Previous studies show they have a giving-up density of 2.249 ± 0.045 g and that they respond more to owls than snakes (Bleicher 2015). They also perceive the presences of snakes under a full moon as more risky than at the new moon (Bleicher 2015).

Cerastes cerastes – Saharan Horned Viper

Cerastes cerastes (subfamily Viperinae) are convergent on, but lack the sensory pits of the sidewinder rattlesnake. Saharan horned vipers are found across much of the Middle East and North Africa. They can grow in length to 80 cm, but average 30-60 cm. The horns on their head are each made up of a single supraocular scale, which makes them distinct from other *Cerastes* species. They are most active during late April to early October and enter torpor during the winter months. Saharan horned vipers use sidewinding locomotion and prey upon small rodents, birds, and lizards that they detect using ground-borne vibrations and visual cues (Young and Morain 2002). Vertical burrowing is commonly employed to escape predators, ambush prey, and possibly thermoregulate (Young and Morain 2003).

Crotalus cerastes – Sidewinder Rattlesnake

Crotalus cerastes (subfamily Crotalinae) when compared to Saharan horned vipers are highly convergent predators. A potential constraint breaking adaptation of theirs are the two sensory pits on their snouts that allow them to "see" into the infrared. Sidewinders get their name from their sidewinding locomotion (Mosauer 1932, Secor et al. 1992) and dead tissue at the end of their tail that produces a rattling noise when shaken. They are found across the Mojave and Sonoran Deserts of North America and are most active nocturnally from April to October (Secor 1994). Their snout-vent length ranges from 16.5 to 61.5 cm and body mass from 5 to 304 g (Secor 1994), and they have two supraocular scales (horns). Sidewinders often spend daylight hours in rodent burrows, but when above ground may "crater" themselves into the sand at the base of bushes as a method of ambush hunting or thermoregulation (Secor 1994, 1995). *Crotalus cerastes* usually remain in a 30 x 30 m area for 2-3 nights and then will move to new locations (cited in Bouskila 1995). Their diet is split between small mammals and lizards, with an occasional bird (Webber et al. 2012).

Tyto alba (Scopoli 1769) – Barn Owl

Barn owls are a shared common predator found in Middle Eastern and North American deserts among other locations and habitats worldwide. Sound localization (Payne 1971, Takahashi 2010), silent flight (Bachmann et al. 2007), and low-light vision (Orlowski et al. 2012) are adaptations that help make *T. alba* formidable predators of small mammals. Their diets can include reptiles (Roulin and Dubey 2012), amphibians (Roulin and Dubey 2013), and bats (Roulin and Christe 2013), but are dominated by small rodents in open areas with a mean and median mass of 12.3 g and 23 g, respectively (Kotler et al. 1988, Tores and Yom-Tov 2003, Kitowski 2013).

2.1.2. Measuring the Lunar Cycle

Studies typically use the brightness of the moon (e.g. fraction of the moon illuminated, time above the horizon during the night) as a continuous variable to characterize the lunar cycle, but in doing so, may miss the potential importance of the timing of that illuminance (e.g. early in the night or later in the night). In this study, we use two variables (i.e. brightness and its timing) to better characterize the effects of the lunar cycle on foraging rodents. To measure lunar brightness, illuminance measurements were taken using a Solar Light Company's PMA2100 meter with a PMA2131 visible scotopic light detector. The measured illuminance was averaged between astronomical dusk and dawn to obtain a single illuminance value for each night of the experiment. Lunar timing was characterized using the sine of the moons upper meridian transit time (sUMT) calculated as:

$$sUMT = sin(2\pi T / 24) \qquad (eq.\ 8)$$

where T is the upper transit time in decimal hours. Resultant values range from -1 to 1, where -1 represents peak illuminance occurring early in the night at 18:00 local standard time (i.e. a first quarter moon). Values of 0 represent peak illuminance occurring at noon or midnight which is indicative of a new and full moon, respectively. A last quarter moon is represented by a value of 1 where peak illuminance occurs late in the night (06:00 local standard time). Astronomical twilight times and lunar upper meridian transit times were obtained from Her Majesty's Nautical Almanac Office (http://astro.ukho.gov.uk/). Together, the lunar brightness and its timing more accurately describe changes in lighting throughout the lunar cycle enabling a better understanding of how light drives biological behaviors.

2.1.3. Vivarium and Laboratory Methods

The three common garden experiments were 1) *G. a. allenbyi* and *G. pyramidum* 2) *C. penicillatus* and *G. a. allenbyi* and 3) *D. merriami* and *G. pyramidum*. These three experiments took place from May 7th to June 13th, 2014, August 13th to September 13th, 2013 and September 16th to October 18th, 2013, respectively. Experiments were conducted at the Ben-Gurion University of the Negev, in Midreshet Ben-Gurion, Israel (30°51'N, 34°47'E). A 17 x 34 x 4.5 m outdoor vivarium (Fig. 1) divided into quadrants by walls extending one meter below and rising one meter above the ground were used to conduct the experiment. The vivarium is equipped with snake-resistant gates in the walls separating the quadrants that allow foraging rodents to move freely among quadrants, but limit snake movement to within their quadrant. Each quadrant of the vivarium contained a different snake treatment of either no snakes (NONE), two Saharan horned vipers (SHV), two sidewinder rattlesnakes (SWRS), or one Saharan horned viper plus one sidewinder rattlesnake (BOTH). Barn owls also had access to the entire vivarium when present on selected nights. To ensure the IR lighting in the vivarium did not influence SWRS or rodent activity, an study was performed and described in Appendix A.

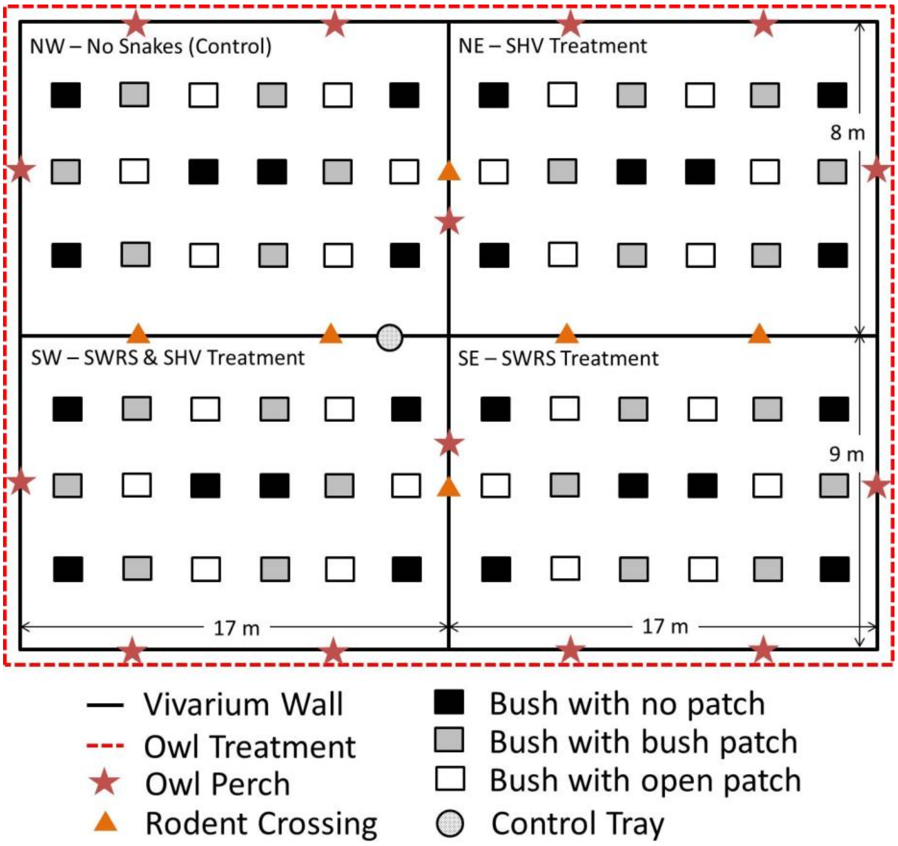

Fig. 1 *Experimental layout in the vivarium (not to scale). Bushes with open patches would be shifted east/west towards the center of the vivarium so their edge is 20 cm away from the patch edge. Bush and open patches alternate on a daily rotation except when owls are present (2 day block). Rodents and owls have free range of the vivarium but snakes are kept in their quadrants. In the experiment with exploratory behavior, snake treatments were replaced with exploratory behavior and rodent crossings were closed*

Three rodents of each of the two species present per experiment were released into each quadrant and allowed three nights to acclimate without predators being present. All rodents were fitted with a uniquely numbered RFID tag (passive induction transponder, or PIT tag) injected subcutaneously. While in the vivarium, rodents were exposed to varying types and levels of direct (e.g. vipers, owls, competitors) and indirect (e.g. microhabitat, illuminance) risk to assess response and ability to mitigate it. After acclimation, two viper predators were added to each of the three quadrants and remained for the duration of the experiment. In the *C. penicillatus* and *G. a. allenbyi* and the *D. merriami* and *G. pyramidum* experiments, the four nights before and after new and full moons were composed of randomized two-night blocks (16 blocks per experiment). During one of the two nights in each block, an owl was released into the vivarium. Outside of the blocked nights, data was still collected but no owl nights occurred. In the *G. a. allenbyi* and *G. pyramidum* experiment, two night-randomized blocks dictating owl nights occurred continuously throughout the experiment (19 blocks) to better balance the different owl treatments. On non-owl nights, each depredated rodent was replaced by adding an additional rodent to the quadrant where its PIT tag was found in order to maintain a consistent density (Embar et al. 2011). Predation events were determined by scanning for PIT tags in predators and their feces or spit pellets whenever found or retrieved.

Each night, foraging rodents could visit any of 48 food patches (43 x 33 x 10 cm plastic assay tray; 12 per quadrant), each of which contained 3 g of millet seed mixed into 3 dm^{-3} of sand. An additional control tray was placed on the center wall. This tray was out of the reach of foragers and controlled for fluctuations in moisture content of the seeds that can influence the weight of the GUDs. Quadrants also contained eighteen low lying, 76 x 60 x 16 cm wooden trellises topped with branches and foliage to create artificial bush microhabitats. Artificial bushes were placed in an alternating pattern so that bush patches had the artificial bush over the patch and open patches had the artificial bush 20 cm away from the patch towards the vivarium center (East/West; Fig. 1). Bush positions at each patch rotated between bush and open microhabitats in 2 day blocks to coincide with owl and non-owl nights.

Each morning, remaining seeds were collected from each tray using a sieve and taken to the laboratory for cleaning and weighing to obtain their GUDs; then assay trays were each replenished with another 3 g of seeds. Rodent tracks found in and around the trays were recorded for species presence. The last species to visit each patch (tracks on top) had the GUD credited to it. Tracks were swept smooth immediately after collecting leftover seeds and re-provisioning trays. To better assess my ability to accurately differentiate between rodent tracks, a RFID reader was placed under one assay tray per quadrant and used to detect RFID chips of the visiting rodents. Due to the limited number of RFID readers available, only tracking data were used in the analysis. In the laboratory, the collected seeds were cleaned of any debris such as feces, sand clumps, and detritus. The remaining mix was gently blown on to rid it of any remaining husks or light materials so that only seeds remained. The mass of remaining seeds were measured to the nearest 0.001 g and recorded as the GUD.

Illuminance measurements, taken every second and averaged every minute, where measured using a solar light PMA2100 data logging radiometer with a PMA2131 scotopic light detector. Mean nightly illuminance was calculated by averaging these measurements between astronomical dusk and dawn obtained from Her Majesty's Nautical Almanac Office (url: http://astro.ukho.gov.uk/). The lunar upper meridian transit times were also obtained from here and used as a variable representing the timing of peak illuminance (sUMT). Together, these two terms of brightness and timing characterize the entire lunar cycle.

2.1.4. Statistical Analysis

Giving-up density thresholds were determined using the mean GUDs of the control tray minus two standard deviations. This threshold was used to distinguish between foraged and unforaged (trays where rodents ran through the sand but did not collect any seeds) trays. Threshold values were chosen in this manor for two reasons 1) it yields threshold values commonly used but not reported in previous studies and 2) it can fluctuate with the methodological and human errors existing in any method. The threshold values for the *G. a. allenbyi* and *G. pyramidum*, *C. penicillatus* and *G. a. allenbyi* and *D. merriami* and *G. pyramidum* were 0.96, 0.94, and 0.96 g dm^{-3}, respectively.

Giving-up densities in the *G. a. allenbyi* and *G. pyramidum* were analyzed using a general least squares (GLS) model since statistical assumptions could not be met. The GUDS in the remaining two experiments were analyzed using an analysis of covariance (ANCOVA) model. Models in each experiment used owl presence, microhabitat, illuminance, timing of illuminance (sUMT), viper species presence, and rodent species as main effects. All two- and three-way interactions with rodent species were included in the model along with the four-way interactions that included illuminance, timing of illuminance, and species. To correct for normality assumptions, square root transformations were used on GUD, but are reported and plotted as untransformed values. Tukey HSD post hoc tests were conducted on main effects only. All statistical tests were performed in R using the car (v2.1-3), nlme (v3.1-128) and multcomp (v1.4-6) packages. R code for each of the three experiments and their ANOVA tables are available in appendix B, C, and D. All tests use $\alpha = 0.05$, and results are reported as means ± 1 standard deviation unless specified.

In these analyses each giving-up density tray is considered its own experimental unit and, therefore, would not be pseudoreplication. This argument is made for two reasons. The first is that foragers have preferences towards trays (e.g. trays closer to walls) that are consistent regardless of the individuals present. In other words, one group of foragers will have preferences towards a certain set of trays and a completely different group will have those same preferences (Kotler et al. 1991). This demonstrates independence between trays. Secondly, the effect of pseudoreplication (i.e. overestimating the error sums of squares) is not observed in these types of experiments. For example, if the daily means of GUDs are used instead, the r^2 of the model should decrease if pseudoreplication is present because estimates of sample size and error sums of squares are now correct since there is no possibility of pseudoreplication. Instead, the use of daily means produces an increase in r^2 values for the models, usually from about 0.4 to over 0.9, demonstrating pseudoreplication is not an issue when using each GUD as its own experimental unit (B.P. Kotler, personal communication). These two reasons support the safe use of GUDs as independent experimental units without pseudoreplicating.

<u>2.2.0. Personality Methods</u>: Variations in risk management between gerbils (*Gerbillus andersoni allenbyi*) with different exploratory/ boldness behaviors

2.2.1. Vivarium methods

This study consisted of one experiment repeated twice (2 rounds), each with different sets of animals, from September 24 to October 17, 2015 and from December 21, 2015 to January 14, 2016 at Ben-Gurion University of the Negev, in Midreshet Ben-Gurion, Israel (30°51'N, 34°47'E). Prior to each experiment, the exploratory behavior (boldness) were determined for each individual gerbil as part of another student's master thesis (Wan 2017). As part of this study, exploratory behavior in two groups (one of 26 and a second of 30) of Allenby's gerbils were assessed using a two-chambered arena, with one serving as a nest box and the other as an "interview" chamber containing novel or familiar objects and environments. These objects and environments included a plastic wrap covered floor, chickpea can, toy metal bird cutout, folded paper bag, dark chamber, light chamber, and a chamber with wind noise. Measurements of gerbil behaviors included time until first look, first entrance, the time spent at certain distances (5, 10, 15, >15 cm) from the center, and total time spent outside the chamber (after (Miller et al. 2006, Dochtermann and Jenkins 2007). Using a principle component analysis (PCA), the scores of individual gerbils for the different treatments were ordered along the first PCA axis. We equated the PCA score of an individual gerbil with its tendency to be exploratory. Gerbils in each group were divided into 4 groups based upon their PCA ranking. The six most exploratory (hereafter referred to as strongly bold) and six least exploratory (hereafter strongly shy) composed two of these groups from the extremes of the PCA ranks. Remaining moderately ranked gerbils formed the last two groups (hereafter, weak bold and weak shy) of six individuals. These four groups provide a gradient across gerbil exploratory behavior.

Members of each group were weighed and released into a separate quadrant of a 17 x 34 x 4.5 m outdoor vivarium (Fig. 1). Quadrants were isolated from each other with rodent-proof fences extending 1 m above and below the ground. At the end of each round, rodents were trapped and weighed again. During the second round in December, each personality group was assigned to the quadrant in the opposite corner to control for any spatial differences between quadrants. Once released, rodents acclimated for five nights to their new environment before data collection started. Data for each round were collected for eight nights centered on both full and new moons for a total of 16 nights each round. As in the rodent community experiment, quadrants each contained 18 artificial bushes (76 x 60 x 16 cm wooden trellises topped with branches) that provide protection from avian predators. Twelve bushes per quadrant contained food patches (43 x 33 x 10 cm plastic assay tray) containing 3 g of millet seed homogenously mixed into 3 dm^3 of dune sand. Half of these patches were placed directly under their bushes, while the other half were placed 20 cm outside the bush, creating bush and open microhabitat food patches. Microhabitats were rotated every two days so that bush patches become open and open patches become bush. Using randomized two-night blocks (8 blocks per experiment), predation risk was manipulated by releasing an owl on one of two nights in the block. On non-owl nights depredated rodents were replaced by adding additional rodents to the quadrant where its pit tag was found in order to maintain a consistent density (Embar et al. 2011). Depredation was determined by scanning for pit tags in spit pellets whenever found or recovered from the owls. Similar to the rodent community methods, control trays were used to correct for methodological error and fluctuations in seed moisture in both microhabitats. Because the amount of moisture (e.g. dew) differes between microhabitats, two control trays (one bush and one open), each with seeds and a 1 cm wire mesh covering (to prevent rodent forging), were placed in the northwest quadrant each night of data collection and their seeds recovered the following morning and weighed (just like a typical tray). Data from control trays were then used to determine the GUD threshold and adjust weights to account for variations in moisture and any methodological errors.

Each morning following a night of gerbil foraging, the remaining seeds were collected from each tray using a sieve and taken to the laboratory for cleaning and weighing. After collection, trays were replenished with another 3 g of millet seed. In the laboratory, the collected seeds were cleaned of any debris such as feces, sand clumps, and detritus. An initial weight of the remaining seeds and husks (BRUTO) was recorded before gently blowing away the husks and taking a second weight of only seeds (giving-up density [GUD]). Giving-up densities are an estimate of the quitting harvest rate and represent the foraging cost (e.g. predation, energetic, competition) of exploiting a patch (Brown 1988). Each GUD was corrected for changes in mass (i.e. moisture) between nights by taking the difference of the initial seed mass (3 g) and the control GUD for each night and multiplying it by the proportion of seeds remaining in the foraged tray. The difference between the BRUTO and GUD equals the mass of husks, which when plotted against the GUD can show the maximum possible husk mass for any GUD. The proportion of the measured husk mass and the maximum possible husk results in the proportion of seeds husked in the tray (HIT; after unpublished methods by J. St. Juliana). Weights were measured to the nearest 0.001 g.

As describe in the rodent community methods, patches were considered exploited if the GUD was less than 3 g minus two standard deviations of the average mass of control tray seeds (0.968 g dm^{-3}). Giving-up densities above this threshold were considered unexploited, although the tray may or may not have been visited by the gerbils. In the second vivarium round, I placed a closed circuit television camera (CCTV) at trays 5 and 8 in each quadrant to record any possible gerbil foraging activity during the entire night. Using our own script in R, we analyzed videos for motion and calculated the times spent by rodents in each tray. Outlying results caused by spiders building webs on the camera or similar events were re-analyzed manually. Visits of 3 s or less were considered a run through and not included in the sum of time spent foraging. Additionally, visits within 8 s of each other were considered one visit because rodents sitting still would not be detected in the script. With the combination of GUDs and the total time spent foraging in the tray, harvest rates based on Holling’s disc equation were calculated and plotted (after Kotler et al. 2010). The resultant curves allow the visualization of differences in time allocation (location of average GUD on the curve relative to the origin) and vigilance / apprehension (slope of the curve).

The lunar cycle was characterized by measuring illuminance and calculating the sine of the upper meridian transit time (sUMT) to represent the timing of peak illuminance. Illuminance measurements were taken using a Solar Light PMA2100 Radiometer with a scotopic light detector (PMA2131) placed on the center wall of the vivarium and averaged across the night between astronomical dusk and dawn. Astronomical twilight times and lunar upper meridian transit times were obtained from Her Majesty's Nautical Almanac Office (url: http://astro.ukho.gov.uk/psp/index_beta.html). Values of sUMT at -1 represent upper meridian transits early in the night (i.e. at 18:00) and values of 1 represent upper meridian transits late in the night (i.e. at 06:00).

2.2.2. Statistical Analysis

The purpose two experiments were to control for any potential biases between vivarium quadrants. For this reason, data from the two experiments were combined into one dataset. A generalized least squares (GLS) model used GUD and HIT as dependent variables in separate analyses with owl presence, microhabitat, illuminance, its timing, personality, their two and three-way interactions with personality, and four-way interactions with personality, illuminance, and its timing as independent variables. Variances were recalculated for each night of data collection. HIT values were square root transformed to better meet normality assumptions. Patch exploitations were analyzed using binomial regression with visit type being the dependent variable. Owl presence, microhabitat, illuminance, its timing, personality, their two-way interactions with personality, and the three-way interaction of illuminance, its timing, and personality were used as independent variables. An analysis of variance analyzed the percent loss of individual body mass in the personality treatments. A post-hoc TukeyHSD test tested for differences between each personality pair. To aid in interpreting data, 3-dimensional figures and harvest rate curves are shown with only strongly bold and strongly shy treatments. The R script for running all analyses and their resulting ANOVA tables can be found in Appendix E. All tests use $\alpha = 0.05$, and results are reported as means ± 1 standard deviation unless stated otherwise.

2.3.0. Theoretical Methods: Patch use as an indicator of habitat preference, predation risk, and competition across space and time

To model the effects of shifts in foraging costs on the lifestyle and grouping of planktivorous reef fishes, each variable of the spatial patch use equation (*eq. 4*) was represented by a logistic function (Table 3). Although other functions can be used, logistic functions were chosen because they assume extreme variable produce less change in energetic costs/gains. For example, fish at various distances close to refuge might exhibit limited differences in predation costs (P_D) because they can easily retreat from an attacking predator. At some distance, the forager's ability to get to safety becomes less certain and the cost of predation increases quicker. If the distance continues to increase, a forager reaches a point that retreating to refuge is futile because the predator will certainly out swim it so the forager relies on other forms of mitigation. Values within these logistic functions were chosen to produce realistic estimates and gradients for each variable based on what is known in scientific literature (Table 3).

To visualize variable gradients, heat maps showing distance to refuge were plotted out to 5 m while nearest neighbor distances were plotted to 1 m. These distances were chosen because most site-attached planktivores will not venture beyond 5 m from their refuge and their schools contain nearest neighbors less than 1 m apart; this conservatively covers all of their foraging space. Calculations were made for each cm^2 within this space. In cases where both horizontal and vertical distance altered the variable (e.g. predation risk, isolation, competition), the distance formula was used to calculate a single 3-dimensional distance.

Table 3 *Base equations for the variables representing the spatial environment and spatial interactions of site attached planktivorous fishes. Variables include the harvestable prey density (*H_D*), energetic gain from forager interactions (*H_C*), energetic cost of a position (*E_D*), energetic cost of interactions (*E_C*), predation costs of a position (*P_D*), and the cost of isolation (*I*)*

Variable	Equation
Logistic Equation	$\frac{L}{1+e^{a(x+b)}}$
H_D	$\frac{12}{1+e^{-(x-1)}}$
H_C	$\frac{0}{1+e^{2(x-1)}}$
E_D	$\frac{3}{1+e^{-2(x-2)}}$
E_C	$\frac{3}{1+e^{5(x-0.9)}}$
P_D	$\frac{3}{1+e^{-(x-2)}}$
I	$\frac{3}{1+e^{-5(x-1)}}$

$$d_{3D} = \sqrt{d_z^2 + d_{xy}^2} \qquad \text{(eq. 10)}$$

When variables only changed along a single axis (e.g. prey or energy), the distance along that axis was used. These heatmaps, created using R (see Appendix F for script), make for an easy and visual portrayal of how each variable changes across its vertical and horizontal environment (Fig. 2). Darker green colors represent the most optimal area for a forager while red shows the least optimal.

The heat maps representing each variable (Fig. 2) were compared with estimates of real values and their distribution across space. Based upon the energy of an average prey item and the number of prey items consumed per unit time, I estimate a foraging damselfish should harvest (H_D) between 0.298-8.965 J min^{-1} (Forrester 1991, Bhat et al. 1993, González et al. 2008) at a natural foraging position 1-2 m above the reef floor. These values should increase vertically in the water column (Hamner et al. 1988, Holzman et al. 2005, Motro et al. 2005, Yahel et al. 2005, Heidelberg et al. 2010) and can be expected to be greater than 8.965 J min^{-1} higher above the reef where site attached planktivorous fishes do not commonly forage (Fig. 2a). I assume that differences in the energetic costs of a position (E_D) are between 0.16-5.83 J min^{-1} (Nilsson and Ostlund-Nilsson 2008, Johansen and Jones 2011) and are primarily influenced by the current magnitude which increases logarithmically with vertical distance from the reef floor (Fig. 2b; Lueck and Lu 1997). Predation substantially affects foraging damselfish behavior (Holbrook and Schmitt 2002,

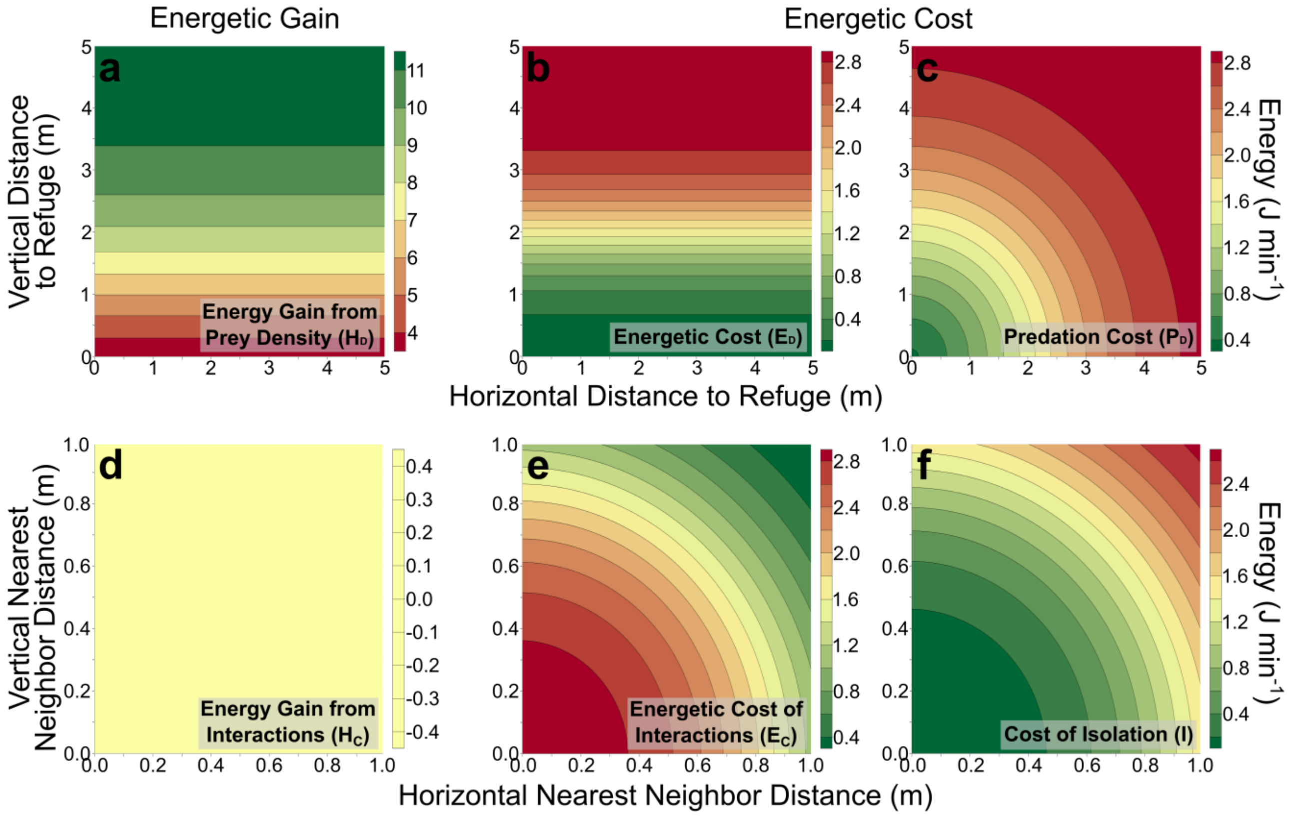

Fig. 2 *Theoretical expectations of how energy costs and gains change across vertical and horizontal space for planktivorous reef fish. Terms describing the spatial environmental via distance to refuge include the a) harvestable prey density, b) energetic costs, and c) predation costs of the position. Forager interactions are also described using nearest neighbor distance as a proxy and include d) energy gains and e) costs from interactions and f) the cost of isolation*

Almany 2004, Stier and White 2014), however, the cost of predation (P_D), in terms of energy, is difficult to directly measure. I assume this cost to increase with distance to refuge and have a similar magnitude as E_D (Fig. 2c) and to increase as a forager moves further from refuge (Hixon and Beets 1993, Holbrook and Schmitt 2002). Planktivorous damselfish are not known to facilitate each other in accessing resources and hierarchical differences were not a focus for this study so H_C was assumed to be zero (Fig. 2d). Because we assume foragers to first select their position/habitat and then select how close they will tolerate competitors, the magnitudes of the energetic cost of interactions (E_C) and the cost of isolation (I) were set lower than other costs. However, both change with distance to nearest neighbor, where E_C decreases and I increases with increasing distance (Fig. 2e, f). Together, these variables produce realistic representations of a planktivorous reef fish's spatial foraging environment, which can be used in the spatial patch use equation.

