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Testing Marginal Value Theorem in *Saimiri sciureus*

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Testing marginal value theorem in *Saimiri sciureus*

By

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A Proposal Submitted to the Honors Council

For Honors in Animal Behavior

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Approved by:

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Abstract

Marginal value theorem (MVT), a key component of optimal foraging theory, aims to model how an individual will most efficiently utilize a resource distributed in patches of varying size and value throughout a habitat. Among the fundamental assumptions of MVT is that foragers will maximize their net energy gain by foraging in a resource patch until reaching the average rate of intake for the habitat. This “give-up time” (GUT) per patch, defined as the time between the final prey capture and departing the patch, should remain constant throughout the habitat as a whole, but vary across habitats of different quality. For example, a rich habitat should have a shorter GUT than that of a poorer habitat because it takes less time to lower the density of each patch to that of the average rate of intake for the habitat. Though tested and supported in avian studies, marginal value theorem has not been thoroughly tested in primates. This study tested whether foraging behavior of captive common squirrel monkeys (*Saimiri sciureus*) conformed to the assumptions of marginal value theorem. In keeping with the predictions of MVT, I hypothesized that there would be a significant difference in GUTs for rich and poor habitat manipulations and no difference in the GUTs of patch types within each manipulation.

Subjects foraged on an experimental tree made out of PVC pipe and consisting of twelve horizontal branches stratified into three layers of four branches. A wooden platform supporting six evenly spaced capped film canisters, each containing a small mealworm, was positioned at the end of each branch with each platform signifying a distinct resource patch. Two individuals were selected for use in data collection based on their willingness and aptitude for navigating between feeding platforms and successfully opening the film canisters containing food rewards. Testing included two experimental manipulations, rich and poor, which varied in the number of canisters on each platform that contained mealworms. The rich habitat contained more mealworms per platform than the poor habitat. Furthermore, both manipulations contained two patch types that also varied in the number of mealworms. Trials consisted of releasing one subject into the enclosure containing the experimental tree and recording arrival at a patch, opening a canister, ingesting a mealworm, and departing a patch until all canisters had been opened. Each subject participated in an equal number of rich and poor manipulation tests.

Two-way repeated measures ANOVA comparing GUTs showed that as predicted, the GUT of the poor manipulation was significantly higher than that of the rich and there was no

significant difference in GUTs between the two patch types in the rich manipulation. However, the two patch types in the poor manipulation were significantly different, which contradicted the predictions of MVT. Results demonstrated some evidence for optimal foraging in squirrel monkeys, providing a basis for continued research in this area.

Introduction

Optimal foraging theory attempts to explain how animals forage in an environment so as to maximize energy intake per unit time, taking into account not only the energy gains for food items, but also the energy costs associated with gathering these items (Stephens & Krebs, 1986). Because acquiring food is essential for fitness, the basic concept of optimal foraging seems intuitive in the context of evolution by natural selection, especially given that food is rarely available in excess. If natural selection maximizes fitness and optimal foraging increases fitness, then through natural selection organisms should evolve to exhibit optimal foraging behavior as they navigate their environment for resources. Consequently, foraging researchers often assume that animals use strategies to maximize their energy intake per time (Stephens & Krebs, 1986). Using examples in human foraging, imagine you are berry picking. You gather the berries from a single bush until the density within that bush decreases to a point at which the berries become difficult to find, but are not necessarily entirely depleted. At this marginal capture rate, you would gather berries at a faster rate by heading to the nearest berry bush than by staying at the same one until none remain. Without really devoting conscious thought to calculating at what point the density has sufficiently decreased before it is worth moving to the next bush, we may have *a priori* knowledge of when to move to a new patch as depletion occurs. Though the example may seem oversimplified for human behavior, optimal foraging has been successfully used at the theoretical level in early hominids (Kurland & Beckerman, 1985) and more directly in modern hunter-gatherer societies (Hill, Kaplan, Hawkes & Hurtado, 1987).