The value of each variable at each cm^2 of space within heat maps were entered into the spatial patch use equation to produce two heat maps showing the net energy gain as distance from refuge or distance to nearest neighbor changes (Fig. 3). While examining variables characterizing the distance to refuge, nearest neighbor distance was held constant at 0.25 m. This allows the effects of distance to refuge to be observed without changes in nearest neighbor distances altering the net energy gain. Similarly, when manipulating variables affecting nearest neighbor distance, a constant vertical height of 1.2 m above the refuge was used. These values were selected because they are the similar to data collected observing *Dascyllus marginatus*, a planktivorous coral reef damselfish (Reuben 2016). The resultant heat maps allow visual examinations to ascertain the optimal positions for a foraging fish to inhabit (Fig. 3; darker green areas where the net energy gain is highest). These heat maps also produce a base result to compare against when foraging costs change.

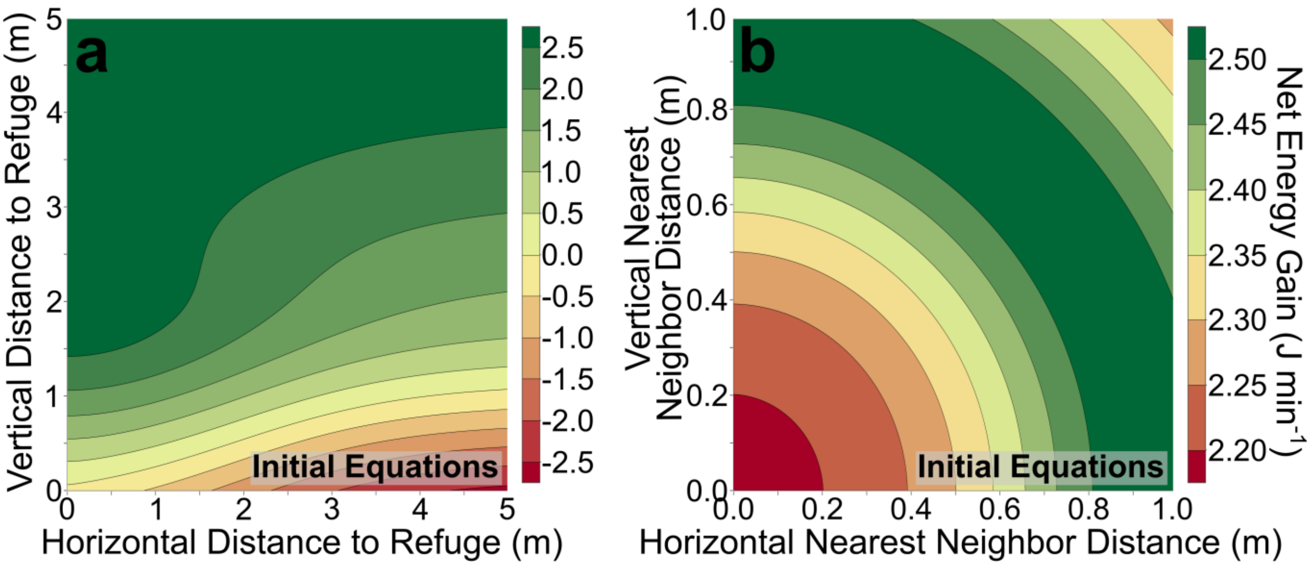

Fig. 3 *Initial model results for planktivorous fish using a spatial patch use equation to determine net energy gained from a forager's a) distance from refuge and b) nearest neighbor distance. When modelling distance to refuge, nearest neighbor distance was held constant at 0.25 m and when modelling nearest neighbor distance, distance to refuge was constant at 1.2 m*

To determine how changes in foraging costs affect the optimal position, each equation's numerator (L) was manipulated to alter the magnitudes of the variable and test the predictions discussed above in the hypothesis (Table 4). Using the same technique used to develop the base heat maps, the resultant heat maps can be compared with the manipulated maps. Rather than comparing absolute values, comparisons looked for shifts in the optimal position being more circular and directly above the refuge (i.e. site attachment) or distributed horizontally across the upper portion of the map (i.e. pelagic). Similarly, the base heat maps for the optimal nearest neighbor distance was examined for shifts in the optimal position moving closer (i.e. schooling) or further (i.e. solitary) from the individual of interest. These results produce general predictions that should apply to planktivorous fishes, but whose absolute values should vary between species and environmental conditions. The purpose of this model is not to provide absolute values for every condition/species but to understand the possible mechanisms producing the different observed lifestyles/aggregations and to produce testable predictions for further studies.

Table 4 *Manipulations of the numerator (*L*) in logistic functions to represent changes in the magnitudes of foraging gains and costs in the spatial patch use equation. Using site-attached planktivorous fish as an example, their resulting distribution are included. Variables manipulated include the energetic gain from forager interactions (*$\mathrm{H_C}$*), energetic cost of a position (*$\mathrm{E_D}$*), energetic cost of interactions (*$\mathrm{E_C}$*), predation costs of a position (*$\mathrm{P_D}$*), and the cost of isolation (*I*)*

Change	**Variable**	**New Value (L)**	**Resultant Strategy**
Increase	E_D	6	Site Attachment
	P_D	6	Site Attachment
	E_D & P_D	5 & 5	Site Attachment
	H_C	3	Isolated/Solitary
	E_C	6	Aggregated/Schooling
	I	6	Aggregated/Schooling
Decrease	E_D	1	Pelagic
	P_D	1	Pelagic
	E_D & P_D	2 & 2	Pelagic
	E_C	1	Isolated/Solitary
	I	1	Isolated/Solitary

<u>2.4.0. Damselfish Methods</u>: A mechanistic approach to understanding the spatial structure of site attached planktivores

2.4.1. Study Organisms

To test the hypotheses of this study, the site-attached planktivorous marginate dascyllus, *Dascyllus marginatus*, was chosen. This species is found across the Red Sea, Gulf of Oman, and western portions of the Indian Ocean at depths of 1-15 m (Lieske & Myers 2004; url:fishbase.org). They are hosted by several coral species including, *Stylophora pistillata*, *Stylophora wehisi*, *Acropora* spp., and *Porites* spp., to which they quickly retreat when frightened (Lieske and Myers 2004, Shashar et al. 2005). Individuals can reach 6 cm total length and school in groups of up to 25 individuals, despite preferring sizes of three or less (Kent et al. 2006). While foraging, they are believed to prey on zooplankton (primarily copepods) greater than 200 µm (Fishelson et al. 1974). Their similar foraging behavior to other site attached planktivorous fishes (Fishelson 1998) combined with a relatively high abundance in the northern Red Sea (Brokovich et al. 2006), make them an excellent candidate for this study.

2.4.2. Measuring Foraging Behavior

This study took place at the Interuniversity Institute (IUI) for Marine Sciences in Eilat, Israel from the 18-24th of August 2014. A 32 x 25 x 15 cm *Acropora* coral with 10 *Dascyllus marginatus* was taken from the coral nursery at the IUI and placed on a 1 m high stand, at a depth of 8.8 m, on the cobble-bottomed area about 100 m north of the institute's pier in the Gulf of Eilat. The fish acclimated here for two weeks prior to the start of data collection where they were exposed to naturally occurring variations of

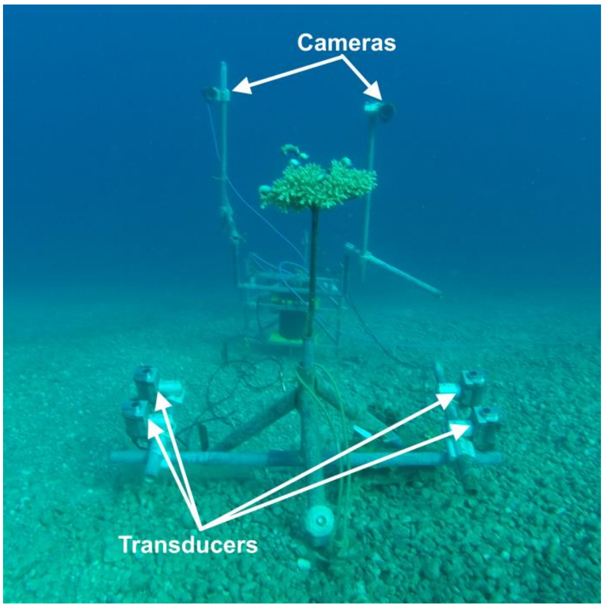

Fig. 4 *Photograph showing a new setup of Zooplankton Sonar (ZOOPS). Its two cameras are zoomed out and placed in a stereo array to determine the positions of fish. Four acoustic transducers, in two pairs of two, are placed parallel with the current upstream and downstream of a coral containing individuals of the site attached planktivorous fish,* Dascyllus marginatus

current magnitude, prey density, and prey flux (current magnitude x prey density). An acoustic Doppler current profiler (RD Instruments, Workhorse 600; ADCP) was placed 7.25 m northward of the coral at 10.8 m depth to allow the first 0.5 m bin to read the current at the same depth of the fish. Current magnitude was measured every second and averaged together every five minutes. To measure prey abundance and fish behavior, a modified setup of ZOOPlankton Sonar (ZOOPS) was used. Zooplankton sonar is a broadband echosounder with coordinated stereo-optical imaging (Roberts and Jaffe 2007, 2008, Briseño-Avena et al. 2015). This tool was developed to study zooplankton distributions in the ocean, but by zooming out the cameras and orienting ZOOPS transducers vertically in the water column, a fish's position in space can be determined and the density of prey available measured (Fig. 4).

ZOOPS acoustic transducers operate within 1.5-2.5 MHz frequency range and return the target distance and strength, allowing an estimation of zooplankton size within a given range (Roberts and Jaffe 2007, 2008). Pings were transmitted every 0.5 or 1 ping s^{-1} depending upon the run. Two transducers 11 cm apart were placed 1 m north and another two placed 1 m south of the coral head so one pair could always measure the upstream prey density. Periodic checks using fluorescein and monitoring of current direction from the ADCP helped ensure the parcel of water being measured was the same parcel being foraged. Using a level, the transducers were placed at equal depths and oriented vertically in the water column. Plankton abundance was measured from 85 to 103 cm above the transducers, which encompasses the top of the coral (93 cm from the reef floor) to the maximum height the fish were observed to forage (17.6 cm above the coral). Acoustic targets were considered planktivorous prey if they had a target strength between -110 and -85 db. This was estimated by comparing target abundances from ZOOPS during preliminary runs with those simultaneously collected by divers pulling a 200 µm plankton net adjacent to the ZOOPS setup. These acoustic techniques allow for an initial measurement of properly sized prey items in the parcel of water passing through the school of planktivorous fish.

Prior to collecting data, the intrinsic parameters of ZOOPS cameras were calibrated (after Briseño-Avena et al. 2015) using the stereo calibration toolbox for MATLAB (Jena-Yves Boguet, http://www.vision.caltech.edu/bouguetj/calib_doc/) and a checkerboard with 39 mm squares. Two screws on a level, easyWand and the digitizing tools software were used to calibrate the camera space (Theriault et al. 2014) within a global coordinate system. During the ZOOPS runs, stereo images were taken once 10 s^{-1}. Using DLTdv5 software, each visible fish's X, Y, and Z coordinates were calculated (Hedrick 2008). Additionally, coordinates of the vertically aligned pole holding the coral were obtained to allow orientation of the fish coordinates to horizontal and vertical space. Using a point on the pole holding the coral, the coral's center was determined and used as the origin of the camera space. Fish within the coral or a 12 cm ellipsoid buffer around the coral were considered not to be foraging and were removed from the analysis. Additionally, fish below the origin were also removed to keep a more natural perspective of fish foraging above the coral. Using these coordinates, the Euclidian distance to refuge and the nearest neighbor distance along the vertical, horizontal, and 3-dimensional axes were calculated for each fish using MATLAB.

The clocks of the ADCP and ZOOPS were synchronized allowing measurements of current magnitude, prey density, and fish positions to be compared over a select period. Runs were started remotely from the lab when current magnitudes increased and fish left their coral to forage; runs ended when they ceased foraging and returned to their coral. Because the ADCP required 5 min of measurements to give an accurate mean current magnitude, all other data were divided into these same 5 min bins and averaged together for that period. Thus, for each 5 min period measuring current, one mean would result for the vertical, horizontal, and 3-dimensional distance to refuge and nearest neighbor distance. Any measurements that did not completely fill a 5 min bin were removed from the study.

The resulting means were analyzed using a type III analysis of covariance (ANCOVA) in R (car v. 2.1-2) where distance (e.g. distance to refuge or nearest neighbor distance along 3-dimensional, horizontal, or vertical dimensions) was used as the dependent variable and an environmental factor (e.g. prey density, current magnitude, or prey flux) as the independent variable. The resulting models tested positive for auto-correlation using a Durbin-Watson test. To correct for auto-correlation, a second independent variable was added containing the distance value for the previous time step and the models were re-run. Since a significant change in distance does not indicate a difference in use of vertical and horizontal space, a second ANCOVA was used to compare the two slopes and see if the fish use these axes differently if both slopes were significantly different from zero. Such a difference occurs when the interaction of the environmental variable and the dimension (z or xy) are significant, the slopes are significantly different. Although prey density, current magnitude, and flux were all analyzed and reported, the focus of the study is on prey density due to the complicated correlation between current and flux affecting both H_D and E_D. A logistic regression was used to examine the probability of fish being present outside the coral buffer. The R script and its resulting ANOVA tables are available in Appendix G. All tests use $\alpha = 0.05$, and results are reported as means ± 1 standard deviation.

3.0.0. RESULTS

3.1.0. Desert Rodent Communities Results: Effects of constraint breaking adaptations on three experimental desert rodent communities

3.1.1. Gerbillus andersoni allenbyi *and* Gerbillus pyramidum

RFID readers agreed with track assessments 70% of the time, suggesting tracking data in this study are reliable. As with previous studies, open microhabitats (GLS, $F_{(1,1235)} = 1149.45$, $p < 0.001$) and the presence of owls (GLS, $F_{(1,1235)} = 615.70$, $p < 0.001$) increased giving-up densities. The presence of an owl increased the foraging costs of *G. andersoni allenbyi* more than *G. pyramidum* (GLS, $F_{(1,1235)} = 12.98$, $p < 0.001$), suggesting the latter, larger species handles risk from avian predators better than the former. This

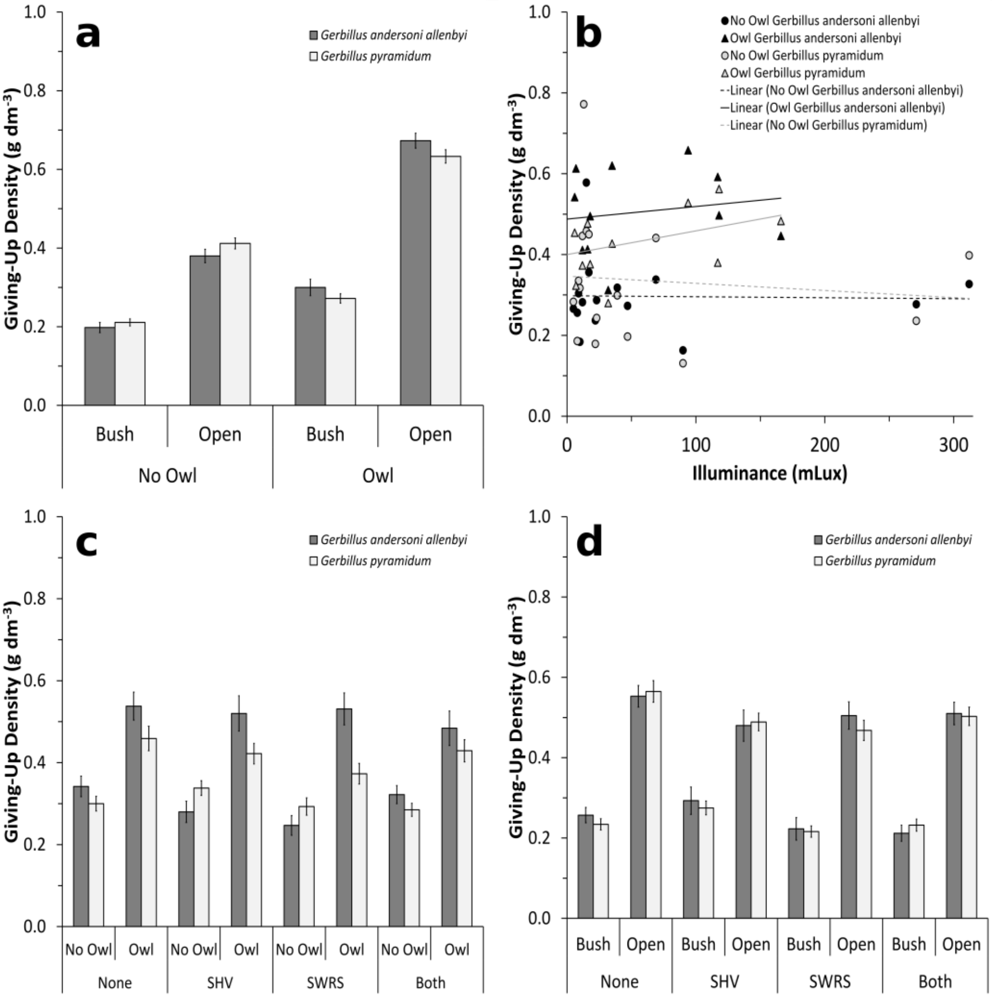

Fig. 5 *Giving-up densities showing the interaction of a) owl presence (Owl / No Owl), microhabitat (Bush / Open), and rodent species (*Gerbillus andersoni allenbyi / Gerbillus pyramidum*), b) owl presence, average nightly lunar illuminance, and rodent species, c) owl presence, rodent species, and viper treatment, and d) microhabitat, rodent species, and viper treatment in an artificial community. Viper treatments include no vipers (None), two sidewinder rattlesnakes (SWRS;* Crotalus cerastes*), two Saharan horned vipers (SHV;* Cerastes cerastes*), and one SWRS with one SHV (Both). Values represent the mean ± SE*

trend is also supported in the interaction between rodent species, owl presence, and microhabitat (GLS, $F_{(2,1235)} = 63.49$, $p < 0.001$) where *G. andersoni allenbyi* is more efficient in both bush and open habitats when owl is absent, and *G. pyramidum* when owl is present (Fig. 5a). Treatments containing greater risk (i.e. open microhabitat or owl presence) show greater differences between species. The interaction between rodent species, owl presence, and lunar brightness was also significant (GLS, $F_{(2,1235)} = 10.95$, $p < 0.001$), further demonstrating a lesser ability of *G. andersoni allenbyi* to mitigate risk from owls (Fig. 5b). This interaction also showed foraging costs increased at a greater rate across illuminance when an owl was present, suggesting an added difficulty of mitigating multiple risks. These results suggest the larger species, *G. pyramidum*, better handles direct risk cues from owls, while *G. andersoni allenbyi* is more efficient under indirect cues or a lack of risk.

Contrary to some studies (Kotler et al. 1993a, 2016, Bleicher et al. 2016), but consistent with others (Bleicher 2015), viper presence lowered the giving-up density (GLS, $F_{(3,1235)} = 15.50$, $p < 0.001$), with trays in the presence SWRS having the lowest GUD. *Gerbillus andersoni allenbyi* was the more efficient forager only in the presence of homogeneous snake treatments (SHV or SWRS) without owls (GLS, $F_{(6,1235)} = 3.81$, $p < 0.001$), suggesting they are better able to handle viper predators (Fig. 5c). A second possibility is

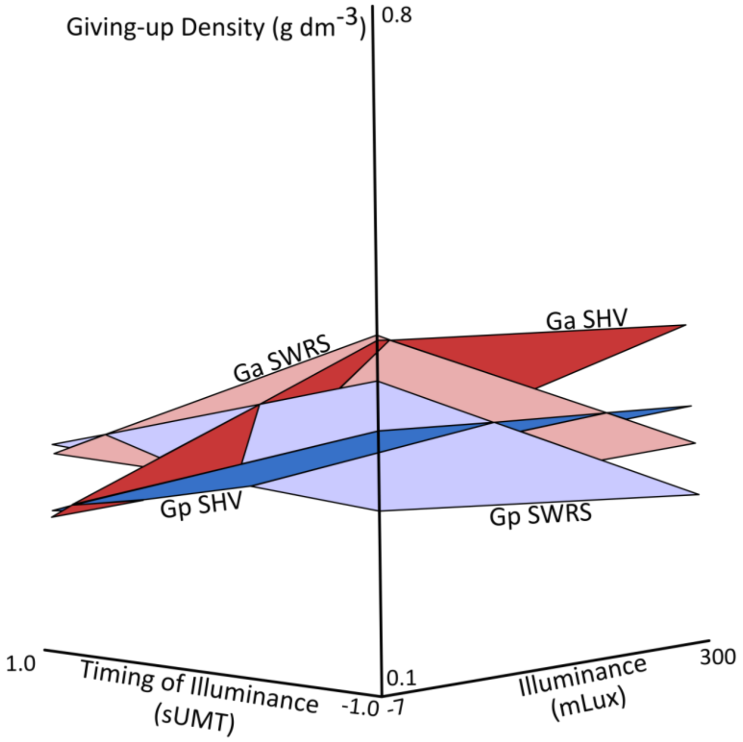

Fig. 6 *Giving-up densities showing the interaction of rodent species (Ga =* Gerbillus andersoni allenbyi */ Gp =* G. pyramidum*), average nightly lunar illuminance, the timing of illuminance, and viper treatment in an artificial community. Viper treatments include no vipers (None), two sidewinder rattlesnakes (SWRS;* Crotalus cerastes*), two Saharan horned vipers (SHV;* Cerastes cerastes*), and one SWRS with one SHV (Both). sUMT is calculated by taking the sine of the moon's upper meridian transit time. Values closer to -1 (18:00) represent illuminance occurring earlier in the night while values closer to 1 (06:00) represent later illuminance. Each point represents a mean value*

that interference competition pushed them from quadrants with low snake activity into more risky ones since previous studies showed all species to prefer the absence of snakes or lower viper activity (Kotler et al. 2016) and we observed *G. andersoni allenbyi* to be most efficient in the presence of vipers (Fig. 5c). This would require the cost of competition to be greater than the cost of predation. Although the interaction between microhabitat, viper treatment, and rodent species was significant (GLS, $F_{(6,1235)} = 3.81$, $p < 0.001$), no clear trends between rodent species were observed (Fig. 5d). These results again suggest the inability of *G. andersoni allenbyi* to handle multiple levels of risk compared to *G. pyramidum*, and that interference competition may occur, pushing the smaller species into more dangerous treatments.

Although illuminance showed no significant effect on GUDs by itself, GUDs were significantly higher when illuminance occurred later in the night (GLS, $F_{(1,1235)} = 244.05$, $p < 0.001$). The interaction of illuminance, its timing, and rodent species shows *G. andersoni allenbyi* has lower GUDs than *G. pyramidum* during the waning mooning phase when brightness is later in the night (GLS, $F_{(2,1235)} = 107.55$, $p < 0.001$). However, when illuminance, viper treatment, and rodent species interacted, this decline with illuminance was most prevalent for *G. andersoni allenbyi* in the presence of SHV (GLS, $F_{(6,1235)} = 3.38$, $p = 0.003$). Giving-up densities had the highest rate of increase in the viper treatment with both species (BOTH) where *G. andersoni allenbyi* had the higher GUDs. This suggests rodents may detect the differences in viper behaviors and perceive greater risk when multiple types of risk are present. One such behavioral difference possibly produced by the viper's sensory pits is seen in the interaction with viper

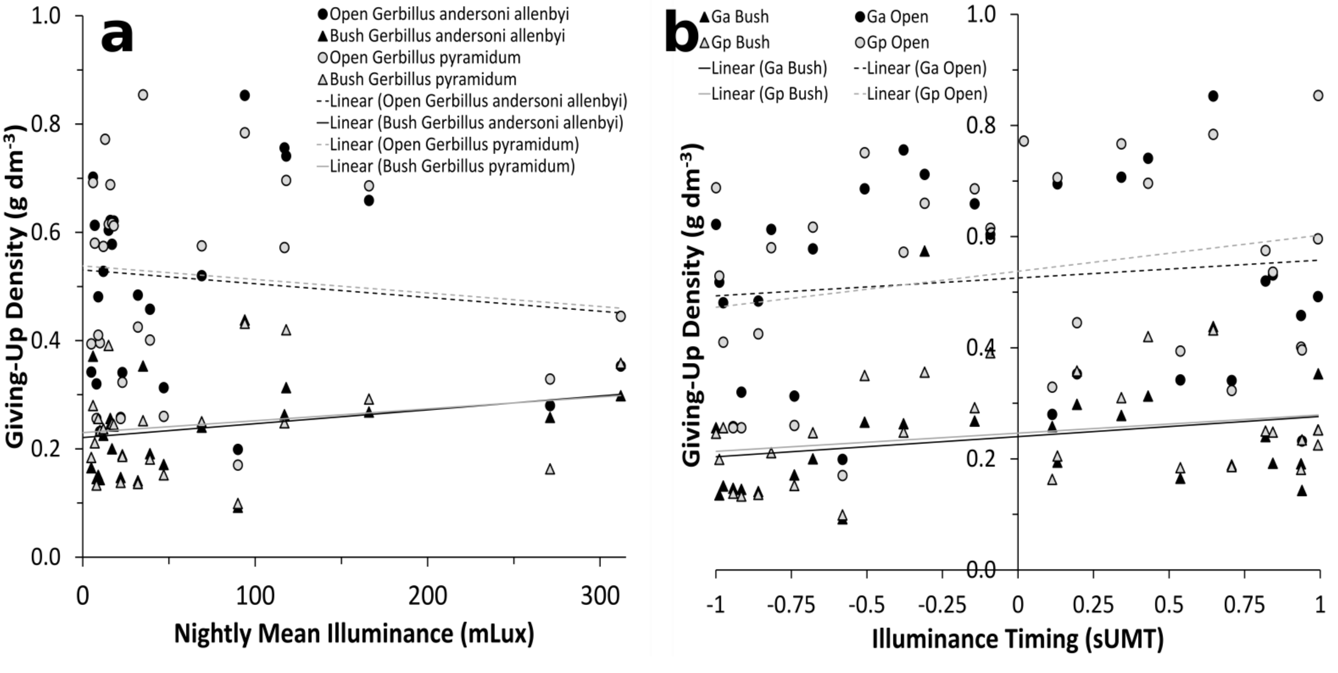

Fig. 7 *Giving-up densities showing the interaction of a) microhabitat (Bush / Open), average nightly lunar illuminance, and rodent species (*Gerbillus andersoni allenbyi / G. pyramidum*) and b) microhabitat, rodent species, and the timing of lunar illuminance (sUMT) in an artificial community. sUMT is calculated by taking the sine of the moon's upper meridian transit time. Values closer to -1 (18:00) represent illuminance occurring earlier in the night while values closer to 1 (06:00) represent later illuminance. Each point represents a mean value*

treatment, illuminance timing, and rodent species (GLS, $F_{(6,1235)} = 31.76$, $p < 0.001$). *Gerbillus andersoni allenbyi* had higher GUDs when brightness was earlier in the night, except in the presence of SWRS where both *G. andersoni allenbyi* and *G. pyramidum* showed a high rate of increase in GUD as illuminance came later in the night. The combined effect of these two interactions are seen when comparing the lunar cycle (illuminance and its timing) with snake and rodent species (GLS, $F_{(6,1235)} = 4.33$, $p < 0.001$). In the presence of the single species viper treatments (SHV and SWRS), *G. andersoni allenbyi* had lower GUDs during the waning crescent (weaker and later illuminance) while *G. pyramidum* was more efficient the rest of the cycle (Fig. 6). Giving-up densities increased with illuminance and earlier timing in the presence of SHV while GUDs decreased with illuminance and were relatively consistent across timing in the presence of SWRS. This suggests sensory pits may not increase risk by themselves, but rather alter the periods when risk is greatest, thereby changing the forager's behavior and temporal foraging activity patterns.

Giving-up densities were affected by the interaction of microhabitat, illuminance, and rodent species (GLS, $F_{(2,1235)} = 4.75$, $p = 0.009$). *Gerbillus andersoni allenbyi* had lower GUDs except in the bush when illuminance was above ~250 mLux. In the bush, GUDs increased with illuminance for both species, while in the open they decreased (Fig. 7a). Microhabitat and rodent species also interacted significantly with the timing of illuminance (GLS, $F_{(2,1235)} = 5.54$, $p = 0.004$). Here, *G. andersoni allenbyi* had the lowest GUDs except when illuminance in the open occurred early in the night. Both species and microhabitats showed GUDs increasing as illuminance occurred later (Fig. 7b). This suggests that rodents may exploit open microhabitats based on timing of when in the night the risk occurs, while they may exploit bush microhabitats based on how much light is penetrating through the foliage.

3.1.2. C. penicillatus *and* G. andersoni allenbyi

Tracking data for the last rodent visiting the tray in the *C. penicillatus* and *G. andersoni allenbyi* experiment agreed with RFID readings 82% of the time, suggesting results to be reliable. Rodents in this experiment responded as expected by increasing GUDs in the presence of owls (ANCOVA, $F_{(1,644)} = 3.63$, $p = 0.057$), in open microhabitats (ANCOVA, $F_{(1,644)} = 11.04$, $p < 0.001$), with increasing illuminance (ANCOVA, $F_{(1,644)} = 9.47$, $p = 0.002$), with later illuminance (ANCOVA, $F_{(1,644)} = 27.52$, $p < 0.001$), and in the presence of snakes (ANCOVA, $F_{(3,644)} = 4.46$, $p = 0.004$). Although GUDS for only the SHV (Tukey, $p < 0.001$) and BOTH (Tukey, $p = 0.034$) snake treatments were significantly greater than for NONE, giving-up densities were significantly lower in the presence of SWRS than SHV (Tukey, $p = 0.012$).

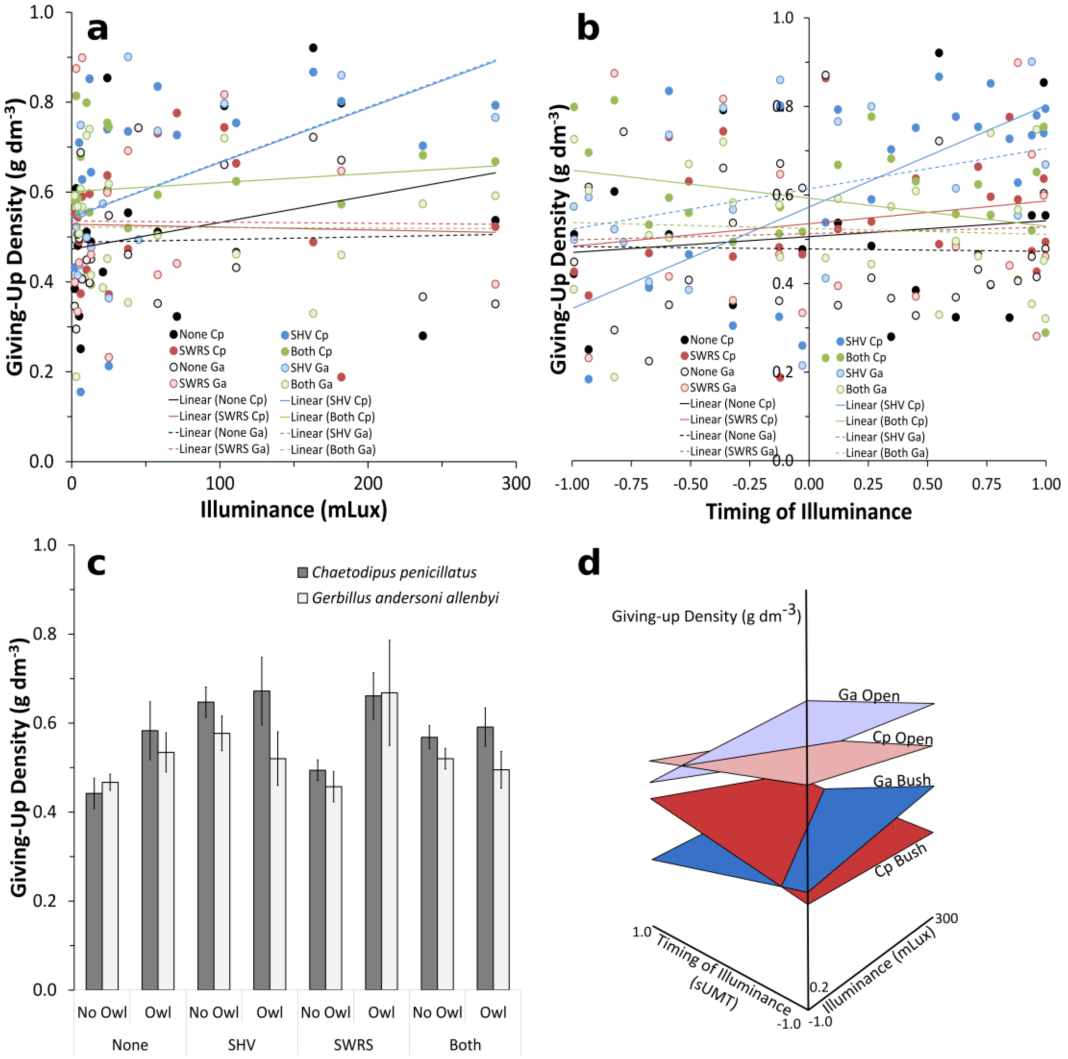

Fig. 8 *Giving-up densities showing the interactions of rodent species (Cp =* Chaetodipus penicillatus*, Ga =* Gerbillus andersoni allenbyi*) with a) lunar illuminance and viper treatment, b) the timing of lunar illuminance (sUMT) and viper treatment, c) owl presence and viper treatment, and d) microhabitat (bush/open), lunar illuminance, and its timing. Viper treatments include no vipers (None), two sidewinder rattlesnakes (SWRS;* Crotalus cerastes*), two Saharan horned vipers (SHV;* Cerastes cerastes*), and one SWRS with one SHV (Both). sUMT is calculated by taking the sine of the moon's upper meridian transit time. Values closer to -1 (18:00) represent illuminance occurring earlier in the night while values closer to 1 (06:00) represent later illuminance. Points represents a mean value and planes represent a linearly regression of mean points*

Chaetodipus penicillatus had marginally lower GUDs than *G. andersoni allenbyi* when illuminance was early in the night and increased its GUD as illuminance came later at night (ANCOVA, $F_{(1,644)} = 3.68$, $p = 0.056$). Alternatively, *G. andersoni allenbyi* decreased its GUD as illuminance came later in the night. The interaction of illuminance, its timing, and rodent species showed a tradeoff in foraging efficiency (lower GUDs being most efficient) along the axis of illuminance timing while both species increased their GUD with increasing illuminance (ANCOVA, $F_{(2,644)} = 4.18$, $p = 0.016$). Foraging costs were also affected by the interaction of viper treatment, rodent species, and illuminance (Fig. 8a; ANCOVA, $F_{(6,644)} = 3.82$, $p < 0.001$). Here, GUDs increased in both rodent species at a greater rate in the presence of SHV, while the presence of SWRS was relatively constant or even declining as illuminance became brighter. Similarly, rodents (especially *G. andersoni allenbyi*) in the presence of SHV changed their GUDs at a much greater rate as illuminance came later in the night (Fig. 8b; ANCOVA, $F_{(6,644)} = 5.50$, $p < 0.001$). Most importantly, *Gerbillus andersoni allenbyi* had lower GUDs than *C. penicillatus* in almost every case when predators were present (Fig. 8c; ANCOVA, $F_{(6,644)} = 2.35$, $p = 0.030$). This was particularly true when its natural SHV and barn owl predators were present. When the novel SWRS and natural owl predators were present, *G. andersoni allenbyi* increased its GUDs to a comparable level with *C. penicillatus*, which had the lowest GUD when no predators were present.

Rodents also increased their GUDs in open microhabitats (ANCOVA, $F_{(1,644)} = 11.04$, $p < 0.001$) where both species had similar GUDs. However, in bush microhabitats *G. andersoni allenbyi* had marginally lower GUDs than *C. penicillatus* (ANCOVA, $F_{(1,644)} = 4.10$, $p = 0.043$). This interaction combined with Illuminance showed that *C. penicillatus* increased their GUDs at a lower rate in the bush while *G. andersoni allenbyi* did so at a lower rate in the open (ANCOVA, $F_{(2,644)} = 8.69$, $p < 0.001$). However, *G. andersoni allenbyi* still had lower GUDs than its competitor in the bush while *C. penicillatus* showed lower GUDs in the open. Species showed that *C. penicillatus* showed little change in GUDs with the timing of illuminance in the open habitat, although in the bush, GUDs increased as illuminance became later (timing of illuminance X habitat X rodent species; ANCOVA, $F_{(2,644)} = 13.29$, $p < 0.001$). Alternatively, *G. andersoni allenbyi* GUDs did not alter its GUD in the bush with changing timing of illuminance, but in the open GUDs decreased as illuminance became later in the night suggesting potential temporal partitioning. The interactions of illuminance and its timing combined with habitat and rodent species was significant, continuing to show the general trends of *C. penicillatus* being most efficient during the waxing moon and *G. andersoni allenbyi* in the waning moon (Fig. 8d; ANCOVA, $F_{(2,644)} = 10.90$, $p < 0.001$).

3.1.3. D. merriami *and* G. pyramidum

The ability to distinguish the last rodent foraging agreed with the RFID system 48.9% of the time, which should be taken under consideration when interpreting the result from this experiment. *Dipodomys merriami* had slightly lower GUDs (0.376 ± 0.238 g dm^{-3}) than *G. pyramidum* (0.389 ± 0.233 g dm^{-3}; ANCOVA, $F_{(1,830)} = 4.72$, $p = 0.030$). Both species increased GUDs as illuminance increased (ANCOVA, $F_{(1,830)} = 5.87$, $p = 0.016$), however, *G. pyramidum* did so at a greater rate and was the more efficient forager below nightly mean illuminances of ~100 mLux. With the timing of illuminance, *G. pyramidum* increased its GUD at a lower rate than *D. merriami* (ANCOVA, $F_{(1,830)} = 9.07$, $p = 0.003$). *Dipodomys merriami* was the more efficient forager when illuminance occurred earlier in the night. The lunar cycle (illuminance and its timing) significantly interacted with species to show that *D. merriami* dominated the waxing gibbous portion of the lunar cycle and *G. pyramidum* the waning crescent portion (ANCOVA, $F_{(2,830)} = 10.36$, $p < 0.001$).

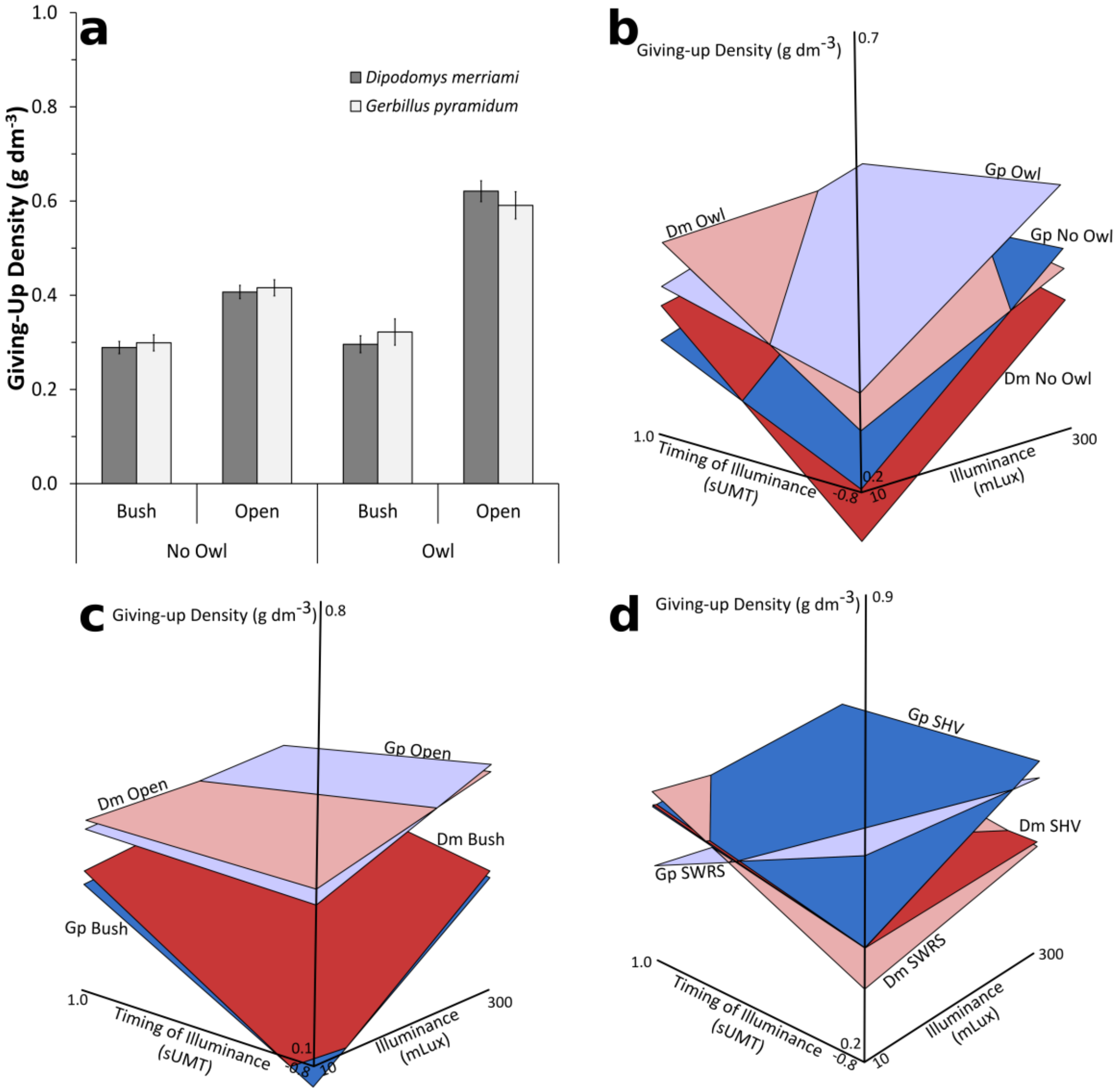

Fig. 9 *Giving-up densities showing the interactions of rodent species (Dm =* Dipodomys merriami, *Gp =* Gerbillus pyramidum*) with a) microhabitat and owl presence, b) lunar brightness, its timing, and owl presence, c) lunar brightness, its timing, and microhabitat, and d) lunar brightness, its timing, and homogeneous viper treatments (SHV = Saharan horned viper, SWRS = Sidewinder Rattlesnake). sUMT is calculated by taking the sine of the moon's upper meridian transit time. Values closer to -1 (18:00) represent illuminance occurring earlier in the night while values closer to 1 (06:00) represent later illuminance*

Giving-up densities without snakes (0.313 ± 0.227 g dm^{-3}) were significantly lower (ANCOVA, $F_{(3,830)} = 21.42$, $p < 0.001$) than in the presence of SHV (Tukey, $p < 0.001$; 0.469 ± 0.234 g dm^{-3}) and SWRS (Tukey, $p < 0.001$; 0.437 ± 0.236 g dm^{-3}), but similar to BOTH (Tukey, $p < 1.000$) where snake activity appeared much lower. *Dipodomys merriami* responded similarly to both SHV and SWRS viper treatments by increasing its GUD, but changed at a lower rate as illuminance increases (ANCOVA, $F_{(6,830)} = 3.29$, $p = 0.003$). *Gerbillus pyramidum*'s response to SWRS was similar to *D. merriami*, but it increased its GUD at a much greater rate in the presence of SHV. The response of *D. merriami* to the timing of illuminance did not change in the presence of SHV or SWRS (ANCOVA, $F_{(6,830)} = 4.79$, $p < 0.001$). However, *G. pyramidum* increased its GUD at a similar rate as illuminance came later in both the absence and presence of SHV. In the presence of SWRS, its GUDs remained constant regardless of the timing of illuminance suggesting it may be responding to the sensory pits of SWRS. These trends were also observed in the interaction of illuminance, its timing, viper treatment, and rodent species, which significantly affected GUDs (Fig. 9d; ANCOVA, $F_{(6,830)} = 6.45$, $p < 0.001$).

Open microhabitats increased GUDs (ANCOVA, $F_{(1,830)} = 8.58$, $p = 0.003$) and contained lower rates of increase for both species as illuminance came later (ANCOVA, $F_{(2,830)} = 4.55$, $p = 0.011$). In the open, *D. merriami* had lower GUDs when illuminance was earlier, while *G. pyramidum* had lower GUDs when illuminance was later and in bush microhabitats. The interaction of illuminance, its timing, microhabitat, and rodent species was also significant (Fig. 9c; ANCOVA, $F_{(2,830)} = 8.20$, $p < 0.001$), showing *D. pyramidum* had slightly lower GUDs during gibbous portions of the lunar cycle. Microhabitat, owl presence, and rodent species interacted affecting GUDs, although no trends stood out (Fig. 9a; ANCOVA, $F_{(2,830)} = 17.13$, $p < 0.001$). The interaction of the lunar cycle, owl presence, and rodent species was also significant, but did not show any clear trends (Fig. 9b; ANCOVA, $F_{(2,830)} = 5.52$, $p = 0.004$).

3.2.0. Personality Results: Variations in risk management between gerbils (*Gerbillus andersoni allenbyi*) with different exploratory/ boldness behaviors

3.2.1. Giving-up density results

As has been shown previously, these gerbils respond to risk factors of microhabitat, the lunar cycle, and owls. Gerbils had higher GUDs in the open microhabitats ($F_{(1,1291)} = 663.74$, $p < 0.001$) where they are more exposed to predators. Higher GUDs were also measured when greater illuminance was present ($F_{(1,1291)} = 1113.70$, $p < 0.001$) and when this illuminance occurred later in the night ($F_{(1,1291)} = 198.12$, $p < 0.001$), exposing the game between risk and energetic state (Kotler et al. 2010). The presence of owl was marginally significant ($F_{(1,1291)} = 2.88$, $p = 0.090$), suggesting that GUDs increased when owls were present.

Exploratory behavior type affected patch use. In regards to giving-up densities, bolder individuals had lower GUDs (Fig. 10a; Strong Bold: 0.524 ± 0.280; Weak Bold: 0.533 ± 0.269; Weak Shy: 0.568 ± 0.282; Strong Shy: 0.574 ± 0.287; $F_{(3,1291)} = 13.57$, $p < 0.001$), i.e., they exploited patches more thoroughly and left them at lower quitting harvest rates under the same ecological conditions. These values produce an increasing GUD gradient as individuals become less exploratory/ shyer. Thus, exploratory behavior helps determine an ecologically relevant behavior.

In addition, exploratory behavior affected how individuals responded to the various risk factors. The interaction of exploratory behavior and microhabitat showed different responses based on behavioral

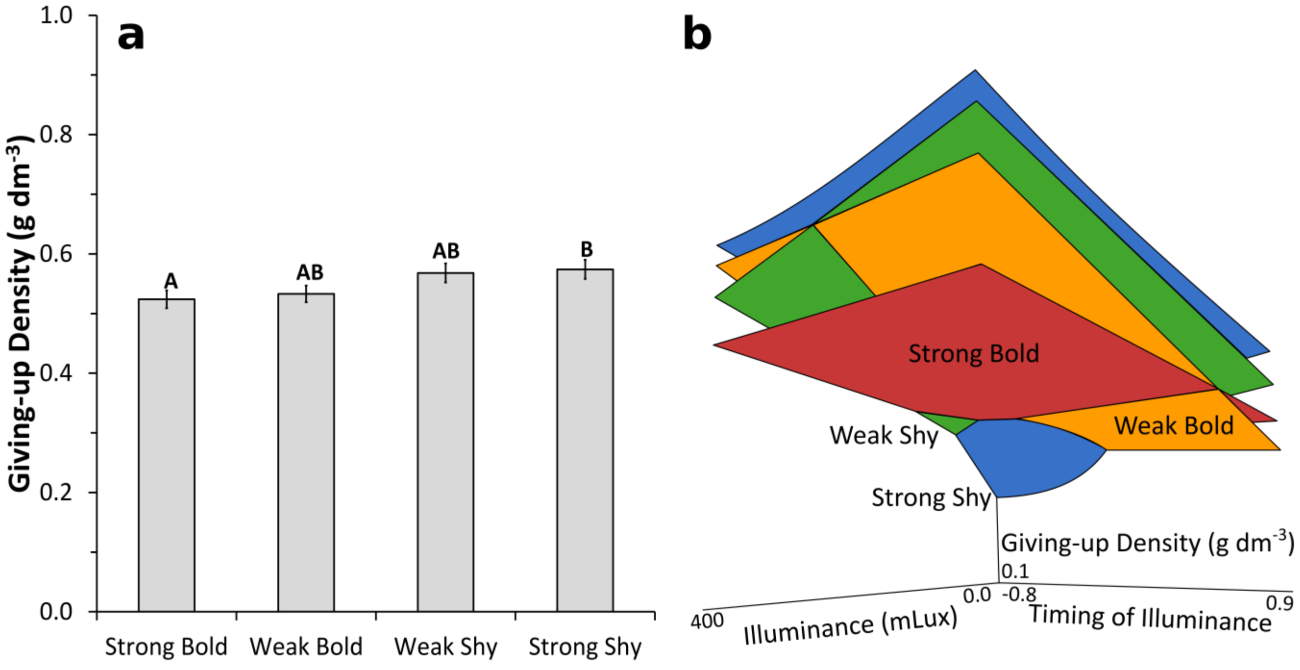

Fig. 10 *Giving-up densities of* Gerbillus andersoni allenbyi *from two one month long vivarium experiments with two different sets of rodents. In a), differences in exploratory behavior/ boldness are shown and in b), these giving-up densities are shown across the lunar cycle where each category of exploratory behavior is most efficient during a portion of the cycle. Error bars show standard error*

type ($F_{(3,1291)} = 15.54$, $p < 0.001$). Giving-up densities in the bush microhabitat were unimodal across the spectrum of exploratory behaviors, where stronger exploratory behaviors (especially bold) had the lowest GUDs. Alternatively, GUDs in the open were bimodal across the spectrum of exploratory behavior, with strong exploratory behavioral types exhibiting the highest GUDs. Although each behavioral type increased its GUD with increasing illuminance, the shyer groups did so at a greater rate than bolder groups ($F_{(3,1291)} = 41.11$, $p < 0.001$). Illuminance timing also affected each exploratory behavioral type differently ($F_{(3,1291)} = 14.20$, $p < 0.001$). Bolder types were most efficient when illuminance occurred later in the night and increased their GUD as it became earlier. Shyer types did the opposite, with lower GUDs when illuminance was earlier suggesting there might be temporal preferences for when each type prefers to forage since they are known to avoid illuminance. Owl presence produced similar GUDs across all exploratory behavior

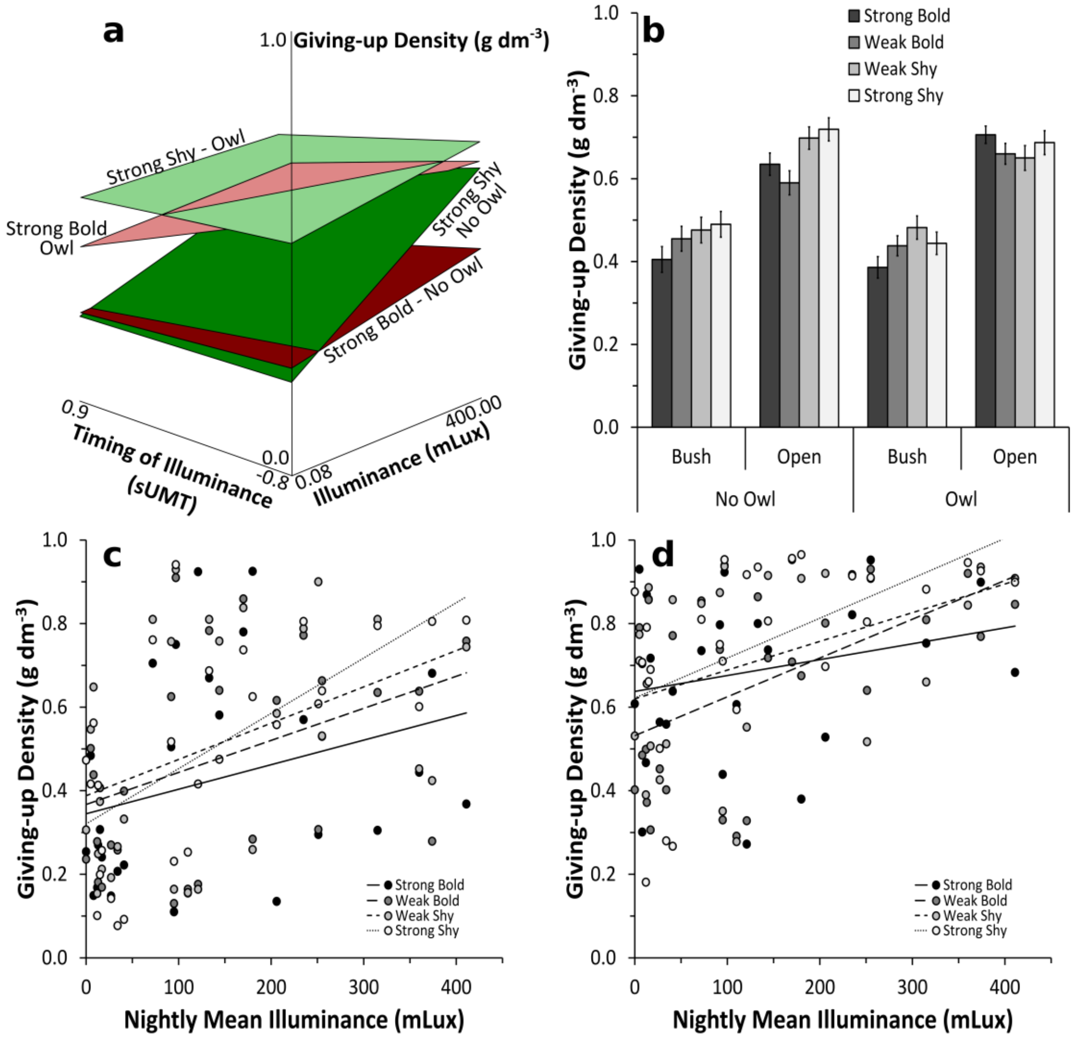

Fig. 11 *Giving-up densities of* Gerbillus andersoni allenbyi *exploratory behavior interacting with a) microhabitat, illuminance, and the timing of illuminance, b) microhabitat and owl presence, c) bush microhabitat and illuminance and d) open microhabitat and illuminance. More exploratory behaviors are labeled bold and lesser as shy. Values for the timing of illuminance nearing -1 represent illuminance occurring earlier in the night while values approaching 1 represent later illuminance. Due to the complexity, 3-dimensional plots only include strong behaviors to make them easier to read. Error bars show standard error*

types, but when absent, bolder types had significantly lower GUDs than shyer types ($F_{(3,1291)} = 12.23$, $p < 0.001$).

Personality types also affected how gerbils responded to the interaction of the risk factors. Owl, habitat, and exploratory behavior interacted significantly ($F_{(4,1291)} = 2.84$, $p = 0.023$), showing bolder types to have the lower GUDs when the owl is absent and lower GUDs in the bush microhabitat only compared to shyer types when owls are present. When risk is higher (i.e. open microhabitat with owls present), a bimodal distribution occurs where strong types have higher GUDs and weak types are most efficient (Fig. 11b).

The timing of illuminance, owl presence, and exploratory behavior also interacted significantly ($F_{(4,1291)} = 7.01$, $p < 0.001$). When owls were absent, bolder types were more efficient when illuminance was later and shyer types when it was earlier (same as above). However, when owls were present, all exploratory behavioral types, but especially shyer types, increased their GUDs as illuminance came later in the night.

Microhabitat, illuminance, and personality interacted significantly ($F_{(4,1291)} = 3.46$, $p = 0.008$). In the bush, strongly shy individuals were the most efficient when dark and least efficient forager when illuminance was above ~150 mLux (Fig. 11c). Weakly bold individuals dominated darker nights in open microhabitats while strongly bold dominated brighter ones (Fig. 11d). These results suggest shyer individuals are better under direct risk while microhabitat may also offer an avenue for weaker personalities to coexist.

The interaction of personality, illuminance, and its timing showed each exploratory behavioral type possessed the lowest GUD during a portion of the lunar cycle (Fig. 10b; $F_{(4,1291)} = 48.17$, $p < 0.001$). Strongly shy individuals were most efficient in the waxing crescent (early dim illuminance) while strongly bold individuals dominated the waning gibbous (late bright illuminance) and pushed into surrounding phases. Weakly bold individuals were most efficient in the waning crescent (late dim illuminance), and weakly shy individuals had the mid-portions of the waxing gibbous moon (early bright illuminance). These tradeoffs during the lunar cycle appear to provide the conditions necessary for the coexistence of each behavioral type.

A significant interaction between owl presence, illuminance, the timing of illuminance, and personality also occurred (Fig. 11a; $F_{(4,1291)} = 4.64$, $p = 0.001$) showing a shift in the portion of the lunar cycle dominated with the presence and absence of owls. Shyer individuals dominated the darker crescent moon when owls are absent, but only the waxing crescent when owls are present. These results show that different exploratory behavioral types possess different foraging costs and responses to interacting risks.

3.2.2. Husk results

The proportion of seeds husked in the tray decreased with owl presence ($F_{(1,1289)} = 9.93$, $p = 0.002$) and in open habitat ($F_{(1,1289)} = 92.09$, $p < 0.001$) but increased with increasing illuminance ($F_{(1,1289)} = 8.57$, $p = 0.003$). Personalities formed a unimodal distribution with weakly bold individuals husking the most and strongly bold individuals husking the least (Fig. 12a; $F_{(3,1289)} = 98.02$, $p < 0.001$). Although strongly bold individuals had the lowest overall GUD (harvested the most seeds), they husked the lowest proportion, suggesting they grab seeds and cache or husk them elsewhere. Husking in the tray increased with illuminance in all behaviors ($F_{(3,1289)} = 4.30$, $p = 0.005$). Our results suggest that bolder individuals forage earlier and shyer later based on bolder individuals husking greater proportions when illuminance occurs earlier and shyer individuals husking more when illuminance occurs later ($F_{(3,1289)} = 16.08$, $p < 0.001$). This temporal partitioning is inferred by comparing the response to illuminance with the response to the timing of illuminance. For example, husking increases with illuminance, so when husking increases

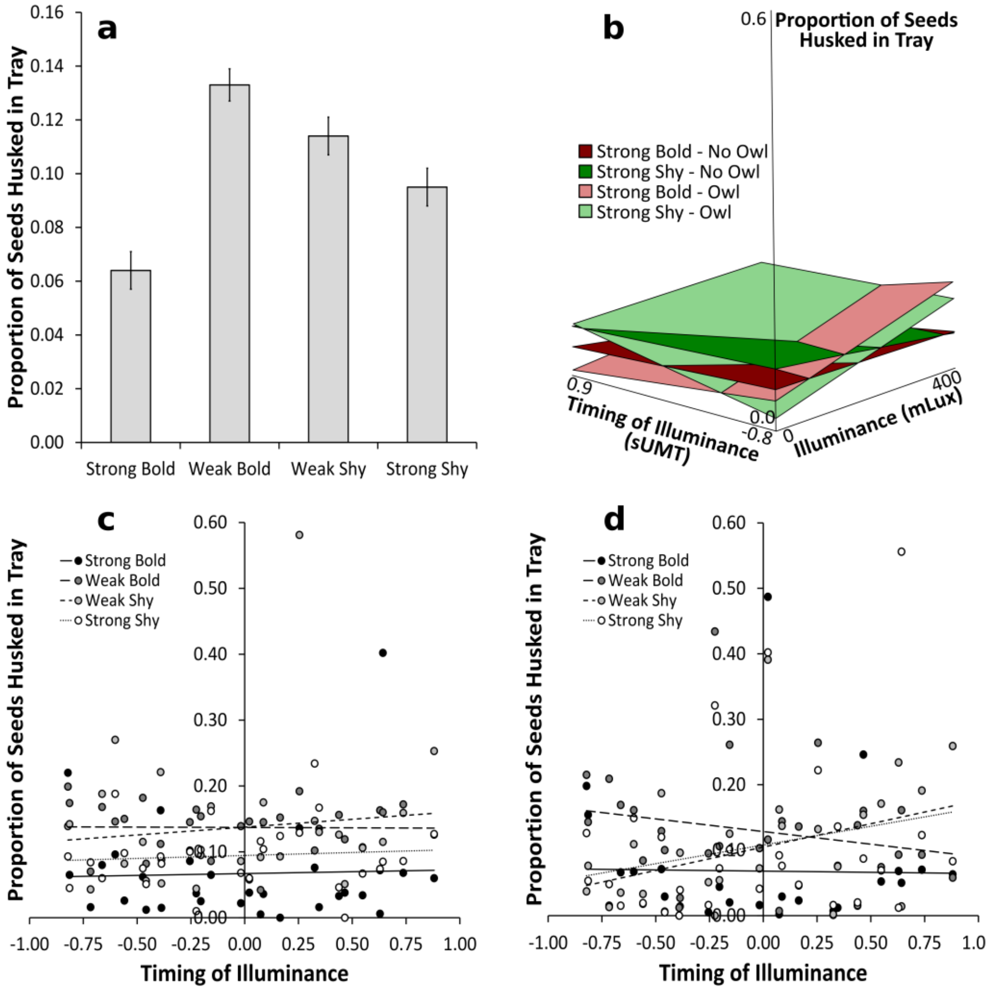

Fig. 12 *a) Proportion of seeds husked in the tray by* Gerbillus andersoni allenbyi *of differing exploratory behaviors (bolder is more exploratory). Subsequent plots show the interactions of exploratory behavior with b) owl presence, illuminance, and timing of illuminance c) bush microhabitat and timing of illuminance and d) open microhabitat and timing of illuminance. Values for the timing of illuminance nearing -1 represent illuminance occurring earlier in the night while values approaching 1 represent later illuminance. Due to the complexity, 3-dimensional plots only include strong behaviors to make them easier to read. Error bars show standard error*

with the timing of illuminance, it may be a result of the animal's increased presence. Lunar illuminance, its timing, and exploratory behavior interacted together significantly ($F_{(4,1289)} = 4.93$, $p < 0.001$) although no obvious trends appear.

The presence of owls decreased the proportion of seeds husked in the trays exploited by gerbils with strong exploratory behavior ($F_{(4,1289)} = 3.95$, $p = 0.003$) and also interacted with the lunar cycle (Fig. 12b; $F_{(4,1289)} = 6.65$, $p < 0.001$). When owls were present, the proportion of seeds husked increased at a greater rate with increasing illuminance than when owls were absent. Additionally, when owls were absent, the tradeoff between bolder and shyer individuals over the timing of illuminance disappeared.

Although significant, no trends were apparent from the habitat and personality interaction ($F_{(3,1289)} = 3.99$, $p = 0.008$), but their interaction with the timing of illuminance also showed the removal of the tradeoff between bold and shy in bush microhabitats (Fig. 13c,d; $F_{(4,1289)} = 3.19$, $p = 0.013$). These last results may suggest that husking in trays may be an anti-predator behavior that reduces movement and the risk of being detected.

3.2.3. Patch visit results

The probability of visiting a patch decreased significantly in the open (Logistic, $X^2_{(1,1447)} = 21.56$, $p < 0.001$), when owls were present (Logistic, $X^2_{(1,1447)} = 21.56$, $p < 0.001$), with increasing illuminance (Logistic, $X^2_{(1,1447)} = 14.50$, $p < 0.001$), and when illuminance occurred earlier (Logistic, $X^2_{(1,1447)} = 7.19$, $p = 0.007$). The interaction of personality, illuminance, and its timing was significant (Logistic, $X^2_{(4,1447)} = 12.64$, $p = 0.013$), but did not show any clear trends.

3.2.4. Harvest Rate Curves

Overall, GUD trays averaged 1660.6 ± 1441.8 s of rodents foraging per night, with 38.6 ± 33.9 visits, each averaging 41.0 ± 24.3 s per visit. Trays visited by strongly shy types averaged 1598.6 ± 1597.3 s of foraging per night with an average of 37.9 ± 36.2 visits each averaging 36.9 ± 20.3 s. The trays foraged by strongly bold types averaged more foraging time (1753.9 ± 1674.4 s) per night, a greater average number of visits (45.0 ± 44.6), but shorter average visits (34.5 ± 16.7 s) than shyer types. This supports bolder types foraging more, but for shorter periods, while shyer types spent more time per visit, but less time overall.

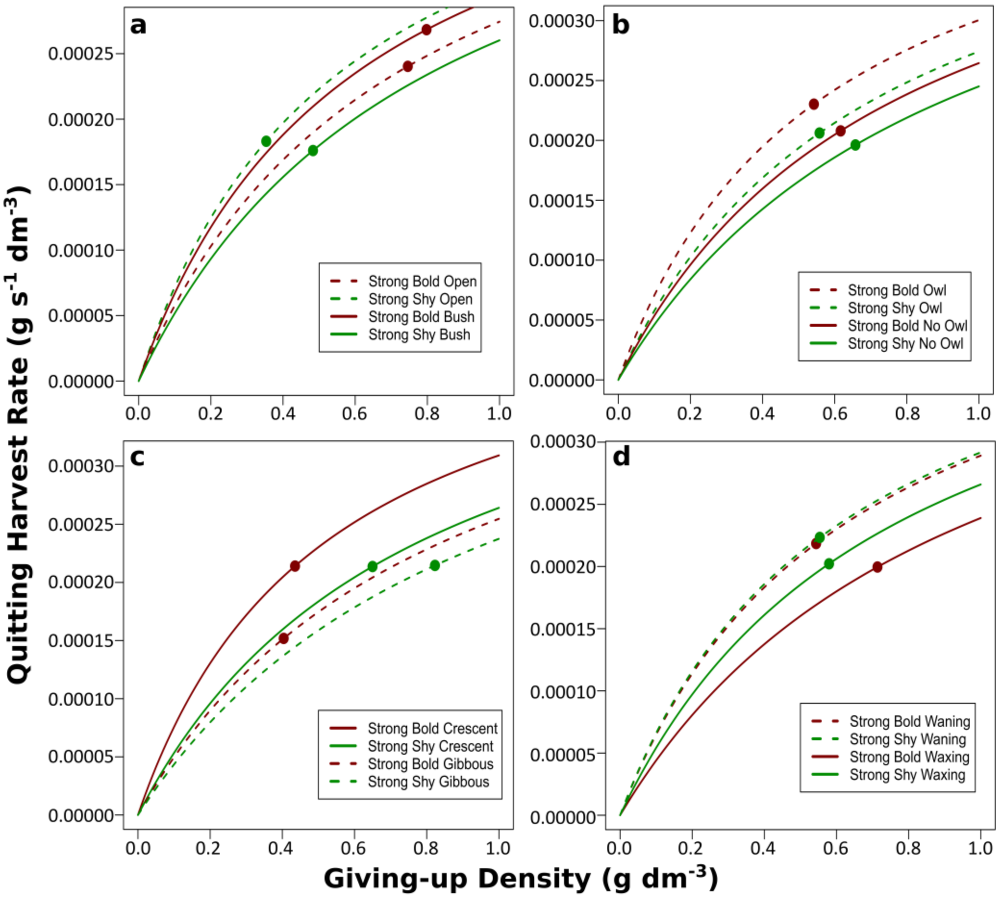

Fig. 13 *Harvest rate curves of more (strongly bold) and less (strongly shy) exploratory behavior in Gerbillus andersoni allenbyi. These show differences in time allocation and vigilance by the behavioral types when interacting with a) microhabitat, b) owl presence, c) lunar brightness, and d) the timing of lunar brightness. Vigilance is changes in giving-up densities (the point) along the x-axis while time allocation is seen by changes along the y-axis (Kotler et al. 2010)*

Comparisons of the harvest rate curves show differences in time allocation (point closer to the origin indicates more time) and vigilance (shallower curve indicates more vigilance) between strongly bold and strongly shy individuals. Bold types had GUDs occurring higher along the y-axis, implying higher quitting harvest rates (QHR) in both bush and open microhabitats than shyer types. Shy types used mostly differences in vigilance (i.e. shallower or steeper curves) while bold individuals used primarily time allocation (i.e. GUD occurring closer to or farther from the origin) to mitigate risk between bush and open microhabitats (Fig. 13a). In the presence of owls, both bold and shy individuals behaved similarly, using a combination of time allocation and vigilance (Fig. 13b). Response to lunar brightness (gibbous vs. crescent) showed similar results to microhabitat, with bold individuals using time allocation and shy individuals using vigilance (Fig. 13c). Combinations of time allocation and vigilance were also used for lunar timing (waxing vs. waning), although bolder individuals showed a greater shift in vigilance than shy individuals (Fig. 13d).

3.2.5. Body Mass Loss

Strongly bold individuals lost significantly less proportion of body mass than weakly shy (Tukey, p

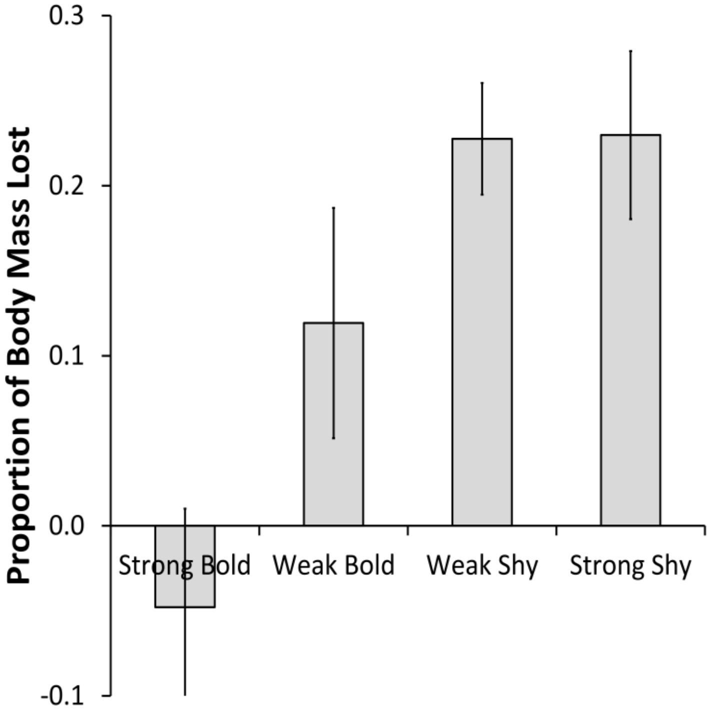

Fig. 14 *Proportion of* Gerbillus andersoni allenbyi *body mass lost in vivarium experiments. Negative values represent a gain in body mass and error bars show standard error*

= 0.019) and strongly shy (Tukey, p = 0.012) individuals (Fig. 14; ANOVA, $F_{(3,15)} = 5.58$, p = 0.009). In fact, strongly bold individuals increased in mass (0.05 ± 0.13 increase) while weakly bold lost less (0.12 ± 0.15 loss). Weakly shy (0.23 ± 0.07 loss) and strongly shy (0.22 ± 0.11 loss) individuals lost the greatest proportion of mass during the study.

<u>3.3.0. Theoretical Results</u>: Patch use as an indicator of habitat preference, predation risk, and competition across space and time

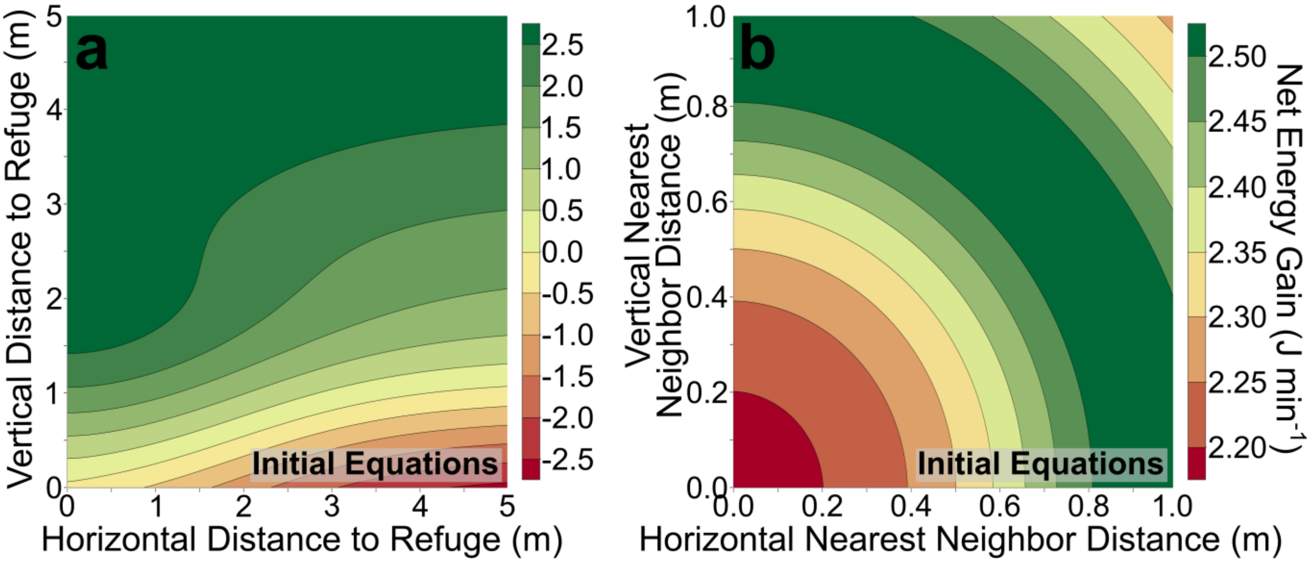

Fig. 3 *Initial model results for planktivorous fish using a spatial patch use equation to determine net energy gained from a forager's a) distance from refuge and b) nearest neighbor distance. When modelling distance to refuge, nearest neighbor distance was held constant at 0.25 m and when modelling nearest neighbor distance, distance to refuge was constant at 1.2 m*

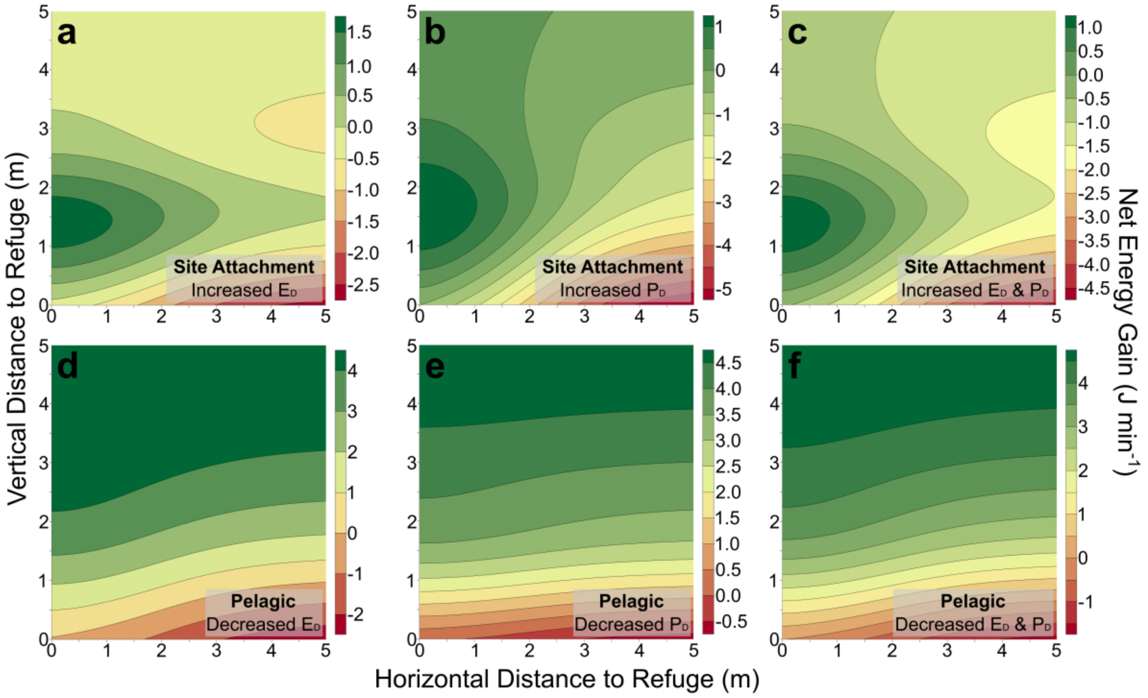

Fig. 15 *By increasing or decreasing certain costs of the initial patch use equation modeled in Fig. 4, site attached and pelagic lifestyles can be inferred by assuming planktivorous fish will forage where net energy gain is maximized. Increases in a) energetic costs, b) predation costs, and c) both energy and predation costs produced heat maps indicative of site attachment while decreases in d) energetic costs, e) predation costs, and f) both energy and predation costs produced a heat map indicative of a pelagic lifestyle*

The non-manipulated base equations shows foragers with a mix between pelagic and site attached distributions in the environment (Fig. 3a) while keeping a distance of 1 m to neighbors (Fig. 3b). The increase of energetic (E_D) and/or predation (P_D) costs supported our predictions by creating heat maps more indicative of site attachment (Fig. 15a,b,c). When the optimal position in each was ~1-2 m above the refuge, positions with positive net energetic gains for increased E_D were elongated horizontally (Fig. 15a). Alternatively, increased P_D produced a vertical elongation of positive net energy gain (Fig. 15b). The combination of increased energetic (E_D) and predation (P_D) costs produced the most indicative heat map of site attachment where foragers are only present in a small area above the refuge (Fig. 15c). Pelagic environmental distributions were produced, as predicted, when energetic (E_D) and/or predation (P_D) costs were reduced (Fig. 15d,e,f). Results here were all very similar with positive net energy gain starting within the first meter and maximum net energy gain around 3 m and above.

The model also produced expected results demonstrating how changes in the energetic cost of interactions (E_C), cost of isolation (I), and the energetic gain from interactions (H_C) create more solitary or aggregate distributions (Fig. 16). Increases in the energetic cost of interactions (E_C) increased the optimal nearest neighbor distance to ~1.2 m while having positive net energy gain up to 0.8 m from each other (Fig. 16a). Similarly, a decrease in the cost of isolation (I) pushed individuals farther apart, although, all mapped distances between fish had a positive net energy gain (Fig. 16b). Aggregation was predicted by the model when the energy gain from interactions (H_C) increased (Fig. 16c), the cost of isolation (I) increased (Fig.

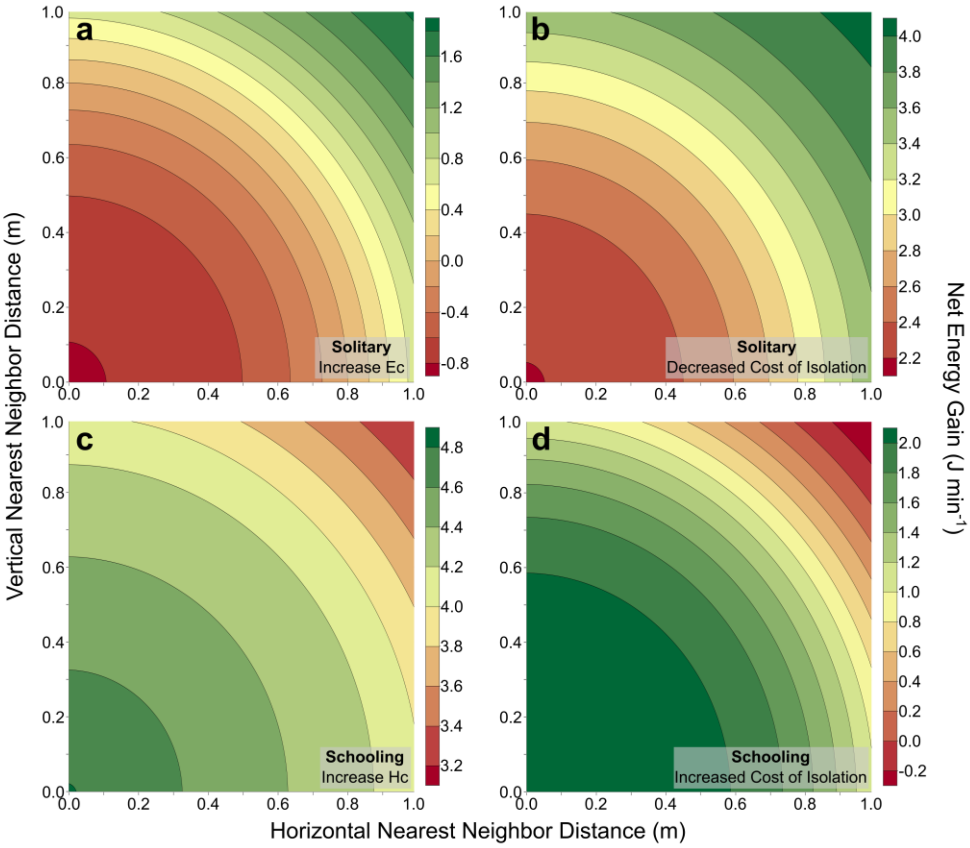

Fig. 16 *Using a spatial patch use equation, planktivorous fish could be shown to school more closely when a) the energy gains were greater than the costs of forager interactions or b) when the cost of being isolated was high. Similarly, a more solitary distribution is predicted when c) energy costs are greater than energy gains from forager interactions or d) when the cost of isolation is low*

16d), and the energetic cost of interactions decreased. These results demonstrate that relatively small changes (Table 4) in foraging costs may be able to produce the many different distributions across the environment and between individuals observed in nature.

<u>3.4.0. Damselfish Results</u>: A mechanistic approach to understanding the spatial structure of site attached planktivores

Fifty-seven 5-minute periods of fish foraging outside the coral were collected from seven different runs totaling 475 minutes and averaging 67.8 ± 44.6 minutes each. During these runs, current magnitudes ranged from 0.01 to 0.17 m s^{-1}, averaging 0.08 ± 0.05 m s^{-1}. Prey densities ranged from 310 to 3,049 individuals m^{-3} with an average of 1,030 ± 542 individuals m^{-3}. These two environmental conditions were significantly correlated (Pearson's, t = 7.23, df = 89, $p < 0.001$, r = 0.608), suggesting an association between zooplankton abundance and current magnitude rather than only an increased prey flux. Fluxes produced by these currents and densities ranged between 2 to 327 individuals s^{-1} m^{-2} and averaged 93 ± 89 individuals s^{-1} m^{-2}.

The probability of finding fish outside the coral buffer increased significantly with increasing current magnitude (Logistic, $\beta_{(1,70)} = 62.2$, $p < 0.001$), prey density (Logistic, $\beta_{(1,70)} = 0.0012$, p = 0.018), and prey flux (Logistic, $\beta_{(1,70)} = 0.0286$, $p < 0.001$), suggesting their activities outside the refuge relate to foraging and prey availability. Equal probability of being inside or outside the coral occurred when the current was at 0.06 m s^{-1}, prey density was 914 individuals m^{-3}, and prey flux was 59 individuals m^{-2} s^{-1}. Below these thresholds, *D. marginatus* was more likely to remain in the coral and above these thresholds, more likely to be seen outside the coral.

Dascyllus marginatus significantly decreased their 3-dimensional distance to refuge as current magnitude (ANCOVA, $F_{(1,53)} = 4.61$, p = 0.036) and prey flux (ANCOVA, $F_{(1,53)} = 4.12$, p = 0.048) increased. However, an increase in prey density only resulted in a marginally significant decrease (ANCOVA, $F_{(1,53)} = 3.14$, p = 0.082; Fig. 17a). These decreases of 3-dimensional distance to refuge indicate overall decreases in predation costs (via distance to refuge) and possibly energetic costs (via the vertical current gradient). Three dimensional nearest neighbor distances increased significantly with increasing prey density (ANCOVA, $F_{(1,30)} = 7.33$, p = 0.011; Fig. 17a), current magnitude (ANCOVA, $F_{(1,30)} = 12.05$, p = 0.002), and prey flux (ANCOVA, $F_{(1,30)} = 14.23$, $p < 0.001$), indicating an increase in isolation costs and a decrease in competition costs. These 3-D movements with increasing patch richness show fish favored safety by decreasing their distance to refuge. However, fish also increased predation risk by moving further apart from each other, indicating a more complex interplay.

When examining foraging behavior along the vertical axis, *D. marginatus* decreased its vertical distance to refuge with increasing prey density (ANCOVA, $F_{(1,53)} = 17.40$, $p < 0.001$; Fig. 17b), current magnitude (ANCOVA, $F_{(1,53)} = 17.88$, $p < 0.001$), and prey flux (ANCOVA, $F_{(1,53)} = 24.35$, $p < 0.001$). These decreases in distance to refuge along the vertical axis indicate decreases in predation (P_Z) and energetic (E_Z) costs. Energetic gains (H_Z) would also increase, decrease, or remain constant depending upon the steepness of the prey gradient. Vertical nearest neighbor distances did not significantly change in response to increasing prey density (ANCOVA, $F_{(1,30)} = 0.68$, p = 0.416; Fig. 17b), current magnitude

(ANCOVA, F$_{(1,30)}$ = 2.18, p = 0.150), and prey flux (ANCOVA, F$_{(1,30)}$ = 1.70, p = 0.203), suggesting the cost of competition and isolation are not managed along the vertical axis. These results suggest the vertical axis is used to control energy and predation risk.

Along the horizontal plane, *D. marginatus* significantly increased its distance to refuge with increasing prey density (ANCOVA, F$_{(1,53)}$ = 4.14, p = 0.047; Fig. 7c) and prey flux (ANCOVA, F$_{(1,53)}$ = 4.70, p = 0.035) but the increase in current magnitude was only marginally significant (ANCOVA, F$_{(1,53)}$ = 3.30, p = 0.075). This change should not affect the energetic costs as prey, current, and therefore flux, primarily change along the vertical axis within *D. marginatus*' foraging space. The increase in distance indicates an increase in the cost of predation for the fish. However, the overall 3-dimensional decreases in distances indicate the horizontal increase here is less than the vertical decrease. Nearest neighbor distances also increased significantly along the horizontal plane with increasing prey density (ANCOVA, F$_{(1,30)}$ = 7.62, p = 0.010; Fig. 7c), current magnitude (ANCOVA, F$_{(1,30)}$ = 12.81, p = 0.001), and prey flux (ANCOVA, F$_{(1,30)}$ = 14.62, p < 0.001). Such changes indicate reductions in competition costs (C_{XY}) and increases in the isolation costs (I_{XY}). The horizontal axis appears to be used to control for competition, which may also cause a slight increase in horizontal distance to refuge.

Vertical and horizontal slopes of distance to refuge differed significantly with prey density (ANCOVA, F$_{(1,110)}$ = 35.86, p < 0.001), current magnitude (ANCOVA, F$_{(1,110)}$ = 29.82, p < 0.001), and prey flux (ANCOVA, F$_{(1,110)}$ = 41.94, p < 0.001). These results suggest *D. marginatus* uses vertical and horizontal axes differently for distance to refuge.

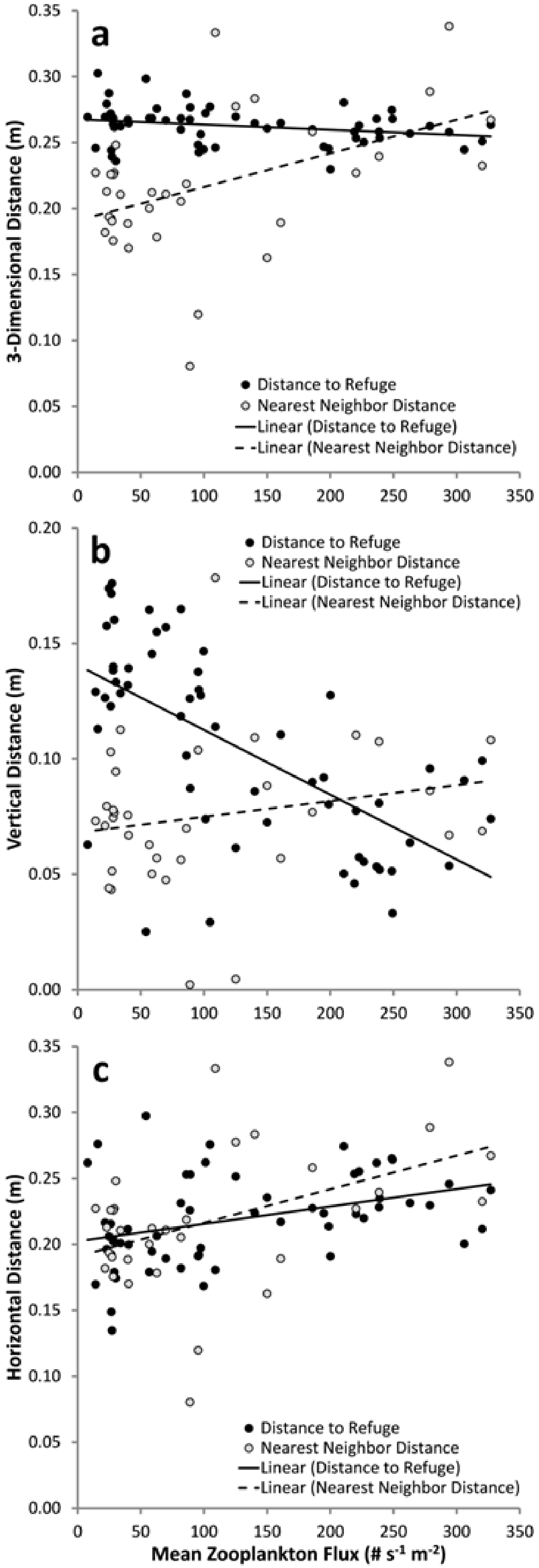

Fig. 17 *Changes in mean distance to refuge and nearest neighbor distance of* Dascyllus marginatus *as zooplankton flux increases. Distances are shown for (a) 3-dimensional space, (b) the vertical axis, and (c) the horizontal plane. Similar trends also occurred with current magnitude and prey density*

4.0.0. DISCUSSION

4.1.0. Desert Rodent Communities Discussion: Effects of constraint breaking adaptations on three experimental desert rodent communities

4.1.1. Gerbillus andersoni allenbyi *and* Gerbillus pyramidum

This study examines the effects of sensory pits in viper predators on a "natural" experimental rodent community of two differently sized rodents exposed to various combinations of risk (i.e. owl, vipers, microhabitat, illuminance). Using giving-up densities, inferences into the mechanisms of coexistence can be discussed by examining community characteristics indicative of certain community structures. For example, along a single axis of heterogeneity, coexistence may occur if each species is the most efficient (lower GUD) along a certain portion of the axis (Kotler and Brown 1988, Brown 1989b); without this tradeoff, the species with the lower GUD should competitively exclude the other (Hardin 1960). The results of this study 1) suggests coexistence can be aided by temporal advantages at different parts of the lunar cycle, according to illuminance and its timing, 2) are consistent with centrifugal community organizations, and 3) demonstrates the ability to recreate many characteristics indicative of natural Gerbilline communities. These results also build from single species experiments to show the effects of interspecific competition on communities and lay the foundation for further experiments focusing on potential constraint breaking adaptations of granivorous desert rodents.

This study is the first to look at rodent giving-up densities as they relate to the lunar cycle's illuminance and the timing of illuminance together. The results suggest that species coexistence may be aided by temporal advantages during different parts of the lunar cycle. Illuminance timing seemed particularly important as *G. andersoni allenbyi* and *G. pyramidum* displayed a tradeoff of foraging efficiencies along this axis of heterogeneity. Such tradeoffs occurring at the scale of a complete lunar cycle may aid coexistence by emphasizing nightly tradeoffs more or less. For example, *G. pyramidum* is known to forage preferred habitats early in the night, thus forcing *G. andersoni allenbyi* later in the night (Ziv et al. 1993). This means that dependent upon the timing of illuminance and the forager's reaction to the magnitude of the brightness, foraging costs can be increased for one species and decreased for the other, allowing more seed to be harvested and state to be replenished (Kotler et al. 2010). Such temporal refuges in resources may aid the stable coexistence in these gerbil species.

The lower GUDs of *G. andersoni allenbyi* in the absence of owls, but lower GUDs of *G. pyramidum* in the presence of owls, regardless of microhabitat (Fig. 5a) is consistent with centrifugal community organizations. Centrifugal organization occurs when preferred habitat (e.g. semi-stabilized dunes) are shared between species, but their secondary habitat preferences (e.g. stabilized dunes and unstabilized dunes) differ (Rosenzweig and Abramsky 1986). Although the stabilized dunes were shown to contain greater foraging costs (Wasserberg et al. 2005), these costs are not necessarily related to predation costs and could include greater competition or energetic costs to obtain resources. If this is the case, the centrifugal organization of these two species may occur due to the differences in ability to mitigate risk and the different levels of risk provided by different levels of shrub cover in the two habitats. In this scenario, *G. andersoni allenbyi* could competitively exclude (due to lower GUDs) *G. pyramidum* in the safer stabilized dunes and *G. pyramidum* could competitively exclude *G. andersoni allenbyi* in the more risky unstabilized dunes while competition dictates the semi-stabilized use.

Sensory pits in the pit vipers were not viewed as creating more risk in themselves, but rather they can lead to more risk during different temporal periods. Previous work showed *G. andersoni allenbyi* did not alter GUDs in response to the two different vipers (Bleicher et al. 2016), however this difference may be due to differences in how the lunar cycle was broken apart in the data analysis. The single species studies compared full and new moon categorically, while this one included illuminance and its timing as continuous variables. Our study shows that pit-vipers are treated by rodents as more dangerous on dark nights while true-vipers are treated so on bright nights. But the timing of this illuminance was also shown to be important. Vipers, although active throughout the night, are likely most active early in the night when temperatures are warmer (Heckrotte 1975, Clark et al. 2016). Our study supports this notion because SWRS with their sensory pits were more risky during the waning moon when dark hours come early and illuminance occurs later in the night. Alternatively, SHV were more risky in the waxing moon when illuminance occurs early in the night. By shifting risk into the darker portions of the lunar cycle, or by being risky throughout the entire lunar cycle, foragers may have no respite from vipers or predators in general. Because of this, communities in the Mojave may have adapted to cope with this risk through mechanisms of microhabitat partitioning (Brown and Lieberman 1973, Kotler 1984a, Brown 1989b) rather than foraging efficiency when respite from risks are present.

Our study also showed evidence that interference competition and body size may also be important in structuring communities. Previous studies showed *G. andersoni allenbyi* preferred treatments with no snakes (Bleicher et al. 2016, Kotler et al. 2016), however, here we find *G. andersoni allenbyi* had its lowest GUDs in the presence of homogeneous viper treatments. This is likely due to interference competition from *G. pyramidum* which can push it into lesser preferred habitats or times (Ziv et al. 1993). Alternatively, *G. andersoni allenbyi* may be better adapted for dealing with viperian threats. Their smaller body size and quadrupedal locomotion may allow *G. andersoni allenbyi* to forage in denser vegetation where snakes are rarely found (Clark et al. 2016). Besides predation costs, the inability of *G. pyramidum*'s larger body side to maneuver within these microhabitats may also reduce the cost of competition for *G. andersoni allenbyi*. These factors may contribute to the importance of body size difference as it relates to microhabitat preference and access to resources.

One possibility for the decrease of GUDs in the presence of vipers may be due to the intense risk of predation and competition throughout this month-long study that likely created relatively high marginal values of energy for the rodents and contrasting risks. This may have pushed rodents to ignore indirect risk cues while responding to the most imminent and lethal risk cues such as the presence of owl (Brown 1999, Cresswell and Quinn 2013). Additionally, viper risk may be actively reduced by rodents through harassment (e.g. hopping up and down and kicking sand) of any encountered viper until it leaves the vicinity. This behavior can also explain why managing multiple risks is difficult. Owls are attracted to rodent activity (Embar et al. 2014a), so defensive activity against snakes likely increases risk from any nearby owls as well as distracting the rodents from detecting those owls. However, *G. pyramidum* did show greater capabilities in mitigating multiple risks, including owls. This could be in part due to larger auditory bullae (Webster 1961, 1962, Nikolai and Bramhle 1983) that allow the larger species to use hearing to better detect the low auditory frequencies generated by the wingbeats of attacking owls. Thus body size in itself cannot only be important for interference competition, but also the ability to detect, avoid, and evade multiple types of predators.

Microhabitat use, although significantly different between rodent species, did not show trends with snake species, but did with the lunar cycle. The decline of GUDs with illuminance in the open microhabitat is inconsistent with other studies (Kotler 1984b, Kotler et al. 1994, 2010) and may be caused by the low number of nights with high illuminance that occur in the lunar cycle (A. K. Dixon, unpublished data). Combinations of contrasting risks and the presence of snakes possessing sensory pits may also have influenced GUDs in this period. However, the timing of illuminance in the open habitat did show differences between species, suggesting the timing of illuminance has a greater effect in microhabitats exposed to the illuminance.

This study replicated many of the characteristics indicative of natural Gerbilline communities in an artificial setting, allowing future studies to build from and further manipulate artificial communities. We show that tradeoffs in species' foraging efficiency over the lunar cycle may aid species coexistence through temporal refuges allowing energetic state to rebuild. Our results further suggest body size may be an important characteristic defining mechanisms used in desert rodent communities due to their influence on energetic demands, interference competition, and antipredator benefits. Support for constraint breaking adaptations affecting community structure was also found by observing differences in rodent foraging costs in the face of mortality risk arising from true vipers versus pit-vipers across the lunar cycle. Pit-vipers were most costly during the darker crescent portion of the cycle while true vipers were most costly during brighter gibbous portions. Adaptations like sensory pits may not necessarily be constraint breaking due to a superior "technology," but break constraints because of the manner in which the species applies the adaptation.

4.1.2. C. penicillatus *and* G. andersoni allenbyi

In the experiment contrasting *C. penicillatus* and *G. andersoni allenbyi, C. penicillatus* possessed higher GUDs, which while consistent with other studies in artificial settings (Kotler et al. 2016), does not capture the lower GUDs observed in nature (Brown et al. 1988). One possible cause for this is a greater risk of predation. While the artificial bushes provide some protection from avian predators, the limited risk imposed upon the predator when attacking rodents at bushes may keep the cost of predation high (Embar et al. 2014b). Also, the lack of dense branches along the base of the artificial bush may also increase predation costs from viper predators (Clark et al. 2016). A second possible cause for the high GUDs could be an increase in the cost of competition caused by the presence of a competitor, *G. andersoni allenbyi*. However, GUDs of *C. penicillatus* in this experiment are slightly lower than other studies in the same vivarium (Bleicher 2015) suggesting predation risk and habitat complexity are likely the cause for increased GUDs here.

This study also showed *G. andersoni allenbyi*'s ability to better mitigate threats and combinations of threats suggesting body size is, in this case, more important than external cheek pouches in mitigating risk. A previous study comparing *G. andersoni allenbyi* and *G. pyramidum* also supports body sizing being an important characteristic, showing the larger *G. pyramidum* to better mitigate risk. This beneficial effect of body size may come from several aspects. In rodents, larger body size mean larger auditory bullae (Webster 1961, 1962, Nikolai and Bramhle 1983), allowing for increased detection of low auditory frequencies, including those generated by the wingbeats of attacking owls. Additionally, larger rodents tend to run faster (Thompson 1985) and can likely jump higher or farther to evade predatory attacks (Bartholomew, Jr. and Caswell, Jr. 1951, Longland and Price 1991). Overall, possessing a larger body size may mitigate risks allowing for otherwise inaccessible resources to be foraged.

The timing of illuminance in this study supported the temporal partitioning of rodent species due to interference competition. Because *C. penicillatus* had lower GUDs when illuminance occurred earlier and it is known to increase its GUD with illuminance, *C. penicillatus* likely forages later in the night when it is more efficient. Similarly, *G. andersoni allenbyi* was more efficient than *C. penicillatus* when illuminance occurs early in the night and less when it occurs later. This tradeoff in foraging efficiencies produced by the risk caused by illuminance is indicative of interference competition where the larger species, *G. andersoni allenbyi*, pushes the smaller species to later periods of the night (Ziv and Kotler 2003). Foraging later may also reduce predation costs of the smaller species as many predators are less active later in the night (Clark et al. 2016), which further adds to the different effects of body size and predation risk.

As with previous studies (Bleicher 2015, Kotler et al. 2016), the rodents in this study changed their GUDs in response to the different viper predators. The shifts in GUDs in the presence of snakes with sensory pits both here and elsewhere support pit-vipers causing more costly foraging in rodents on darker nights. These differences in the temporal foraging efficiencies of each species may have the potential to affect the temporal refuges of species in a manner that break constraints.

4.1.3. D. merriami *and* G. pyramidum

In the experiment contrasting *D. merriami* and *G. pyramidum*, *G. pyramidum* behaved as previously reported by changing its GUD in response to illuminance and viper treatment. However, *D. merriami* responded similarly to both homogeneous viper treatments. This difference raises the question of whether *D. merriami* noticed the difference between vipers or whether it cares about that difference. In similar single-rodent experiments, *D. merriami* was shown to have higher GUDs in the presence of SWRS (Bleicher 2015), suggesting it can distinguish between vipers. One difference between these studies is the presence of interspecific competitors. For *D. merriami*, the similar GUDs between viper treatments may be obtained if both species use the safer habitat more and *D. merriami* were to lose in competition. This lose could drive up the cost of competition in one shared habitat but not the other. Despite this possibility, it seems unlikely the larger *D. merriami* would be interfered with by *G. pyramidum*, leaving further studies to be conducted.

The larger species present in this study appeared to not be affected as much by the risk of avian predators. While bipedal locomotion of *D. merriami* and the reduced accuracy of tracking in this study could be responsible for not seeing a difference in owl response between species, it could also mean that body size is a factor. Barn owls are known to hunt larger rodents, but primarily consume rodents with a mean and median mass of 12.3 g and 23 g, respectively, well below the mean mass of *D. merriami* and *G. pyramidum* (Kotler et al. 1988, Tores and Yom-Tov 2003, Kitowski 2013).

4.1.4. General Discussion of Community Experiments

Both studies containing similarly sized rodents displayed a lack of community characteristics indicative of granivorous rodent coexistence observed in nature, but rather that of competitive exclusion. This result relates back to the concept of limiting similarity, where the frequency of traits or resources exploited are limited by how similar they can be (MacArthur and Levins 1967). In both experiments presented here, rodents of similar sizes showed characteristics of the larger excluding the smaller. Because coexistence requires a tradeoff along an axis of environmental heterogeneity (Kotler and Brown 1988, Brown 1989b), the similarities in body size likely restricts foraging to similar habitats and predator combinations (Longland and Price 1991, Kotler et al. 1993c) due to their energetic demands, foraging ability, and capacity to mitigate predation. Constraint breaking adaptations may still be important in structuring communities, but they may only be inside the invasion window if species are dissimilar enough.

In both studies, the viper treatment containing BOTH viper species often appeared to have a reduced or negligible effect on rodent giving-up densities. This may be caused by the two viper species interfering with each other (Embar 2013, Bleicher 2015). In these experiments I observed noticeably less viper tracks in the BOTH treatment than the SWRS or SHV treatments (A. Dixon, personal observation), suggesting that decreased viper activity when both snake species were present reduced predation costs of the rodents. This potential interference between viper species was also observed in previous studies (Embar 2013, Bleicher 2015). Although I am uncertain of the cause, one possibility may be differences in activity cycles of the vipers throughout the lunar cycle. For example, if SHV are much less active during the crescent moon, the activity in BOTH should be half the tracks found in SWRS. Further studies and analysis should be conducted to determine the interactions occurring here.

Because these studies took place during different years and months, it is possible that seasonal differences influenced the results in some minor ways. For example, cooler nightly temperatures towards the end of the *G. pyramidum* and *D. merriami* experiment may have reduced foraging activity (increased costs) of both rodents (Kotler et al. 1993b) and their viper predators (Putman and Clark 2017). However, changes in the known response to vipers in this experiment were not observed, suggesting any effects were minimal. Instead, a different response was observed in the *G. a. allenbyi* and *G. pyramidum* experiment where GUDs increased in the presence of vipers. This response could have been because the snakes, all of which were male, were more focused on finding mates than foraging since this took place during their breeding season (Webber et al. 2012). Behaviors and missed opportunity costs could have also differed in this earlier experiment because of more water availability and rodent breeding opportunities (Sarli et al. 2015). Such an interest in reproduction could have increased the marginal value of energy while devaluing predation.

Overall, these experiments suggest that, in the case of desert granivorous rodents, external cheek pouches and bipedal locomotion do not appear to be constraint breaking adaptations. While they likely contribute to rodent fitness, the presence or absence of these adaptations do not seem to give the species possessing them an advantage over another. Instead, body size appears to be important in competition and mitigating predation as well as allowing the conditions necessary for coexistence to occur. When compared with previous studies, characteristics indicative of species coexistence only occurred when body sizes were further apart. The presence of viper predators with sensory pits did produce changes in most rodents' foraging behaviors, suggesting that the different temporal risk associated with them may have the ability to break community constraints by the altering of temporal refuges.

4.2.0. Personality Discussion: Variations in risk management between gerbils (*Gerbillus andersoni allenbyi*) with different exploratory/ boldness behaviors

Our results show bold individuals primarily used time allocation to mitigate risk. In doing so, they gathered more food, visit patches earlier, and maintained a greater body mass, suggesting an advantage in competition for resources. Based on our results, we propose exploratory behaviors in gerbils may largely be produced and maintained through variations in risk management tactics, including differences in the use of time allocation and apprehension/ vigilance. We demonstrate several axes of heterogeneity along which tradeoffs occur between gerbils groups displaying different exploratory behaviors. These may allow each personality type to coexist within populations in a manner similar to mechanisms that promote the coexistence between species (e.g., Brown 1989). Thus, the generation and maintenance of personalities may not require new mechanisms, but rather the same mechanisms used on a smaller scale.

The smaller proportion of seeds husked in the trays by bolder individuals suggest the use of a “grab and go” tactic. Bolder individuals would come, collect seeds from the tray, and carry them off to consume or cache them in a safer area. where they would husk a smaller proportion of seeds in the tray. To be effective, this tactic uses time allocation, which favors the first foragers in a patch because they would yield a higher harvest rate. As a patch is depleted, more time would need to be spent to obtain a given amount of resources (Kotler and Brown 1990). Our GUD results across the lunar cycle suggest that bolder individuals forage earlier in the night based on observed responses to the lunar cycle. Trapping observations at the conclusion of the experiment also support this since gerbils from quadrants holding bolder animals were captured earlier in the night than gerbils from quadrants holding shyer animals (A.K. Dixon, pers. obs.). Bolder individuals are also known to move more than shyer individuals (Ciuti et al. 2012), which may require greater energy costs, but provide greater and more accurate information on resource depletion. Such costs, greater information, and earlier foraging periods likely contribute to the gathering of the greater resources observed here and in other studies (Mella et al. 2015). Bolder individuals gained more body mass, a feature that would likely contribute to greater reproductive success (Smith and Blumstein 2008) and greater ability to interfere with others (Ziv et al. 1993). This further insures the ability to obtain resources first, favoring yet more time allocation. Such a tactic is frequency dependent as only a certain number of individuals can consistently be the first to a patch. Aggressiveness is also linked to resource use (Biro and Stamps 2008), and would further promote time allocation strategies, resulting in a correlation between exploratory behavior/boldness and aggressiveness (a behavioral syndrome; Sih et al. 2004). Time allocation strategies may explain a resource driven strategy in bolder individuals and demonstrate one way that personalities and behavioral syndromes may be generated and maintained evolutionarily.

Gerbils that are unable to consistently arrive to patches first and defend them from competitors (shyer individuals) likely used a tactic focused more on apprehension/vigilance. Thus they mitigate predation risk differently by seeking to detect threats rather than avoid them. Apprehension and vigilance also allow for the detection of competitors including larger bolder gerbils that may seek to chase shyer individuals from a resource patch (Ziv et al. 1993). To best use vigilance, foragers must devote time to scanning the environment (Lima 1987b, Kotler et al. 2004a, Embar et al. 2011), meaning they must move less to successfully use this tool (Ciuti et al. 2012). Motionlessness is also advantageous in avoiding detection by predators and competitors (Lima 1987b, Lima and Dill 1990, Griffin et al. 2005, Embar et al. 2014a, Casillas-Barragán et al. 2016), which both contribute to foraging costs. While both time allocation and vigilance tactics can adequately mitigate risk, time allocation seems to better maximize resource harvest while vigilance affects the detection of foragers and threats. Thus, bolder individuals likely have better information on the resource landscape while shyer individuals have better information of risks (predation and competition).

While foragers may choose to use one tactic more prominently, it is important to note that portions of both time allocation and vigilance are used. For example, shyer individuals foraged later in the night, which may allow them to be vigilant early on or wait until times when predators are less active (Embar et al. 2014c). In nature where the different exploratory behaviors coexist, foraging later in the night may be further enforced by more aggressive and bolder individuals (Ziv et al. 1993). The two tactics may also be affected by the accuracy of indirect and direct cues of risk. When risk is low, emphasis on indirect cues and obtaining resources (boldness) should be a winning tactic but when risk is high, vigilance (shyness) should dominate (Bell and Sih 2007, Dingemanse et al. 2007, Stamps 2007). This is because rodent predators are drawn to activity (Embar et al. 2014a), so the more emphasis on time allocation and movement, the greater actual risk a rodent likely faces. Resource driven strategies, like those observed within bolder individuals should be negatively frequency dependent because as more individuals become bold, each individual obtains less resources. At a certain frequency threshold, individuals may achieve greater fitness by being shy and focusing on vigilance rather than time allocation. This negative frequency dependence may maintain the existence of bolder and shyer personalities within a population.

Coexistence of personalities appear to occur along axes of illuminance and its timing (Kotler and Brown 1988), suggesting a tradeoff of food and safety. Our study showed each behavioral group was most efficient during a different portion of the lunar cycle. Strongly bold individuals dominated the gibbous phase, demonstrating time allocation’s efficiency when dealing with indirect cues. During the crescent phase, bold and shy gerbils showed a tradeoff their responses to the timing of illuminance, where vigilance was the most efficient strategy when illuminance was early, allowing for darker periods later in the night when shy individuals foraged. Waning (illuminance later) portions of the lunar cycle may have remained dominated by bolder personalities due to their more aggressive nature and higher marginal value of energy during this portion of the lunar cycle (Kotler et al. 2010). Besides frequency dependence, personalities may be maintained through typical coexistence mechanisms.

Our study also suggested weaker personalities might perform better in open microhabitats than bush microhabitats. Rather than pure time allocation or vigilance (strong personalities), weaker personalities utilizing a greater mix of the two may be best in the most risky environments by limiting exposure costs and maximizing detection. Bush microhabitats might reduce the chance of error in time allocated strategies by foraging in an environment where they are safer from owls (Kotler et al. 2004a, Embar et al. 2011). Similarly, shy vigilant individuals might find bushes to provide relatively safer positions and efficiently observe the environment (Embar et al. 2011). It is also worth pointing out the lack of differences between personalities and patch exploitations, which show that even shy vigilant individuals visited the same number and type of patches as bolder ones. These differences may further help to maintain a range of personalities within a population.

Despite the advantages of behavioral flexibility (Sih et al. 2004), consistencies in the environment including resource abundance and distribution, predation risk, and competition may influence the repeatability of some behaviors. Our study helps to explain how the evolutionary process may drive the generation and maintenance of personalities through differences in risk management and tradeoffs in food and safety (Kotler and Brown 1988). This process may also blur the line between species as differences in personalities or tactics used within a population may eventually become different enough to be labeled distinct species.

4.3.0. Theoretical Discussion: Patch use as an indicator of habitat preference, predation risk, and competition across space and time

This model extends the temporal patch use equation described by Brown (1988), allowing characteristics of the spatial environment and interactions to be considered alongside temporal changes. The model allows predictions about the spatial distributions of planktivorous fishes within the environment and between each other. While these predictions will need to be experimentally tested, it describes possible mechanisms other than recruitment that may produce the spatial structuring of coral reefs (Shulman 1985, Sale 2004).

While energetic costs (E_D) showed some ability to produce site attachment, predation costs (P_D), or the combination of the two appeared more important for site attachment. As seen in the models (Fig. 15), higher predation costs were important for reducing the horizontal range of optimal foragers while both energetic and predation costs controlled the vertical movement. These differences may contribute to observed differences observed in planktivorous fish foraging behavior. Anthias (*Pseudanthias squamipinnis*), which move more horizontally (Shapiro and Genin 1993), may be one species that exhibits relatively lower levels of predation costs. Armored catfish of the family Loricariidae may also possess lower predation costs in deeper waters where subcutaneous bony plates protect them from predators (Power 1984). However, the latter example would also have an inverted prey distribution (H_D) contributing to their more demersal/benthic lifestyles. These predictions complement previous studies suggesting predation is an important component of spatial structuring (Fricke 1977, Hixon and Beets 1993)

Predictions from this model may also clarify confusion between the existence and strength of competition between fishes (Roberts and Ormond 1992). Results here (Fig. 3b, Fig. 16) suggest optimal distances for fish to maintain between each other because of energy (H_C and E_C) and safety from predation (I). Once hierarchical positions are determined within a group (Forrester 1991, Booth 1995, Reuben 2016), subordinate fish would have little to gain from violating the optimal distance, which could result in depredation or a losing clash. Similarly, dominant fish gain nothing from pushing fish beyond the optimal distance. This ‘cooperative’ competition would result in reduced energetic costs and clashes (Roberts and Ormond 1992) while holding to the strict spatial structuring observed (Reuben 2016).

Similar studies modeled the positions of Arctic grayling in rivers and found fishes sought out positions that maximized net energy gains (Hughes and Dill 1990, Hughes 1992). These models also examined the hierarchy of positions in the streams based on environmental conditions and their ability to find and consume prey. While such models are accurate and useful in specific situations, the fitness functions and patch use equations used here can have much broader uses. The games and movements of foragers between patches and refuges (e.g. Fortin et al. 2005) could be better understood by measuring or modelling foraging costs throughout a landscape over time. Such studies, like those measuring landscapes of fear (e.g. Shrader et al. 2008; Iribarren and Kotler 2012), fail to examine changes across multiple instants. Other studies (e.g. Ciuti et al. 2012) focus more on temporal changes by measuring activity and mortality events. The expanded model presented here has the capacity to extend spatial predictions across time. For example, as the sun sets, the density of harvestable prey (H_D) would change as the intensity and angle of light change with each time step (H_T), resulting in changes of foraging behavior (Rickel and Genin 2005).

Forager densities or group sizes will also influence the terms of the patch use equation in one of two ways: 1) by affecting the space itself, or 2) affecting the "exchange rate" (marginal value) a variable. Imagine a higher density of foragers that are not competing directly with the focal forager. These additional foragers will still deplete the spatial landscape, reducing H_D. In a second scenario, foragers may have to travel longer distances to perform alternative activities affecting fitness (e.g. finding a mate, socialize, etc.) when densities are low. Such energetic costs should decrease the denominator in the marginal rate of substitution (i.e. "exchange rate"), devaluing the performance these alternative activities. As time moves forward, this distance may decrease as individuals get closer and increase the marginal value of such activities until it becomes too costly not to perform them. It is also worth mentioning that densities, or other factors, can cause variables of the patch use equation to change in an opposite manor than presented here. For example, if a school of fish attracts predators rather than diluting the risk, the cost of isolation would be high when foragers are close and decrease as they move apart.

This model may also be relevant for fission-fusion social groups including those found in bats (Kerth and Konig 1999, Willis and Brigham 2004), elephants (Couzin 2006), dolphins (Bräger 1999, Pearson 2009, Parra et al. 2011), chimpanzees (Symington 1990), and buffalo (Cross et al. 2005). Individuals in these groups may fuse to minimize missed opportunity costs (MOC) by engaging in mating, playing, or other social behaviors and minimize the cost of isolation (I) by diluting the probability of an individual being depredated. However, while in a fused group, a forager's resources are depleted and renewal rates are low so the marginal rates of substitution can change to value energy over safety and alternative activities, resulting in fission and organisms seeking food in smaller groups. This argument helps may explain fission-fusion in ungulates (e.g. Sundaresan et al. 2007) whose gut size can limit resource absorption (Belovsky 1997), thus changing the marginal value of energy throughout the day and leading to the dynamic described above.

Although this study was not intended to be a quantitative one, it is worth discussing the sizable differences between net energy gains of site-attached planktivores (~1.5 J min^{-1}) verses pelagic planktivores (~4.5 J min^{-1}). Such differences are largely caused by the steepness of the plankton gradient combined with the reduction of certain terms. For example, as current and/or predation become less costly they make the richer areas more accessible to the forager. Given equal costs between a rich and poor patch, an optimal forager should choose the rich patch (MacArthur and Pianka 1966, Fretwell and Lucas, Jr. 1969). It is also interesting that most planktivorous reef fishes foraging higher in the water column tend to be larger (e.g. *Caesio* sp. compared to *Dascyllus* sp.). Because larger body sizes require greater energetic intake because of greater metabolic demands (Brown et al. 2004, Speakman 2005), such foragers would likely not forage close to the reef floor because the lower harvest rates would be below their quitting harvest rate due to higher energetic demands from metabolisms. Such a scenario could allow coexistence where smaller fish species then forage below the larger ones, similar to the coexistence of gerbils in the Negev desert (Kotler et al. 1993d, Ziv et al. 1993).

Our extension incorporates spatial components into patch use equations and can produce predictions for a wide range of systems, organisms, and lifestyles. We demonstrated how simple differences in foraging costs may produce the differences observed on coral reefs in planktivorous fish distributions. Subtitle differences between species may further contribute to our understanding of high species diversity and coexistence of coral reefs and in other systems.

4.4.0. Damselfish Discussion: A mechanistic approach to understanding the spatial structure of site attached planktivores

The fitness function and expanded patch use equation presented earlier allow for the spatial use of planktivorous site-attached reef fishes to be analyzed and dissected to better understand their use of space. *Dascyllus marginatus* responded similarly to increasing patch richness via prey density, current magnitude, and prey flux by exchanging energy for safety. Rather than doing this through simple decreases in distance to refuge and/or nearest neighbor distance, as we predicted. A complex dynamic was shown to exist where risk drastically decreased via the vertical distance to refuge in order to allow a slight increase in risk via horizontal distance to refuge and isolation costs. These results contribute to understanding how reef fish view their space, which can help lead to an understanding of coral reef spatial structure.

The interpretation of the effects of prey density is rather straightforward since it only influences H_Z. However, current magnitude and prey flux can affect both H_Z and E_Z. To simplify this, these terms can be combined into the net energy gain along the vertical axis. In doing so, foraging should cease when the net energy gain becomes equal to the cost of competition, predation, and isolation (Brown 1988). In other words, when a forager is foraging, the net energy gain must be positive and large enough to account for the remaining foraging costs. When foraging ceases and fish return to the coral, it is possible that the net energetic gain has become negative due to a decrease in prey density or a reduction in current and the rate at which prey are replenished. However, it is possible for the net energy gain to still be positive but not be great enough to be greater than the remaining foraging costs (i.e. competition, predation, and isolation).

The selection by *D. marginatus* to use the vertical dimension to control energy demands corresponds to our understanding of energetic heterogeneity via the vertical plankton gradient (Holzman et al. 2005, Yahel et al. 2005, Heidelberg et al. 2010) and current gradient (Hobson and Chess 1978, Bray 1981, McFarland and Levin 2002). Because horizontal prey flux is considered relatively spatially uniform, to adjust harvest rates, fish must rely on temporal changes of current magnitude and/or adjust their spatial position along the vertical gradient. Predation costs also were controlled along the vertical axis, even though distance to refuge along any axis has the same effect. The reason for selecting the vertical axis is likely due to energetics and prey flux being controlled along it. For a selected position of net energy gain, the position with the lowest foraging cost will be the shortest distance to refuge, which is directly above the coral. By moving horizontally outward from refuge, a forager only increases its distance to refuge (predation risk) without any increase in net energy gained. Site-attachment is therefore the optimal behavior as horizontal movement increases costs while net energy gains remains constant, thus decreasing fitness.

Our results are consistent with previous studies (Harrington and Losey 1990) that suggest competition is controlled along the horizontal plan, rather than the vertical axis, when competition (i.e. multiple fish) is present. In this study, we assumed all horizontal directions are equivalent, which ignores potential benefits of being upstream and not in the "shadows" of competitors (Kiflawi and Genin 1997). Other studies support such differences by showing the dominant "alpha" *D. marginatus* will always select a position upstream and slightly in front of its refuge (Reuben 2016). This behavior suggests competition may push dominant individuals to a position that, if alone is less optimal, but with competitors, prevents others from foraging upstream of them. Although not the ideal position for a lone fish, the slight increase in predation costs (i.e. distance to refuge) would need to be less than the cost of competition of foraging in a shadow.

The role of competition in coral reef fishes is controversial and opinions have changed over the decades from being thought to be widely prevalent, to unimportant, to somewhere between (Webster and Hixon 2000). But the foraging and mechanistic understanding described here may help shed light on this confusion. While some benefits of competition exist (Deelder 1951, Foster 1985), it is commonly viewed as a cost to foraging fish (McCormick 2012, McCormick and Weaver 2012, Bostrom-Einarsson et al. 2013). When the latter is true, individuals should seek to minimize competition costs. This can be done by establishing territories in strategic positions that minimize competition for prey (Reuben 2016). Such territories could help prevent a "tragedy of the commons" where both competitors loose (Berger-Tal et al. 2015). Instead, periodic tests, observed as by ecologists as competition, reinforce the status quo or produce a change in hierarchy. Missed opportunity costs can relate to competition. If an individual selects a territory too close to a dominant fish, frequent contests would reduce the time spent foraging and, therefore, potentially the fitness (Brown 1988). In this mechanism, competition is prevalent; producing the territories and spatial structuring of fishes, however, because it is costly, fish prefer to spatially select territories to minimize its costs.

Within the 3 dimensions of space, this study shows *D. marginatus* behaves as expected by an optimal forager; decreasing its costs as the environment becomes richer (i.e. the marginal value of energy decreases). This produces a cone-like shape where the group is closer together while higher up in the water column above the coral head, but farther apart when lower in the water column, suggesting fish may change how they mitigate predation risk with changing distance to refuge. For a forager, predation risk should increase with distance to refuge until the point that the refuge in unobtainable within the timeframe of a predator attack. Beyond this point, the predation costs from the distance to refuge should remain constant. But foragers too far from refuge can still reduce predation risk through other mechanisms, including group vigilance and the dilution effect (Foster and Treherne 1981) by reducing the cost of isolation. Reducing isolation costs will increase an individual's probability of survival, but at the cost of increased competition, creating a tradeoff of food and safety. In this study, competition costs of *D. marginatus* appear to be greater than isolation costs within the conditions and locations examined. This is likely caused by a greater reliance by *D. marginatus* on mitigating predation risk through distance to refuge. Differences in strategies of mitigating predation costs may explain differences between pelagic fishes that school for safety (i.e. rely on reducing the cost of isolation; Brock & Riffenburgh 1960) and fishes that are seen in groups, but rely on refuge more than schooling. It may also explain why schooling may not always be observed in schooling fishes placed in new environmental conditions (Ryer and Olla 1996). Thus, *D. marginatus* may not school in the pelagic sense, but rather obtain a clumped distribution due to habitat selection.

This study showed the probability of observing damselfish outside the coral buffer was significantly associated with current magnitude, prey density, and prey flux. Because each influence the amount of harvestable prey available, it is likely that the dominant activity conducted outside the coral is foraging. The threshold for current magnitude observed here is consistent with the lower range of flow speed where feeding rates peaked in laboratory flow chambers (Kiflawi and Genin 1997). Variations in threshold values would be expected as foraging costs and marginal rates of substitution (i.e. the value of energy) are manipulated (Brown 1988). For example, an increase in perceived predation risk, including anthropogenic fishing or motor boat presence, would increase these thresholds to higher levels (Madin et al. 2010, Bracciali et al. 2012). Although the probability of observing damselfish outside the coral buffer was significant for current magnitude, prey density, and prey flux, the p-value was much smaller for current magnitude and prey flux. This may suggest that while prey density is important, planktivorous site attached fish place a greater emphasis on the rate of prey item renewal at a given position (i.e. current magnitude) rather than the instantaneous prey density. This contrasts with many terrestrial studies where resource renewal is often slower (Brown 1989a, Kotler et al. 1994, Abu Baker and Brown 2009). Additionally, the ~1 m height placement of the coral head in our experiment would place fish in a richer environment than fish attached to corals on the reef floor (i.e. prey and current gradients), allowing the fish to further reduce foraging cost, including distance to refuge or time spent foraging. Thus, prey renewal rates could be important for site attachment since reduced rates could result in starvation if a forager remains at a single position.

For site attachment to occur, we suggest that 1) energy and predation must optimally be managed along the vertical axis and 2) prey replenishment must occur at a high enough rates to allow the organism to survive. When multiple individuals are attached to a single refuge, competition costs must be low enough to make remaining at the site worthwhile. Through a foraging ecology approach, combined with a theoretical framework, we demonstrate new methods of testing and looking at the spatial structure of coral reefs while addressing many other areas to which this framework may be applied.

4.5.0. General Discussion

Each experiment in this study has made advances in its own right. Rodent community experiments demonstrated how constraint-breaking adaptations could alter tradeoffs in food and safety and potentially change the mechanisms of coexistence operating within the community. Tradeoffs of food and safety were also shown to exist between different exploratory behaviors within a single rodent population and help explain their natural maintenance within the population. Expansions to existing theoretical work added spatial variables to the patch use equation allowing for additional applications and studies of tradeoffs of food and safety. This expanded equation was then used to understand the use of tradeoffs of food and safety on spatially structured coral reefs, which may lead to better understanding the mechanisms behind coral reef spatial structure. While each step in these contrasting fields contributes to advances of understanding the effects of tradeoffs of food and safety, are there any commonalities that can be drawn from such different studies.

One result, common to the desert rodent community studies and the personality study was the important role of body size within populations and the community. Unlike some communities, granivorous rodents do not seem to partition themselves across seed size (Price 1983). When multiple species coexist on a single resource, interference competition, and therefore body size, should be limited in how similar they can be (MacArthur and Levins 1967, Wilson 1975, Abrams 1983). The community experiments presented here showed rodents of similar size displayed results indicative of competitive exclusion, which support the idea of limiting similarity. Competitive exclusion of species on a shared resource should continue to occur until a tradeoff in foraging efficiency (ratio of energy gained to the total energy expended) can occur at different resource availabilities (Basset 1995), such as observed in native Negev rodent communities (Kotler et al. 1993d, Ziv et al. 1993).

Body size may also affect foraging efficiencies besides affecting the overall energy required to survive. Larger body size may aid a forager's ability to escape (e.g. jump higher or run farther quicker) or affect the predation risk (e.g. too large or risky to try to eat or too small to bother eating) from certain predators. For example, while barn owls will eat larger rodents, they primarily consume rodents with a mean and median mass of 12.3 g and 23 g, respectively (Kotler et al. 1988, Tores and Yom-Tov 2003, Kitowski 2013). This could mean larger rodents are less affected by owl predation as observed in the *G. pyramidum* and *D. merriami* experiment where owl was insignificant. While in this case, body size reduces predation risk, and therefore increases foraging efficiencies, the opposite could be true if a different predator targeting larger body sizes were present.

Within a population, the personality experiment suggests body size is also important for possessing a time allocated strategy, which is maximized by being the first forager in a patch. To be first, foragers must interfere and control patches which is easier for larger individuals (Vance 1984, Ziv et al. 1993, McCormick and Weaver 2012). Not only does this reinforce the importance of body size in the coexistence of phenotypes and personalities but it also hints that mechanisms of coexistence for these phenotypes and personalities are likely the same types of mechanisms acting between species within communities (Polis 1988).

Tradeoffs of food and safety were capable of explaining aspects of both community and population coexistence and the behaviors and distributions observed within them. The general applicability of this concept is encouraging when seeking to find generalized ecological concepts. While the reality of simple processes producing vastly different outcomes due to slight variations in initial conditions is frustrating to simplify, it is marveling how such simple differences produces the complex communities observed today. Continued advances in the application of tradeoffs of food and safety in less studied areas such as coral reefs and spatial distributions may one day further simplify our understanding of community structure and species coexistence.

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Appendix A - Effects of IR Light on SWRS Methods

Introduction

Previous 'common garden' experiments (e.g. Embar et al. 2014c, Bleicher et al. 2016, Kotler et al. 2016) have utilized nocturnally active pit vipers (e.g. sidewinder rattlesnakes *Crotalus cerastes*) under the presence of infrared (IR) light. Doing so is necessary for cameras to record the behaviors of the various rodents, vipers, and owls present within the experimental arena. However, pit vipers possess special sensory pits on the tip of their snout that allow them to "see" into the infrared spectrum (Lynn 1931, Noble and Schmidt 1937). This begs to question if the behaviors of pit vipers under IR lighting in previous studies could have been altered by the presence of the lighting.

While varying magnitudes of IR light may yield different results (i.e. inhibit or facilitate the snakes ability to "see"), here I examine the behavior of *Crotalus cerastes* and its prey under similar lighting conditions used by current and previous studies. I expect to see one of three results: 1) IR light inhibits the vipers by masking the rodents causing a decrease in viper activity and a decrease in rodent giving-up densities (rodents forage more food due to less risk), 2) IR light facilitates the vipers by lighting up darker portions of the landscape causing an increase in viper activity and an increase in rodent giving-up densities, 3) viper activity and rodent giving-up densities will not differ between IR lit nights and non-IR lit nights indicating no visible effect on behaviors.

Methods

This study took place between July 9-23, 2015 at the Jacob Blaustien Institute for Desert Studies in Midreshet Ben-Gurion, Israel. These dates are centered on the new moon to reduce any effects of visible light, thereby maximizing any effects of IR lighting. Since potential effects of IR should be most prominent when visual light is least abundant, the experiment was centered on new moon. A vivarium (34 x 17 x 5 m) was divided into four quadrants. Each quadrant contained 16 artificial bushes (trellises with shade cloth and branches) and 8 GUD trays (Fig. 1). These trays were filled and collected using the same methods as described in Section 2.1.3. Two sidewinder rattlesnakes were placed in three of the four quadrants, leaving one as a control for gerbil behavior. Tracking data on snake activity was collected by scoring their tracks using two methods. First, the number of sides (1-4) with snake tracks around and under the bushes containing trays were measured. Secondly, four 17 m transects were swept smooth before sunset and then counted after sunrise for the number of entries/exits across transects and the number of "J's" which are a distinct track feature left by the tail end of the snakes when sidewinding. Snake 'craters' (i.e. burrowing down into the substrate) next to patches were also recorded but did not yield a high enough sample size to warrant an analysis. To incentivize snake activity, four lab born and raised *Gerbillus gerbillus* were added to each quadrant and given six nights to acclimate prior to collecting data. Sidewinder rattlesnakes were then allowed three nights of acclimation prior to collecting data. Using two night blocks, infrared lighting was randomly selected to be present for one of the two nights. Each quadrant contained four diffused IR floodlights hung along the walls of the vivarium at 5 m height. They were angled to, as evenly as possible, cover the entirety of the quadrant. Each of the four types of tracking data was averaged together for each night x quadrant combination. These means and GUDs were used as dependent variables in separate analyses of variance (ANOVA) to test for differences caused by IR presence.

Results

Rodents did not significantly alter their GUDs when IR light was present (ANOVA, $F_{(1,239)} = 1.14$, $p = 0.287$), suggesting the foraging cost of predation did not change. However, snake tracks did suggest an increase in snake activity. No significant changes were observed in the number of sides with snake tracks around (ANOVA, $F_{(1,40)} = 1.84$, $p = 0.182$) or under bushes (ANOVA, $F_{(1,40)} = 2.23$, $p = 0.143$). The number of entries and exits (ANOVA, $F_{(1,40)} = 0.89$, $p = 0.352$) and "J's" (ANOVA, $F_{(1,40)} = 2.29$, $p = 0.138$) also showed no significant differences between IR treatments. These results suggest IR lighting within the vivarium do not influence the activity of pit-vipers or the foraging costs of gerbils.

Discussion

IR lighting showed no effect on pit-viper activity or rodent foraging costs. This supports the third hypothesis that IR lighting within the vivarium settings does not influence the outcome of such studies. Such results alleviate any concerns regarding invalid results due to IR lighting from previous and current studies.

R Script for IR experimental statistics

```
library(car)    # For type III ANOVA
data=read.csv(file.choose(),na.strings="-")  # Load data file

#--------------------------------------------------------------------------
# Snake track Transect Analysis
#--------------------------------------------------------------------------
  # Prepare data for analysis
  sub = data[1,]

  for(i in 1:length(unique(data$Date))){
    for(j in 1:length(unique(data$Quadrant))){
      temp = subset(data,data$Date == unique(data$Date)[i] & data$Quadrant
        == unique(data$Quadrant)[j])
      temp$Js[1] = mean(temp$Js)
      temp$EE[1] = mean(temp$EE)
      sub = rbind(sub, temp[1,])
    }
  }
  sub = sub[2:dim(sub)[1],]
  rm(temp)

  # Analyze Snake Tracks
  res = lm(Js~IR, data=sub)
```

```
  res = lm(EE~IR, data=sub)

  layout(matrix(1,1,1)); hist(resid(res));
  layout(matrix(c(1,2,3,4),2,2)); plot(res);
  Anova(res,type="III")

#---------------------------------------------------------------------------
# Snakes around and under (ANCOVA)
#---------------------------------------------------------------------------
  sub = data[1,]

  for(i in 1:length(unique(data$Date))){
    for(j in 1:length(unique(data$Quadrant))){
      temp = subset(data,data$Date == unique(data$Date)[i] & data$Quadrant
        == unique(data$Quadrant)[j])
      temp$skAround[1] = mean(temp$skAround)
      temp$skUnder[1] = mean(temp$skUnder)
      sub = rbind(sub, temp[1,])
    }
  }
  sub = sub[2:dim(sub)[1],]
  rm(temp)

  SA = lm(skAround~IR,data=sub)
  Anova(SA,type="III")

  SU = lm(skUnder~IR,data=sub)
  Anova(SU,type="III")

#---------------------------------------------------------------------------
# GUD Analysis
#---------------------------------------------------------------------------
   data=read.csv(file.choose(),na.strings="-")  # Load data file
   sub = subset(data,data$GUD < threshold.G & data$Visits == "Visited" &
      data$Snake == "SWRS")
   GUD = lm(sqrt(GUD)~IR,data=sub)
   layout(matrix(1,1,1)); hist(resid(GUD));
   layout(matrix(c(1,2,3,4),2,2)); plot(GUD);
   Anova(GUD,type="III")
```

ANOVA Tables for IR experiment

The ANOVA comparing the number of “J” tracks with IR treatment produced:

	Sum Sq	Df	F value	Pr(>F)
(Intercept)	12691.15	1	56.62072	3.52E-09
IR	512.7515	1	2.287607	0.138272
Residuals	8965.726	40		

and for the number of entries/exits across transect lines produced:

	Sum Sq	Df	F value	Pr(>F)
(Intercept)	1678.574	1	60.9543	1.45E-09
IR	24.38095	1	0.885349	0.352389
Residuals	1101.53	40		

The ANOVA table for snake tracks around the bush resulted in:

	Sum Sq	Df	F value	Pr(>F)
(Intercept)	64.75074	1	60.14375	1.70E-09
IR	1.982515	1	1.84146	0.182389
Residuals	43.06399	40		

while tracks under the bush resulted in:

	Sum Sq	Df	F value	Pr(>F)
(Intercept)	20.0119	1	38.2943	2.57E-07
IR	1.166667	1	2.232505	0.142982
Residuals	20.90327	40		

The ANOVA with giving-up density as the response variable yielded:

	Sum Sq	Df	F value	Pr(>F)
(Intercept)	85.86847	1	5471.99	1.03E-166
IR	0.017886	1	1.139761	0.286780059
Residuals	3.750475	239		

Appendix B – *G. a. allenbyi* and *G. pyramidum* experiment statistics

The model run for this experiment used the following R code:

```
library(nlme)   # For gls
library(multcomp) # For gls post-hoc
data=read.csv(file.choose(),na.strings="-")  # Load data file
threshold.G = 0.963503599785624 # =1-2SD; < Exploited; >= Not Exploited
colnames(data)[2] = "Snake"
levels(data$Snake) = c("SHV","None","SWRS","Both")

model.matrix.gls <- function(object, ...) model.matrix(terms(object), data
   = getData(object), ...)
model.frame.gls <- function(object, ...) model.frame(formula(object), data
   = getData(object), ...)
terms.gls <- function(object, ...)    terms(model.frame(object),...)

sdata = subset(data,data$GUD < threshold.G & data$Visits == "Visited")
GUD = gls(sqrt(GUD) ~ Owl + Habitat + Illum + sUMT + Snake + rLast +
   rLast:Owl + rLast:Habitat  + rLast:Illum + rLast:sUMT + rLast:Snake +
   rLast:Owl:Habitat + rLast:Owl:Illum + rLast:Owl:sUMT + rLast:Owl:Snake +
   rLast:Habitat:Illum + rLast:Habitat:sUMT + rLast:Habitat:Snake +
   rLast:Illum:sUMT + rLast:Illum:Snake + rLast:sUMT:Snake +
   Illum:sUMT:Snake:rLast + Illum:sUMT:Owl:rLast +
   Illum:sUMT:Habitat:rLast, weights = varIdent(form=~1|Date), data=sdata,
   na.action = na.omit)
layout(matrix(1,1,1)); hist(resid(GUD));
layout(matrix(c(1,2,3,4),2,2)); plot(GUD);
anova(GUD)

# Post-hoc tests of main effects
pht = glht(GUD, linfct = mcp(Snake = "Tukey"))
summary(pht)
```

and yielded the following ANOVA table for the response variable sqrt(GUD):

	numDF	F-value	p-value
(Intercept)	1	30641.32	0
Owl	1	615.7007	1.31E-110
Habitat	1	1149.446	1.21E-178
Illum	1	0.304169	0.581380296
sUMT	1	244.0507	2.43E-50
Snake	3	15.49774	6.71E-10
rLast	1	1.351116	0.245307758
Owl:rLast	1	12.98299	0.000326832
Habitat:rLast	1	1.152947	0.283142775
Illum:rLast	1	0.012635	0.910519171
sUMT:rLast	1	1.531011	0.216195972
Snake:rLast	3	0.684892	0.561316105
Owl:Habitat:rLast	2	63.48787	5.69E-27
Owl:Illum:rLast	2	10.94638	1.94E-05
Owl:sUMT:rLast	2	1.355441	0.258216789
Owl:Snake:rLast	6	3.806512	0.000916023
Habitat:Illum:rLast	2	4.750582	0.008805298
Habitat:sUMT:rLast	2	5.538435	0.004030983

Habitat:Snake:rLast	6	3.811172	0.000905518
Illum:sUMT:rLast	2	107.5485	8.74E-44
Illum:Snake:rLast	6	3.379069	0.002612397
sUMT:Snake:rLast	6	31.76307	1.14E-35
Illum:sUMT:Snake:rLast	6	4.328425	0.000248592
Owl:Illum:sUMT:rLast	2	2.481048	0.084072424
Habitat:Illum:sUMT:rLast	2	1.441691	0.236925266

Appendix C – *C. penicillatus* and *G. a. allenbyi* experiment statistics

The model run for this experiment used the following R code:

```
library(car)    # For type III ANOVA
data=read.csv(file.choose(),na.strings="-")  # Load data file
threshold.G = 0.938425760966096 # =1-2SD; < Exploited; >= Not Exploited
colnames(data)[2] = "Snake"
levels(data$Snake) = c("SHV","None","SWRS","Both")
sub = subset(data,data$GUD < threshold.G & data$Visits == "Visited")
GUD = lm(sqrt(GUD) ~ Owl + Habitat + Illum + sUMT + Snake + rLast +
   rLast:Owl + rLast:Habitat + rLast:Illum + rLast:sUMT + rLast:Snake +
   rLast:Owl:Habitat + rLast:Owl:Illum + rLast:Owl:sUMT + rLast:Owl:Snake +
   rLast:Habitat:Illum + rLast:Habitat:sUMT + rLast:Habitat:Snake +
   rLast:Illum:sUMT + rLast:Illum:Snake + rLast:sUMT:Snake +
   rLast:Illum:sUMT:Owl + rLast:Illum:sUMT:Habitat +
   rLast:Illum:sUMT:Snake, data=sub)
layout(matrix(1,1,1,byrow=TRUE)); hist(resid(GUD))
layout(matrix(c(1,2,3,4),2,2,byrow=TRUE)); plot(GUD);
Anova(GUD,type="III")
```

and yielded the following type III ANOVA table for the response variable sqrt(GUD):

	Sum Sq	Df	F value	Pr(>F)
(Intercept)	6.372911	1	329.7207	8.25E-60
Owl	0.070157	1	3.629787	0.057199
Habitat	0.213397	1	11.0407	0.000942
Illum	0.183018	1	9.468938	0.002178
sUMT	0.531855	1	27.51705	2.12E-07
Snake	0.258607	3	4.459919	0.00412
rLast	0.016324	1	0.844567	0.358438
Owl:rLast	0.014617	1	0.756272	0.384822
Habitat:rLast	0.079177	1	4.096467	0.043385
Illum:rLast	0.014432	1	0.74666	0.387857
sUMT:rLast	0.071094	1	3.678227	0.055569
Snake:rLast	0.071311	3	1.229822	0.297938
Owl:Habitat:rLast	0.006178	2	0.159825	0.852327
Owl:Illum:rLast	0.062188	2	1.608749	0.200941
Owl:sUMT:rLast	0.026108	2	0.675389	0.509318
Owl:Snake:rLast	0.272901	6	2.353218	0.029525
Habitat:Illum:rLast	0.336024	2	8.692593	0.000188
Habitat:sUMT:rLast	0.513605	2	13.28641	2.22E-06
Habitat:Snake:rLast	0.086334	6	0.744453	0.614
Illum:sUMT:rLast	0.161622	2	4.180982	0.0157
Illum:Snake:rLast	0.443352	6	3.823009	0.000939
sUMT:Snake:rLast	0.63836	6	5.504564	1.42E-05
Owl:Illum:sUMT:rLast	0.015251	2	0.394526	0.674162
Habitat:Illum:sUMT:rLast	0.408636	2	10.57097	3.04E-05
Illum:sUMT:Snake:rLast	0.153947	6	1.327484	0.242488
Residuals	12.44737	644		

Appendix D – *D. merriami* and *G. pyramidum* experiment statistics

The model run for this experiment used the following R code:

```
library(car)    # For type III ANOVA
data=read.csv(file.choose(),na.strings="-")  # Load data file
threshold.G = 0.96311395232855 # =1-2SD; < Exploited; >= Not Exploited
colnames(data)[2] = "Snake"
levels(data$Snake) = c("SHV","None","SWRS","Both")
sub = subset(data,data$GUD < threshold.G & data$Visits == "Visited")
GUD = lm(sqrt(GUD) ~ Owl + Habitat + Illum + sUMT + Snake + rLast +
   rLast:Owl + rLast:Habitat + rLast:Illum + rLast:sUMT + rLast:Snake +
   rLast:Owl:Habitat + rLast:Owl:Illum + rLast:Owl:sUMT + rLast:Owl:Snake +
   rLast:Habitat:Illum + rLast:Habitat:sUMT + rLast:Habitat:Snake +
   rLast:Illum:sUMT + rLast:Illum:Snake + rLast:sUMT:Snake +
   rLast:Illum:sUMT:Owl + rLast:Illum:sUMT:Habitat +
   rLast:Illum:sUMT:Snake, data=sub)
layout(matrix(1,1,1,byrow=TRUE)); hist(resid(GUD))
layout(matrix(c(1,2,3,4),2,2,byrow=TRUE)); plot(GUD);
Anova(GUD,type="III")
```

and yielded the following type III ANOVA table for the response variable sqrt(GUD):

	Sum Sq	Df	F value	Pr(>F)
(Intercept)	8.141695	1	512.9235	8.44E-89
Owl	0.017062	1	1.074869	0.30015
Habitat	0.136152	1	8.577546	0.003496
Illum	0.00651	1	0.410126	0.522082
sUMT	0.037963	1	2.391634	0.122367
Snake	1.020133	3	21.42264	2.26E-13
rLast	0.074987	1	4.724136	0.030024
Owl:rLast	0.048219	1	3.037766	0.081718
Habitat:rLast	0.007357	1	0.46348	0.496192
Illum:rLast	0.093245	1	5.874383	0.015576
sUMT:rLast	0.143923	1	9.06711	0.002681
Snake:rLast	0.034021	3	0.714444	0.543491
Owl:Habitat:rLast	0.543873	2	17.1319	5.12E-08
Owl:Illum:rLast	0.050683	2	1.596492	0.203228
Owl:sUMT:rLast	0.031706	2	0.99873	0.368789
Owl:Snake:rLast	0.13343	6	1.401004	0.211307
Habitat:Illum:rLast	0.019582	2	0.61683	0.539899
Habitat:sUMT:rLast	0.144566	2	4.553807	0.010791
Habitat:Snake:rLast	0.140533	6	1.475591	0.183494
Illum:sUMT:rLast	0.329706	2	10.38568	3.51E-05
Illum:Snake:rLast	0.313576	6	3.292526	0.003301
sUMT:Snake:rLast	0.456536	6	4.7936	8.10E-05
Owl:Illum:sUMT:rLast	0.175189	2	5.518402	0.004161
Habitat:Illum:sUMT:rLast	0.260437	2	8.203707	0.000296
Illum:sUMT:Snake:rLast	0.614134	6	6.448369	1.17E-06
Residuals	13.17469	830		

Appendix E – G. *a. allenbyi* personality experiment statistics

Videos of GUD trays were analyzed using the following R script which was Jorge Menezes coded most of:

```
#--------------------------------------------------------------------------
# Load Libraries and create/organize any global variables
#--------------------------------------------------------------------------
  rm(list=ls())
  cat("\014")
  dev.off(dev.list()["RStudioGD"])
  library(dplyr)
  data=read.csv(file.choose(),na.strings="-",stringsAsFactors = FALSE)
  data$Date_Time = as.POSIXct(data$Date_Time, format="%d-%b-%y %H:%M:%S")
  data$Exp.Night = as.POSIXct(data$Exp.Night, format="%d-%b-%y")
  latency = 8  # Two Visits less than or equal to latency of each other are
   considered 1 visit
  runthru = 3  # Visits less than or equal to runthru are not considered to
   have foraged
  x = unique(data$Channel)


#--------------------------------------------------------------------------
# Determine Entry/Exit/Run Throughs and Duration for each visit
#--------------------------------------------------------------------------
# Add latency, determine, entry, exits, and run throughs
  for(i in x){
sub = mutate(subset(data,data$Channel == i),Difference = NA, EntryExit =
   NA)
    sub = arrange(sub,Date_Time)

  # Calculate the number of seconds between detections
    for(j in 1:(dim(sub)[1]-1)){
sub$Difference[j+1] = as.numeric(difftime(sub$Date_Time[j+1],
   sub$Date_Time[j],units="secs"))}

  # Label 2:end-1 as an entry, exit, delete = between entry & exit, Both =
   1 sec detect
    for(j in 2:(dim(sub)[1]-1)){
      if(sub$Checked[j]=="Yes"){  # I don't want to change videos that were
   manually checked
        if(sub$Difference[j] <= 1 & sub$Difference[j+1] <= 1){
          sub$EntryExit[j] = "Delete"
        }else if(sub$Difference[j] > 1 & sub$Differenc[j+1] <= 1){
          sub$EntryExit[j] = "Entry"
        }else if(sub$Difference[j+1] > 1 & sub$Difference[j] <= 1){
          sub$EntryExit[j] = "Exit"
        }
      }else{
        if(sub$Difference[j] <= latency & sub$Difference[j+1] <= latency){
          sub$EntryExit[j] = "Delete"
        }else if(sub$Difference[j] > latency & sub$Difference[j+1] >
   latency){
          sub$EntryExit[j] = "Delete" # Here we assume single detects are
   an error, as a visit should give 2 detects
        }else if(sub$Difference[j] > latency & sub$Differenc[j+1] <=
   latency){
          sub$EntryExit[j] = "Entry"
```

```
      }else if(sub$Difference[j+1] > latency & sub$Difference[j] <=
   latency){
         sub$EntryExit[j] = "Exit"
      }
    }
  }

# Labels the first and last rows
  if(sub$EntryExit[2]=="Delete"){
    sub$EntryExit[1]="Entry"
  }else{sub$EntryExit[1]="Delete"}  # Here we assume single detects are
   an error, as a visit should give 2 detects
  if(sub$EntryExit[dim(sub)[1]-1]=="Delete"){
    sub$EntryExit[dim(sub)[1]]="Exit"
  }else{sub$EntryExit[dim(sub)[1]]="Delete"}  # Here we assume single
   detects are an error, as a visit should give 2 detects

# Removes all the Delete rows and calculates the duration of visit
  sub = subset(sub,sub$EntryExit != "Delete")
  colnames(sub)[10] = "Duration"    # Ensure Difference is the 10th
   column in final draft
  for(j in 1:(dim(sub)[1]-1)){
    if(sub$EntryExit[j] == "Entry"){
      sub$Duration[j] =
   as.numeric(difftime(sub$Date_Time[j+1],sub$Date_Time[j],units="secs"))
      if(sub$Duration[j] <= runthru){sub$EntryExit[j] = "Run Through"}
    }else{sub$Duration[j] = NA}
  }

# Removes all exits and compiles results to dataframe res
  sub = subset(sub,sub$EntryExit != "Exit")
  if(i == x[1]){res = sub
  }else(res = rbind(res,sub))
}

# Remove columns that are not needed
  res$Presence=NULL

#-------------------------------------------------------------------------
# Calculate Summary Info for each day and tray
#-------------------------------------------------------------------------
# Calculate Summary Tables for Each Day & Tray
  n=0
  sub = as.data.frame(matrix(NA,ncol = 8, nrow =
   (length(unique(res$Channel))*length(unique(res$Exp.Night)))))
  colnames(sub) = c("Date","Channel","Total","Mean","SD","SE","N","NRT")
  for (i in unique(res$Exp.Night)){
    for(j in unique(res$Channel)){
      n=n+1
      temp = subset(res,res$EntryExit=="Run Through" & res$Exp.Night==i &
   res$Channel==j)
      sub$NRT[n] = dim(temp)[1]  # Number of Run Throughs
      temp = subset(res,res$EntryExit=="Entry" & res$Exp.Night==i &
   res$Channel==j)
      sub$Date[n] = i  # Experimental Night
      sub$Channel[n] = j  # Camera Channel
      sub$Total[n] = sum(temp$Duration)  # Total time spent in tray j on
   night i
```

```
        sub$Mean[n] = mean(temp$Duration)  # Mean visit length (excluding run
    thoughs) in tray j on night i
        sub$SD[n] = sd(temp$Duration)  # SD of visit lengths (excluding run
    thoughs) in tray j on night i
        sub$SE[n] = sd(temp$Duration)/sqrt(dim(temp)[1])  # SE of visit
    lengths (excluding run thoughs) in tray j on night i
        sub$N[n] = dim(temp)[1]  # Number of visits (excluding run thoughs)
    in tray j on night i
      }
    }
    sub$Date = as.POSIXct(sub$Date,origin = "1970-01-01 00:00:00 UTC")
    sub$Date = format(sub$Date, "%d-%b-%y")

  # Write Data to csv Files
    write.csv(res,file = "Tray Camera Analysis Full.csv")
    write.csv(sub,file = "Tray Camera Analysis Summary.csv")
```

Harvest rate curves were then calculated using the above output and the following R script:

```
GUDdata=read.csv(file.choose(),na.strings="-",stringsAsFactors = FALSE)  #
   Load data file
Timedata=read.csv(file.choose(),na.strings="-",stringsAsFactors = FALSE)  #
   Load summary data file
cameras = data.frame("Channel" = c(9,10,11,12,13,14,15,16),
                     "Quadrant" = c("SW", "NW", "NW", "SW", "SE", "SE",
                     "NE", "NE"),
                     "Tray" = c(5,5,8,8,5,8,5,8))
data=merge(Timedata,cameras,by=c("Channel"),all=FALSE)
data = merge(data,GUDdata,by=c("Date","Quadrant","Tray"),all=FALSE)
No = 1  # Initial density in tray (g dm-3)

# Calculate ln(No/Nf) and (No-Nf)
sub = subset(data,!is.na(data$GUD) & !is.na(data$Total))
a = log(No/(sub$GUD))
h = No - (sub$GUD)

# Regress to solve for a & h & plot overall HR Curve with GUD
mod = lm(Total~a+h,data=sub)
a = 1/as.numeric(mod$coefficients[2]) # units of (g dm-3 s-1)
h = as.numeric(mod$coefficients[3]) # units of (s g-1 dm3)
curve((a*x)/(1+a*x*h),0,No,xlab = "Giving-Up Density (g dm-3)",ylab =
   "Quitting Harvest Rate (g dm-3 s-1)",lwd=2)
points(mean(sub$GUD), (a*mean(sub$GUD)) / (1+a*mean(sub$GUD)*h), pch=19,
   cex=1.5)
```

The model run for analyzing giving-up densities in this experiment used the following R code:

```
library(nlme)   # For gls
library(multcomp) # For gls post-hoc
data=read.csv(file.choose(),na.strings="-")  # Load data file
threshold.G = 0.968076512279981 # =1-2SD; < Exploited; >= Not Exploited
colnames(data)[2] = "Snake"
levels(data$Snake) = c("SHV","None","SWRS","Both")

model.matrix.gls <- function(object, ...) model.matrix(terms(object), data
   = getData(object), ...)
model.frame.gls <- function(object, ...) model.frame(formula(object), data
   = getData(object), ...)
terms.gls <- function(object, ...)    terms(model.frame(object),...)
```

```
sub = subset(data,data$GUD < threshold.G & data$Visits == "Visited" &
   data$Official == "Yes")
GUD = gls(GUD ~ Owl + Habitat + Illum + sUMT + Personality +
   Personality:Owl + Personality:Habitat + Personality:Illum +
   Personality:sUMT + Owl:Habitat:Personality + Owl:Illum:Personality +
   Owl:sUMT:Personality + Habitat:Illum:Personality +
   Habitat:sUMT:Personality + Personality:Illum:sUMT +
   Owl:Illum:sUMT:Personality + Habitat:Illum:sUMT:Personality, weights =
   varIdent(form= ~1|Date), data = sub)
layout(matrix(1,1,1)); hist(resid(GUD));
layout(matrix(c(1,2,3,4),2,2)); plot(GUD);
anova(GUD)

# Post-hoc tests of main effects
glht(GUD,mcp(Owl = "Tukey"))
```

and yielded the following ANOVA table for the response variable GUD:

	numDF	F-value	p-value
(Intercept)	1	14101.53	0
Owl	1	2.883164	0.089750997
Habitat	1	663.7359	1.93E-118
Illum	1	1113.7	1.38E-176
sUMT	1	198.1156	5.75E-42
Personality	3	20.16494	8.96E-13
Owl:Personality	3	12.23104	6.81E-08
Habitat:Personality	3	15.54431	6.17E-10
Illum:Personality	3	41.11444	2.24E-25
sUMT:Personality	3	14.19632	4.18E-09
Owl:Habitat:Personality	4	2.837351	0.023306686
Owl:Illum:Personality	4	0.80013	0.525087297
Owl:sUMT:Personality	4	7.007297	1.40E-05
Habitat:Illum:Personality	4	3.456732	0.008087472
Habitat:sUMT:Personality	4	0.567816	0.686049128
Illum:sUMT:Personality	4	48.17423	8.48E-38
Owl:Illum:sUMT:Personality	4	4.636111	0.00101824
Habitat:Illum:sUMT:Personality	4	1.108377	0.351008393

Husk data was analyzed similarly using the following R code:

```
sub = subset(data,data$GUD < threshold.G & data$Visits == "Visited" &
   data$Official == "Yes" & !is.na(data$EAT))
Husk = gls(sqrt(EAT) ~ Owl + Habitat + Illum + sUMT + Personality +
   Personality:Owl + Personality:Habitat + Personality:Illum +
   Personality:sUMT + Owl:Habitat:Personality + Owl:Illum:Personality +
   Owl:sUMT:Personality + Habitat:Illum:Personality +
   Habitat:sUMT:Personality + Personality:Illum:sUMT +
   Owl:Illum:sUMT:Personality + Habitat:Illum:sUMT:Personality, weights =
   varIdent(form= ~1|Date), data = sub)
anova(Husk)
layout(matrix(1,1,1)); hist(resid(Husk));
layout(matrix(c(1,2,3,4),2,2)); plot(Husk);
```

which produced the following ANOVA table for the response EAT:

	numDF	F-value	p-value
(Intercept)	1	5935.791	0
Owl	1	9.933117	0.001661
Habitat	1	92.09176	4.12E-21
Illum	1	8.564941	0.003487
sUMT	1	1.895611	0.168809
Personality	3	98.02425	3.74E-57
Owl:Personality	3	1.765477	0.151907
Habitat:Personality	3	3.989889	0.007666
Illum:Personality	3	4.301566	0.004983
sUMT:Personality	3	16.08066	2.89E-10
Owl:Habitat:Personality	4	0.608788	0.656358
Owl:Illum:Personality	4	3.950916	0.003419
Owl:sUMT:Personality	4	0.808222	0.519883
Habitat:Illum:Personality	4	1.317668	0.261266
Habitat:sUMT:Personality	4	3.188391	0.012835
Illum:sUMT:Personality	4	4.932684	0.0006
Owl:Illum:sUMT:Personality	4	6.653274	2.67E-05
Habitat:Illum:sUMT:Personality	4	1.830919	0.120451

Patch visits were analyzed using the following R code:

```
library(car)
sub = subset(data,!is.na(data$GUD) & data$Official == "Yes")
sub$Visits = ifelse(sub$GUD<threshold.G,1,0) # 0 = Not Exploited; 1 =
   Exploited
Visits = glm(Visits ~ Owl + Habitat + Illum + sUMT + Personality +
   Owl:Personality + Habitat:Personality + Illum:Personality +
   sUMT:Personality + Illum:sUMT:Personality, data = sub, family =
   binomial)
layout(matrix(1,1,1)); hist(resid(Visits));
layout(matrix(c(1,2,3,4),2,2)); plot(Visits);
Anova(Visits,type="III")
TukeyHSD(aov(Visits~Personality,data=sub))
TukeyHSD(aov(Visits~Personality:Owl,data=sub))
```

which yielded the following ANOVA table for response variable Visits:

	Df	Deviance	Resid. Df	Resid. Dev
NULL			1470	869.591
Owl	1	38.23516	1469	831.3558
Habitat	1	90.25661	1468	741.0992
Illum	1	44.48946	1467	696.6097
sUMT	1	2.533405	1466	694.0763
Personality	3	13.93062	1463	680.1457
Owl:Personality	3	6.203021	1460	673.9427
Habitat:Personality	3	1.736963	1457	672.2057
Illum:Personality	3	5.001882	1454	667.2038
sUMT:Personality	3	9.997236	1451	657.2066
Illum:sUMT:Personality	4	12.63818	1447	644.5684

Body mass loss was analyzed using following R script:

```
Mass = lm(Loss~Personality)
Anova(Mass,type="III")
TukeyHSD(aov(Loss~Personality))
```

and produced the following ANOVA table for the response variable Loss:

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Personality	3	0.246472	0.082157	5.583839	0.008928
Residuals	15	0.220701	0.014713		

Appendix F – Theoretical model R script

```
library(plotly)   # Used for plot_ly() to plot heatmaps
library(webshot)  # Used to export plotly figures as pdf

# MAPS INDIVIDUAL COSTS & HARVESTS
mapper = function(coef,xdim,ydim,vi,save,col){ # xdim = horizontal distance
   (cm); ydim = vertical distance (cm); vi = variable of interest; hm =
   heatmap?
  map=matrix(NA,nrow=ydim,ncol=xdim)

  for(i in 1:dim(map)[1]){ # Row = Vertical Distance
    for(j in 1:dim(map)[2]){ # Column = Horizontal Distance
      dist = sqrt((i/100)^2+(j/100)^2)
      if(vi=="HD"){
        map[i,j] = coef[1,1]/(1+exp(coef[2,1]*((i/100)+coef[3,1])))
      } else if (vi=="ED") {
        map[i,j] = coef[1,3]/(1+exp(coef[2,3]*((i/100)+coef[3,3])))
      } else if (vi=="PD") {
        map[i,j] = coef[1,5]/(1+exp(coef[2,5]*(dist+coef[3,5])))
      } else if (vi=="HC") {
        map[i,j] = coef[1,2]/(1+exp(coef[2,2]*(dist+coef[3,2])))
      } else if (vi=="EC") {
        map[i,j] = coef[1,4]/(1+exp(coef[2,4]*(dist+coef[3,4])))
      } else if (vi=="I") {
        map[i,j] = coef[1,6]/(1+exp(coef[2,6]*(dist+coef[3,6])))
      } else {print("ERROR: Variable of Interest not Recognized")}
    }
  }
  if(save==TRUE){
    tmp = "C:/Users/User0/Desktop/output.pdf"
    export(plot_ly(z=map,type="contour",colors=col),file=tmp)
  } else {plot_ly(z=map,type="contour",colors=col)}
}

# MAPS NET ENERGY
NEmapper = function(coef,xdim,ydim,vi,constant,save){
  map=matrix(NA,nrow=ydim,ncol=xdim)

  for(k in 1:length(constant)){
    if(vi=="DR"){
      for(i in 1:dim(map)[1]){ # Row = Vertical Distance
        for(j in 1:dim(map)[2]){ # Column = Horizontal Distance
          dist = sqrt((i/100)^2+(j/100)^2)

          HD = coef[1,1]/(1+exp(coef[2,1]*((i/100)+coef[3,1])))
          ED = coef[1,3]/(1+exp(coef[2,3]*((i/100)+coef[3,3])))
          PD = coef[1,5]/(1+exp(coef[2,5]*(dist+coef[3,5])))

          HC = coef[1,2]/(1+exp(coef[2,2]*(constant[k]+coef[3,2])))
          EC = coef[1,4]/(1+exp(coef[2,4]*(constant[k]+coef[3,4])))
          I = coef[1,6]/(1+exp(coef[2,6]*(constant[k]+coef[3,6])))

          map[i,j] = (HD+HC)-(ED+EC+PD+I)
        }
      }
    } else if(vi=="NN") {
      for(i in 1:dim(map)[1]){ # Row = Vertical Distance
        for(j in 1:dim(map)[2]){ # Column = Horizontal Distance
```

```
          dist = sqrt((i/100)^2+(j/100)^2)

          HC = coef[1,2]/(1+exp(coef[2,2]*(dist+coef[3,2])))
          EC = coef[1,4]/(1+exp(coef[2,4]*(dist+coef[3,4])))
          I = coef[1,6]/(1+exp(coef[2,6]*(dist+coef[3,6])))

          HD = coef[1,1]/(1+exp(coef[2,1]*(constant[k]+coef[3,1])))
          ED = coef[1,3]/(1+exp(coef[2,3]*(constant[k]+coef[3,3])))
          PD = coef[1,5]/(1+exp(coef[2,5]*(constant[k]+coef[3,5])))

          map[i,j] = (HD+HC)-(ED+EC+PD+I)
        }
      }
    } else {print("Error: Variable of Interest Unknown")}
  }
  if(save==TRUE){
    tmp = "C:/Users/User0/Desktop/output.pdf"
    export(plot_ly(z=map,type="contour",colors=c("#A50026", "#FBFEA2",
   "#006837")),file=tmp)
  } else {plot_ly(z=map,type="contour",colors=c("#A50026", "#FBFEA2",
   "#006837"))}
}


#---------------------------------------------------------------------------
# EFFECTS OF DISTANCE TO REFUGE ON HABITAT
#---------------------------------------------------------------------------

# SET INITIAL BASE COEFFICIENT VALUES
  Base = matrix(c(12,  0,  3,  3.0,  3,  3,
                  -1,  2, -2,  5.0, -1, -5,
                  -1, -1, -2, -0.9, -2, -
   1),byrow=TRUE,ncol=6,dimnames=list(
                  c("First","Second","Third"),
                  c("HD","HC","ED","EC","PD","I")))

# SET SITE ATTACHED COEFFICIENT VALUES
  SAED = matrix(c(12,  0,  6,  3.0,  3,  3,
                  -1,  2, -2,  5.0, -1, -5,
                  -1, -1, -2, -0.9, -2, -
   1),byrow=TRUE,ncol=6,dimnames=list(
                    c("First","Second","Third"),
                    c("HD","HC","ED","EC","PD","I")))
  SAPD = matrix(c(12,  0,  3,  3.0,  6,  3,
                  -1,  2, -2,  5.0, -1, -5,
                  -1, -1, -2, -0.9, -2, -
   1),byrow=TRUE,ncol=6,dimnames=list(
                    c("First","Second","Third"),
                    c("HD","HC","ED","EC","PD","I")))
  SABoth = matrix(c(12,  0,  5,  3.0,  5,  3,
                    -1,  2, -2,  5.0, -1, -5,
                    -1, -1, -2, -0.9, -2, -
   1),byrow=TRUE,ncol=6,dimnames=list(
                    c("First","Second","Third"),
                    c("HD","HC","ED","EC","PD","I")))

# SET PELAGIC COEFFICIENT VALUES
  PelED = matrix(c(12,  0,  1,  3.0,  3,  3,
                   -1,  2, -2,  5.0, -1, -5,
```

```
                   -1, -1, -2, -0.9, -2, -
  1),byrow=TRUE,ncol=6,dimnames=list(
                    c("First","Second","Third"),
                    c("HD","HC","ED","EC","PD","I")))
  PelPD = matrix(c(12,  0,  3,  3.0,  1,  3,
                   -1,  2, -2,  5.0, -1, -5,
                   -1, -1, -2, -0.9, -2, -
  1),byrow=TRUE,ncol=6,dimnames=list(
                    c("First","Second","Third"),
                    c("HD","HC","ED","EC","PD","I")))
  PelBoth = matrix(c(12,  0,  2,  3.0,  2,  3,
                     -1,  2, -2,  5.0, -1, -5,
                     -1, -1, -2, -0.9, -2, -
  1),byrow=TRUE,ncol=6,dimnames=list(
                      c("First","Second","Third"),
                      c("HD","HC","ED","EC","PD","I")))

# SET DEMERSAL COEFFICIENT VALUES
  DemPD = matrix(c(12,  0,  3,  3.0,  3,  3,
                    1,  2, -2,  5.0, -1, -5,
                   -1, -1, -2, -0.9, -2, -
  1),byrow=TRUE,ncol=6,dimnames=list(
                    c("First","Second","Third"),
                    c("HD","HC","ED","EC","PD","I")))

# SET SOLITARY COEFFICIENT VALUES
  SolEC = matrix(c(12,  0,  3,  6.0,  3,  3,
                   -1,  2, -2,  5.0, -1, -5,
                   -1, -1, -2, -0.9, -2, -
  1),byrow=TRUE,ncol=6,dimnames=list(
                    c("First","Second","Third"),
                    c("HD","HC","ED","EC","PD","I")))
  SolI = matrix(c(12,  0,  3,  3.0,  3,  1,
                  -1,  2, -2,  5.0, -1, -5,
                  -1, -1, -2, -0.9, -2, -
  1),byrow=TRUE,ncol=6,dimnames=list(
                    c("First","Second","Third"),
                    c("HD","HC","ED","EC","PD","I")))

  # SET SCHOOLING COEFFICIENT VALUES
  SchEC = matrix(c(12,  0,  3,  1.0,  3,  3,
                   -1,  2, -2,  5.0, -1, -5,
                   -1, -1, -2, -0.9, -2, -
  1),byrow=TRUE,ncol=6,dimnames=list(
                    c("First","Second","Third"),
                    c("HD","HC","ED","EC","PD","I")))
  SchI = matrix(c(12,  0,  3,  3.0,  3,  6,
                  -1,  2, -2,  5.0, -1, -5,
                  -1, -1, -2, -0.9, -2, -
  1),byrow=TRUE,ncol=6,dimnames=list(
                    c("First","Second","Third"),
                    c("HD","HC","ED","EC","PD","I")))
  SchHC = matrix(c(12,  3,  3,  3.0,  3,  3,
                   -1,  2, -2,  5.0, -1, -5,
                   -1, -1, -2, -0.9, -2, -
  1),byrow=TRUE,ncol=6,dimnames=list(
                    c("First","Second","Third"),
                    c("HD","HC","ED","EC","PD","I")))
```

```
# SITE ATTACHMENT VARIABLE PLOTS
  mapper(Base,500,500,"HD",F,c("#A50026", "#FBFEA2", "#006837"))
  mapper(Base,100,100,"HC",F,c("#A50026", "#FBFEA2", "#006837"))
  mapper(Base,500,500,"ED",F,c("#006837", "#FBFEA2", "#A50026"))
  mapper(Base,100,100,"EC",F,c("#006837", "#FBFEA2", "#A50026"))
  mapper(Base,500,500,"PD",F,c("#006837", "#FBFEA2", "#A50026"))
  mapper(Base,100,100,"I",F,c("#006837", "#FBFEA2", "#A50026"))

# SPATIAL ENVIRONMENT NET ENERGY PLOT
  NEmapper(Base,500,500,"DR",0.25,F)
  NEmapper(SAED,500,500,"DR",0.25,F)
  NEmapper(SAPD,500,500,"DR",0.25,F)
  NEmapper(SABoth,500,500,"DR",0.25,F)
  NEmapper(PelED,500,500,"DR",0.25,F)
  NEmapper(PelPD,500,500,"DR",0.25,F)
  NEmapper(PelBoth,500,500,"DR",0.25,F)
  NEmapper(DemPD,500,500,"DR",0.25,F)

# SPATIAL INTERACTION NET ENERGY PLOT
  NEmapper(Base,100,100,"NN",1.2,F)
  NEmapper(SolEC,100,100,"NN",1.2,F)
  NEmapper(SolI,100,100,"NN",1.2,F)
  NEmapper(SchEC,100,100,"NN",1.2,F)
  NEmapper(SchI,100,100,"NN",1.2,F)
  NEmapper(SchHC,100,100,"NN",1.2,F)
```

Appendix G – Damselfish experiment statistics

The model run for this experiment used the following R code:

```
library(car)    # For type III ANOVA
library(lmtest) # For Durbin Watson Test

#--------------------------------------------------------------------------
# Position Analysis
#--------------------------------------------------------------------------
data=read.csv(file.choose(),na.strings="-"
              ,colClasses = c("NNxyz" = "numeric"
                              ,"NNxy" = "numeric"
                              ,"NNz" = "numeric"))  # Load data file

cor.test(sub$Current,sub$Density)

# Distance to Refuge & Prey Density
sub = subset(data, !is.na(data$DRz))

PV = c(NA,sub$DRxyz[1:length(sub$DRxyz)-1])
res = lm(DRxyz~PV+Density,data=sub)
res = lm(DRxyz~PV+Current,data=sub)
res = lm(DRxyz~PV+Flux,data=sub)

PV = c(NA,sub$DRxy[1:length(sub$DRxy)-1])
res = lm(DRxy~PV+Density,data=sub)
res = lm(DRxy~PV+Current,data=sub)
res = lm(DRxy~PV+Flux,data=sub)

PV = c(NA,sub$DRz[1:length(sub$DRz)-1])
res = lm(DRz~PV+Density,data=sub)
res = lm(DRz~PV+Current,data=sub)
res = lm(DRz~PV+Flux,data=sub)

# Nearest Neighbor Distance
sub = subset(data, !is.na(data$NNz))

PV = c(NA,sub$Nnxyz[1:length(sub$Nnxyz)-1])
res = lm(Nnxyz~PV+Density,data=sub)
res = lm(Nnxyz~PV+Current,data=sub)
res = lm(Nnxyz~PV+Flux,data=sub)

PV = c(NA,sub$Nnxy[1:length(sub$Nnxy)-1])
res = lm(Nnxy~PV+Density,data=sub)
res = lm(Nnxy~PV+Current,data=sub)
res = lm(Nnxy~PV+Flux,data=sub)

PV = c(NA,sub$NNz[1:length(sub$NNz)-1])
res = lm(NNz~PV+Density,data=sub)
res = lm(NNz~PV+Current,data=sub)
res = lm(NNz~PV+Flux,data=sub)

# Test Assumptions & Examine Results
durbinWatsonTest(res)
layout(matrix(1,1,1)); hist(resid(res));
layout(matrix(c(1,2,3,4),2,2)); plot(res);
Anova(res, type = "III")
```

and yielded the following ANOVA table for the response variable 3-D distance to refuge (DRxyz):

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.000836	0.000836	4.628539	0.036021
Density	1	0.000567	0.000567	3.136207	0.082322
Residuals	53	0.009574	0.000181		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.000836	0.000836	4.750064	0.033762
Current	1	0.000811	0.000811	4.610093	0.036378
Residuals	53	0.009329	0.000176		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.000836	0.000836	4.709266	0.034503
Flux	1	0.000731	0.000731	4.11528	0.047535
Residuals	53	0.00941	0.000178		

The above code also yielded the following ANOVA table for the response variable horizontal distance to refuge (DRxy):

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.005132	0.005132	5.038727	0.028984
Density	1	0.004213	0.004213	4.135985	0.047
Residuals	53	0.053985	0.001019		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.005132	0.005132	4.965156	0.030129
Current	1	0.003413	0.003413	3.301733	0.074863
Residuals	53	0.054785	0.001034		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.005132	0.005132	5.088793	0.028233
Flux	1	0.004744	0.004744	4.703701	0.034605
Residuals	53	0.053454	0.001009		

The above code also yielded the following ANOVA table for the response variable verticall distance to refuge (DRz):

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.013165	0.013165	11.11843	0.001565
Density	1	0.020598	0.020598	17.39544	0.000113
Residuals	53	0.062757	0.001184		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.013165	0.013165	11.19503	0.001513
Current	1	0.021027	0.021027	17.8804	9.34E-05
Residuals	53	0.062327	0.001176		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.013165	0.013165	12.217	0.000966
Flux	1	0.026241	0.026241	24.35092	8.35E-06
Residuals	53	0.057113	0.001078		

The above code also yielded the following ANOVA table for the response variable 3-D nearest neighbor distance (NNxyz):

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.010075	0.010075	4.608742	0.040015
Density	1	0.016028	0.016028	7.331876	0.011076
Residuals	30	0.065582	0.002186		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.010075	0.010075	5.191745	0.029981
Current	1	0.023392	0.023392	12.05433	0.001591
Residuals	30	0.058217	0.001941		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.010075	0.010075	5.46027	0.026322
Flux	1	0.026255	0.026255	14.22945	0.000711
Residuals	30	0.055354	0.001845		

The above code also yielded the following ANOVA table for the response variable horizontal nearest neighbor distance (NNxy):

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.008527	0.008527	4.010079	0.054339
Density	1	0.016198	0.016198	7.617283	0.009761
Residuals	30	0.063795	0.002127		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.008527	0.008527	4.563305	0.04094
Current	1	0.023932	0.023932	12.80691	0.001198
Residuals	30	0.056061	0.001869		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.008527	0.008527	4.75677	0.037156
Flux	1	0.026212	0.026212	14.62175	0.000618
Residuals	30	0.053781	0.001793		

The above code also yielded the following ANOVA table for the response variable vertical nearest neighbor distance (NNz):

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.000168	0.000168	0.151942	0.69944
Density	1	0.000755	0.000755	0.681515	0.415582

Residuals	30	0.033251	0.001108

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.000168	0.000168	0.159355	0.692579
Current	1	0.002302	0.002302	2.178457	0.150375
Residuals	30	0.031704	0.001057		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PV	1	0.000168	0.000168	0.156964	0.694771
Flux	1	0.001819	0.001819	1.695676	0.202764
Residuals	30	0.032187	0.001073		

Differences in slopes were tested in R using the following code:

```
data=read.csv(file.choose(),na.strings="-",colClasses = c("NN" =
   "numeric"))  # Load data file

# Compare slopes of distance to refuge
sub = subset(data,!is.na(data$DR))

res = lm(DR~Current*Dim,data=sub)
res = lm(DR~Density*Dim,data=sub)
res = lm(DR~Flux*Dim,data=sub)

# Examine results of model
durbinWatsonTest(res)
shapiro.test(resid(res))
layout(matrix(1,1,1)); hist(resid(res));
layout(matrix(c(1,2,3,4),2,2)); plot(res);
Anova(res, type = "III")
```

and yielded the following ANOVA tables for response variable distance to refuge (DR):

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Current	1	0.005983	0.005983	5.336138	0.022754
Dim	1	0.375033	0.375033	334.4771	3.85E-35
Current:Dim	1	0.03344	0.03344	29.82346	2.97E-07
Residuals	110	0.123338	0.001121		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Density	1	0.003943	0.003943	3.621612	0.059648
Dim	1	0.375033	0.375033	344.4421	1.13E-35
Density:Dim	1	0.039048	0.039048	35.86269	2.71E-08
Residuals	110	0.119769	0.001089		

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Flux	1	0.005624	0.005624	5.437973	0.021524
Dim	1	0.375033	0.375033	362.6261	1.30E-36
Flux:Dim	1	0.043373	0.043373	41.93797	2.72E-09
Residuals	110	0.113764	0.001034		

Logistic regressions were run on presence and absence of foraging fishes using the following R code:

```
data=read.csv(file.choose(),na.strings="-")  # Load data file
sub=subset(data,!is.na(data$PA))

curr = glm(PA~Current,data=sub,family=binomial("logit"))
den = glm(PA~Density,data=sub,family=binomial("logit"))
flux = glm(PA~Flux,data=sub,family=binomial("logit"))

predict(curr,newdata=data.frame(Current=c(0.06117,0.06118)),type="response"
   )  # Middle is 0.0612 m/s
predict(den,newdata=data.frame(Density=c(913.7,913.8)),type="response")  #
   Middle is 914 individuals m-3
predict(flux,newdata=data.frame(Flux=c(58.66,58.67)),type="response")  #
   Middle is 58.7 individuals m-2 s-1

# Model Analysis
Anova(curr,type="III")
Anova(den,type="III")
Anova(flux,type="III")

# Beta Coefficient
exp(coef(curr))
exp(coef(den))
exp(coef(flux))
```

which produced the following ANOVA tables:

	Df	Deviance	Resid. Df	Resid. Dev
NULL			90	120.2761
Current	1	50.12073	89	70.15534

	Df	Deviance	Resid. Df	Resid. Dev
NULL			90	120.2761
Density	1	9.133798	89	111.1423

	Df	Deviance	Resid. Df	Resid. Dev
NULL			90	120.2761
Flux	1	34.11972	89	86.15635

תקציר

קיום בצוותא (coexistence) יכול להתרחש כאשר קיימת הקצאה (עקרון ההקצאה; trade-off principle) בין שני מינים לאורך ציר של הטרוגניות. בהרבה מקרים, ההקצאה כוללת משחר שיותר יעיל בהיעדר סיכון ומשחר שיותר יעיל בנוכחות סיכון, ובכך התלות בהקצאה של מזון ובטחון. למידה של קיום בצוותא והקצאות של מזון ובטחון סייעה בהבנת המנגנונים הפועלים בתוך חברות תוך התייחסות להרבה מהשאלות הקשורות למבנה שלהן. במחקר זה, אני בוחן הקצאות של מזון ובטחון בסביבות מנוגדות; זה כולל אלמוגיות (damselfish) בשוניות האלמוגים בים האדום ומכרסמים גרניבוריים מהמדבריות של מוהאבי והנגב. בבחינה של סביבות אלו, אני משתמש בהקצאות של מזון ובטחון ואקולוגיה של שיחור מזון כדי לקדם את ההבנה של שאלות מסוימות הקשורות למבנה מרחבי, מבנה חברה ואישיות. אך אני גם דן בקווי דמיון פוטנציאליים בין חברות מנוגדות כאלו אשר עשויים לסייע לאקולוגים בעבודה לקראת השגת תיאוריות אקולוגיות כלליות יותר.

החלק הראשון של מחקר זה הוא הרחבה תיאורטית של מודל ניצול כתם אופטימלי (optimal patch use model) של Brown (1988), אשר צופה כי על פרטים לשחר בכתם עד אשר קצב צריכת הכתם (harvest rate) שלהם משתווה למחיר האנרגטי, לסכנת הטריפה ולמחיר של הפסד שיחור בכתם אלטרנטיבי. מודל זה, יחד עם הטכניקה של giving-up densities, יושם באופן נרחב בהרבה תחומים אקולוגיים, כולל אקולוגיה של שיחור מזון, אקולוגיה התנהגותית, אקולוגיה של שימור ואקולוגיה של חברות. למרות זאת, המודל מתעלם מהסביבה המרחבית ומאינטראקציות ישירות של משחרים, אשר מגביל את ההבנה של תפוצת בעלי-חיים וניצול כתם (patch use) לאורך זמן. אנו מרחיבים את המודל המקורי כדי לכלול את האינטראקציות והסביבה המרחבית של המשחר תוך שמירה על הפוטנציאל לשינויים מרחביים לאורך זמן. על-ידי שימוש במודל זה ובאלמוגיות פלנקטיבוריות כדוגמה, אנו עושים תחזיות לגבי מנגנונים המאפשרים צורות חיים של היצמדות לאתר (למשל, *Dascyllus* sp., *Chromis* sp.) ופלגיות (למשל, *Caesio* sp.) שנצפו בדגים פלנקטיבוריים. המודל מציע שהיצמדות לאתר מתרחשת כאשר המחיר האנרגטי ו/או מחיר הטריפה גבוהים והם דוחפים את המשחר קרוב יותר למפלט. כאשר מחירים אלו נמוכים, משחרים צריכים במקום זאת לנוע גבוה יותר לתוך עמודת המים ולהתפשט אופקית. אנו גם משתמשים במודל החדש כדי לחזות תפוצת קבוצות, המראה כי כאשר רווח אנרגטי מאינטראקציות של משחרים גדול מהמחיר האנרגטי שלהם ו/או המחיר של בידוד גדל, אז דגים יוצרים להקות. כאשר ההפך הוא נכון, פרטים יהיו סוליטריים. המשך דיון של תוצאות אלו והרלוונטיות של המודל למערכות אחרות (למשל, דינמיקה חברתית של fission-fusion) מספק תמונה פשוטה, אך יותר שלמה של ניצול כתם לאורך טווח של תחומים וסביבות.

בחלק השני של המחקר, המסגרת התיאורטית משמשת כדי להתחיל בבניית הבנה מנגנונית של מבנה מרחבי בשוניות אלמוגים. מרחב הוא גורם מגביל בשונית אלמוגים אשר הוביל להיפותזות רבות המסבירות את המבנה המרחבי שנצפה. למרות היפותזות רבות אלו במשך עשרות שנים של מחקר, חסרה הבנה מנגנונית המסבירה מדוע התפתחו מבנים מרחביים אלו. אחד המבנים המרחביים הנפוצים ביותר בשוניות אלמוגים הוא היצמדות לאתר (site-attachment) של דגים פלנקטיבוריים. כאן אנו מפעילים טכנולוגיה אקוסטית ואופטית בשיטה חדשה כדי ללמוד את התנהגות שיחור המזון של אלמוגית צמודת-אתר (*Dascyllus marginatus*) והשימוש שלה במרחב. מדידות אקוסטיות של צפיפות טרף, מידת זרם, ושטף טרף כולל, בעוד אופטיקה במערך סטריאו מספקת את קואורדינטות X, Y ו- Z של כל דג בקבוצה. בשילוב עם משוואת ניצול כתם תיאורטית, המיקום של הדגים משווה לעושר הכתם לאורך מימדים מרחביים שונים כדי לקבוע כיצד מופחתות עלויות השיחור. תוצאות המחקר מראות כי *D. marginatus* השתמשה במימד האנכי כדי לשלוט בעלויות האנרגיה וסכנת הטריפה ובמישור האופקי כדי לטפל בעלויות התחרות. תוצאות אלו מציעות שהיצמדות לאתר מתרחשת בגלל ש: 1) ההתנהגות האופטימלית היא לנוע אנכית מעל מפלט, ובכך הבקרה על אנרגיה ובטחון ו-2) טרף חייב להתחדש בקצב גבוה מספיק למניעת רָעָב באתר ההיצמדות. כמו כן, אנו מתארים ספים של התנהגות שיחור מזון ודנים בהשלכות של התוצאות על הבנת היררכיות קבוצתיות. מחקר זה תורם להבנה מנגנונית של המבנה והשימוש במרחב שנצפה בשוניות אלמוגים.

בחלק השלישי, המוקד עובר מאוקיינוסים לסביבות יבשתיות והקצאות של מזון ובטחון בחברות של מכרסמים מדבריים גרניבוריים. מחקרים אקולוגיים של 1960 ו-1970 ועד ימינו הגיעו לרוב למסקנה שכל חברה היא ייחודית ואין חוקים ידועים כלליים או מנגנונים הפועלים ליצירת המבנה הייחודי שלה (Lawton 1999). מאז, הושגה התקדמות בתחומים של מנגנונים של קיום בצוותא, הקצאות של מזון ובטחון, ומשחקי שיחור, אשר עשויים לאפשר לנו להעריך טוב יותר מה גורם לחברות בסביבות דומות להיות כל כך שונות. באמצעות ניסוי גן משותף (Common Garden) בויווריום, אנו מדמים חברה טבעית של מכרסם מדברי של שני מיני גרבילים (*Gerbillus andersoni allenbyi* ו- *Gerbillus pyramidum*) בנוכחות של תנשמות, עכני חרטומים, ועכסנים לא מוכרים. מחקר זה מתבסס על ניסויים חד-מיניים קודמים כדי להראות את ההשפעות של תחרות בין-מינית וגודל גוף על תכונות החברה. בנוסף, ההשפעות של נחשים טורפים בעלי איברי חישת חום על עלויות השיחור של מכרסמים מושוות באמצעות שני מיני הנחשים. התוצאות עולות בקנה אחד עם מאפיינים המעידים על חברות טבעיות כולל ארגון צנטריפוגלי. ראיות התומכות בהשגת דו-קיום נראו בהקצאות בעיתוי הארת ירח במהלך מחזור הירח, אשר עשוי לאפשר למכרסמים לשקם מצב אנרגטי במהלך מקטעים עדיפים. בנוסף, גודל גוף תרם לזכייה בתחרות הפרעה, אך גם הועיל בטיפול במספר רמות סיכון במקביל, יכולת שכנראה הושפעה מבולות שמיעה גדולות. לבסוף, מכרסמים שינו את התנהגות השיחור שלהם בנוכחות הצפעוני-גומה (pit vipers) כדי להימנע ממופע סהרון מחסיר במחזור הירח תוך הימנעות מהעכנים (true vipers) במהלך מופע הירח לקראת מילא. תוצאות אלו מניחות את התשתית לניסויים עתידיים לבחון את ההיווצרות של חברות מכרסמים מדבריות ואת ההשפעות של התאמות שוברות-אילוצים (constraint-breaking adaptations) עליהן.

החלק הרביעי נבנה מהשלישי בכדי לערוך השוואות בין-יבשתיות בחברות מלאכותיות. במהלך העשורים האחרונים, אקולוגים התקדמו בהבנתם של קיום בצוותא ומבנה חברה. עם זאת, אני עדיין לא לגמרי מבין מה מבדיל מנגנונים בחברה אחת ממנגנונים בחברה דומה לכאורה. כאן אני מסתמך על מחקרים קודמים כדי לערוך השוואות בין-יבשתיות בתוך חברות ניסיוניות מלאכותיות כדי לבחון את ההשפעות הפוטנציאליות של התאמות שוברות-אילוצים (כיסי לחיים חיצוניים, תנועה ביפדלית, ואיברי חישת חום). מכרסמים מדבריים דומים בגודלם (*Chaetodipus penicillatus* עם *Dipodomys merriami* ו-*Gerbillus andersoni allenbyi* עם *G. pyramidum*) ממדבריות צפון אמריקה והמזרח התיכון, בהתאמה, שיחרו ממגשי מזון בתנאים משתנים הכוללים נוכחות תנשמת, מיקרו בית גידול, מיני צפע, ומחזור ירח. ה- giving-up densities חשף תמיכה מועטה לכיסי לחיים חיצוניים ותנועה ביפדלית כהתאמות שוברות-אילוצים. במקום זאת, גדלי הגוף הדומים ייצרו מאפיינים המעידים על דחיקה תחרותית, ובכך תומכים בהשערת הדמיון המגביל (limiting similarity hypothesis). אף על פי כן, התאמות שוברות-אילוצים עדיין עשויות להיות חשובות מאחר ואיברי חישת החום בצפעוני-גומה שינו את פעילות השיחור של כל המכרסמים למעט *D. merriami*. אני מציע שהתאמות שוברות-אילוצים כן משחקות תפקיד במנגנונים של קיום בצוותא אבל בחשיבות פחותה לעומת תחרות על משאבים.

בחלק החמישי, המיקוד עובר לרמת האוכלוסייה לבחון כיצד הבדלי הקצאות של מזון ובטחון יכולים לתרום ליצירה ושימור של הבדלי התנהגות בין פרטים. נורמות תגובה של התנהגות, או אישיות, נעשים למובנים יותר, אך הבנת יצירתם ושימורם באמצעות תהליכים אבולוציוניים רק בראשית דרכה. מספר מחקרים מראים כי טריפה ומשאבים הם מרכיבים חשובים של תהליך זה. כאן אנו בוחנים האם אישיות בעלי-חיים קשורה לאופן בו גרבילים מדבריים מנהלים סיכון טריפה ואת ההקצאה של מזון ובטחון. לשם כך, דירגנו פרטים של גרביל אלנבי (*Gerbillus andersoni allenbyi*) לארבע קבוצות לפי התנהגויות גישוש (exploratory behavior) שונות (נועז חזק עם רמת הגישוש הגבוהה ביותר וביישן חזק עם הרמה הנמוכה ביותר) וחשפנו אותם בסביבת ויווריום לסימני סיכון טריפה ישירים ועקיפים, הכוללים נוכחות תנשמת, מיקרו בתי גידול עם ובלי מחסה, ומחזור הירח. עלויות שיחור ופעולות ניצול כתם לכל קבוצה נקבעו מ- giving-up densities (GUD) וקליפות זרעים (husks) לאחר פעילות לילית בכתמי משאבים מלאכותיים (מגשי זרעים). בנוסף, הקלטות וידאו של ניצול כתם, נתוני עקבות, ומסת מכרסם אפשרו חישוב ובחינה של עקומת קצב צריכה, ניצול כתם, ומצב אנרגטי. פרטים נועזים היו בעלי GUD נמוך, קילפו זרעים בכתם בתדירות נמוכה, והשתמשו יותר בחלוקת זמן, התנהגות המצביעה על אסטרטגיה של לתפוס וללכת (grab and go strategy), בעוד שפרטים ביישנים השתמשו בעיקר

בדריכות (vigilance) לניהול סיכון הטריפה. הבחנות כאלה בהתנהגות ניהול סיכונים בין פרטים השונים זה מזה בהתנהגות הגישוש שלהם מציעות כי ייתכן ודפוסי אישיות מגוונים באוכלוסיה נוצרו והשתמרו דרך תלות בתדירות (frequency dependence) ו/או הקצאות מסורתיות לאורך צירי הטרוגניות.

יחד, כל אחד מחמשת מרכיבים אלה מקדם לקראת התמודדות עם שאלות אקולוגיות הכוללות הקצאות של מזון ובטחון ותיאוריית שיחור מזון. הקצאות של מזון ובטחון יכולות להסביר את ההיצמדות לאתר של אלמוגית פלנקטיבורית, מאפשרות השוואות בין-יבשתיות בחברות מכרסמים מלאכותיות, ומציעות מנגנונים לשימור של התנהגויות שונות או דפוסי אישיות בתוך אוכלוסיות מכרסמים. בעוד שתיאורייה כללית של תהליכים אקולוגיים עדיין רחוקה מלהיות מסוכמת, התוצאות שהוצגו כאן מראות כי התנהגות של אורגניזמים שעשויה למקסם כשירות (fitness) יכולה לסייע בהסברת מבנים, חברות ודפוסי אישיות מנוגדים אשר נצפים בטבע.

מילות מפתח: נועזות, תחרות, התאמות שוברות-אילוצים, מבנה מרחבי של שונית אלמוגים, מכרסמים מדבריים, התנהגות גישוש, עלויות שיחור, תיאוריית שיחור מזון, *גרביל, גרביל אלנבי*, giving-up density, *Dascyllus marginatus*, מפרץ אילת/עקבה, עקומת קצב צריכה, ירבועניים, קילוף זרעים, השוואת חברות בין-יבשתיות, אלמוגית שחורת-שוליים, אישיות, צפעון גומה, סיכון טריפה, ניהול סיכונים, אלמוגית פלנקטיבורית צמודת-אתר, ניצול כתם במרחב, ניצול כתם בזמן, חלוקת זמן, הקצאות של מזון ובטחון, דריכות

הצהרת תלמיד המחקר עם הגשת עבודת הדוקטור לשיפוט

:אני אוסטין דיקסון החתום מטה מצהיר/ה בזאת : (אנא סמן)

X חיברתי את חיבורי בעצמי, להוציא עזרת ההדרכה שקיבלתי מאת

X החומר המדעי הנכלל בעבודה זו הינו פרי מחקרי מתקופת היותי תלמיד/ת מחקר.

X בעבודה נכלל חומר מחקרי שהוא פרי שיתוף עם אחרים, למעט עזרה טכנית הנהוגה בעבודה ניסיונית. לפי כך מצורפת בזאת הצהרה על תרומתי ותרומת שותפי למחקר, שאושרה על ידם ומוגשת בהסכמתם.

שם התלמיד/ה : אוסטין תאריך : 10-מרץ-2017 חתימה : ____________________

הצהרה של מחבר התוכן:

בעבודה נכלל חומר מחקרי שהוא פרי שיתוף עם אחרים. ההצהרות הבאות מתארות את התרומות על-ידי ועל-ידי שותפי למחקר, שאושרו על-ידם ומוגשות בהסכמתם.

<u>תיאורטי</u>: ניצול כתם כאינדיקטור להעדפת בית גידול, סכנת טריפה, ותחרות לאורך מרחב וזמן.

אני פיתחתי את התיאוריה ותוצאותיה החזויות. ז׳ורז׳ פ.ס. מנסז וברט פ. קוטלר סיפקו הדרכה וסיוע באיך לבצע מודלים תיאורטיים, לרבות נגזרות מתקדמות ודיונים על הדרך הטובה ביותר לתאר את הטבע באמצעות מתמטיקה.

<u>אלמוגית</u>: גישה מכניסטית להבנת המבנה המרחבי של פלנקטיבורית צמודת-אתר.

הייתי החוקר הראשי במחקר והאחראי על תכנונו, יישומו, ניתוחו וכתיבתו. דימיטרי צ׳ורילוב ואלכסנדרה קרוזמן סייעו בפיתוח השיטות והוצאתו לפועל של ניסוי זה. מלבד סיוע עם העבודה הפיסית של הפעלת סונאר זואופלנקטון ומערכות אחרות, הם עזרו לנתח הרבה מהניתוח הראשוני של מידת הזרמים והשפע של זואופלנקטון. אמציה גנין היה אדיב מספיק כדי לארח אותי והעניק לי גישה חופשית למעבדתו ולמשאביו. בנוסף, הוא וברט פ. קוטלר סיפקו הכשרה והדרכה דרך החלקים השונים של המחקר.

<u>חברת גרבילים</u>: החשיבות של גודל גוף והתאמות שוברות-אילוצים בהַבְנָיַת חברות.

אני גיבשתי את תכנון הניסוי תוך הוספת הארת הירח ועיתויו. בנוסף, אני הרצתי את הניסוי וניתחתי את תוצאותיו. ברט פ. קוטלר יצר את תכנון הניסוי הראשוני וסיפק הדרכה לאורך הניסוי וניתוחו.

<u>השוואות בין-יבשתיות</u>: השפעות של התאמות שוברות-אילוצים על שתי חברות מכרסמים מדבריות מלאכותיות בין-יבשתיות.

אני גיבשתי את תכנון הניסוי תוך הוספת הארת הירח ועיתויו. בנוסף, אני הרצתי את הניסוי וניתחתי את תוצאותיו. ברט פ. קוטלר יצר את תכנון הניסוי הראשוני וסיפק הדרכה לאורך הניסוי וניתוחו.

<u>אישיות</u>: שונות בניהול סיכונים בין גרבילים (Gerbillus andersoni allenbyi) עם התנהגויות גישוש/נועזות שונות.

אני גיבשתי את התכנון והובלתי את עבודת היווריום. אחר-כך, אני גם ניתחתי את הנתונים. ז׳ורז׳ פ.ס. מנזס וקינמון מוריסון סייעו וסיפקו תובנות לאורך התכנון, התפעול, והניתוח של מחקר זה. ברט פ. קוטלר גם סיפק הדרכה בתכנון וניתוח של מחקר זה.

העבודה נעשתה בהדרכת

פרופסור ברט פ. קוטלר
,במחלקה לאקולוגיה על שם מטרני
המכונים לחקר המדבר ע״ש יעקב בלאושטיין
אוניברסיטת בן-גוריון בנגב

עקרון ההקצאה בסביבות מנוגדות:
מהמדבריות של מוהאבי והנגב אל שוניות האלמוגים של אילת

״מחקר לשם מילוי חלקי של הדרישות לקבלת תואר ״דוקטור לפילוסופיה

מאת

אוסטין דיקסון

הוגש לסינאט אוניברסיטת בן גוריון בנגב

מאושר על ידי:

ברט קוטלר
(מנחה)

מיכל שפירא
(דיקן בית הספר ללימודי מחקר מתקדמים ע״ש קרייטמן)

י״ט שבט תשע״ז
10-מרץ-2017
באר שבע

עקרון ההקצאה בסביבות מנוגדות:
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