Optimal foraging theory models several different aspects of foraging including meeting nutrient needs, patch choice, patch residence time, and movement between patches (Pyke,

Pulliam & Charnov, 1977). Furthermore, optimal foraging models diverge into three separate categories that vary by foraging environment. Prey models deal with discrete items as first formulated in Schoener (1971), patch models deal with heterogeneous clumps, and hybrids combine aspects of the previous two (Stephens & Krebs, 1986). This manuscript will focus on patch models. As in the berry picking example, food items generally occur in spatially distinct resource patches that are distributed heterogeneously through an environment. These patches generally vary in value, so foragers must select the most profitable patches, but most of the time the profitability of patches is unknown until sampled by the predator, tying the decision of selecting profitable patches to that of moving from one patch to the next (MacArthur & Pianka, 1966). A decade after MacArthur & Pianka (1966) brought the question of optimal foraging into the fore, a mathematical model called marginal value theorem (MVT) was proposed by Charnov (1976) to explain how foragers navigate their environment so as to maximize energy intake per time based on an optimal patch residence time. MVT operates under the following assumptions:

1. Patches are discrete from one another.
2. Patches are encountered sequentially and never simultaneously.
3. Travel time between patches exceeds the time between prey captures within a patch.
4. Searching for and searching within patches cannot occur simultaneously.
5. Rate of intake within a patch decreases with time spent in that patch.

If these assumptions are met, the following equations should predict the marginal rate that determines the optimal time spent in each of any number of patch types within a given environment. It is also important to note that the travel time between patches should be independent of the time spent within any one patch. The reverse statement, however, is not true because as travel time changes independently, the residence time in that patch must change to

meet the energy costs of travel. In accordance with the methods of this thesis, the equations are shown with two patch types denoted with P_A and P_B for the proportion of total patches in an environment as patch type A or B and T_A and T_B for the time spent in the respective patch type. Furthermore, patch types are defined as varying in the food density they contain and habitat types are similarly delineated by their overall food density. In addition, t represents the travel time between patches. With these variables, the average time to use a single patch (T_u) is the travel time plus the proportion of each patch type times the respective time spent in that patch.

$$(1) T_u = t + P_A T_A + P_B T_B$$

If g is the assimilated energy for foraging after accounting for the cost of searching, the average energy intake from a single patch (E_e) is as follows:

$$(2) E_e = P_A \cdot g(T_A) + P_B \cdot g(T_B)$$

Using results of equations (1) and (2) and denoting the energy associated with travel time as E_T , one can calculate the net energy intake rate (E_n).

$$(3) E_n = (E_e - E_T(t)) / T_u$$

With E_n known, the optimal time for a given patch type can be found with the following equation where T_i is used for either T_A or T_B and ∂ denotes a partial differentiation:

$$(4) \partial E_n / \partial T_i = 0$$

T_i can then be plugged into a final equation to find the marginal capture rate (E_n^*).

$$(5) \partial g(T_i) / \partial T_i = E_n^*$$

Equations (4) and (5) respectively optimize time spent and energy intake rate of a given patch type, but this study is concerned with equation (5) because E_n^* should be constant across all patch types in an environment. MVT therefore makes three predictions:

1. Foragers should depart a patch when the rate of food intake reaches the marginal capture rate.
2. Foragers should consequently stay longer in higher quality patches within a habitat because more time must be spent depleting prey to reach the marginal capture rate.
3. As travel time between patches increases relative to the quality of each patch, time spent within each patch should increase to compensate for energy lost through travelling.

Foragers should accordingly spend more time in patches within a poor habitat than a rich one independent of patch type because travel time has a higher energy cost relative to the overall quality of patches.

After the establishment of MVT, Krebs, Ryan & Charnov (1974) produced one of the first studies supporting Charnov's model (which had not yet been published) by measuring giving-up time (GUT), which is the time between the final food capture within a patch and departing that patch. Originally a term coined by Croze (1970), giving-up time is essentially a measure of persistence, the time a forager is willing to continue searching for a prey item without

success. Prey capture rate within a patch decreases with time as the resource is depleted before reaching a marginal capture rate wherein the energy expenditure of foraging begins to exceed the energy gain of food consumption. With the additional assumption that all prey are of similar size and have a brief handling time, the average capture rate should be the inverse of the average intercatch interval. If one prey item is caught per intercatch interval, then one over the average interval (i.e., unit per time) should yield the average capture rate. Because the marginal capture rate for any patch is based on the average rate for the environment and GUT varies with the intercatch interval, GUT is independent of patch type and similarly the inverse of the average capture rate. Though GUT varies inversely with the average capture rate and so remains the same across patch types, this rate, and consequently GUT, differs across habitats. Rich habitats with a higher prey density will have a higher average capture rate than poorer ones and therefore a shorter GUT. In summary, the rate of prey capture within a patch decreases with the density of prey in that patch. Once this rate falls below the average rate for a habitat, the forager would gain more energy per time by travelling to a new patch with higher density and therefore a higher rate of prey capture. Consequently, optimal foraging theory predicts that rich habitats will have significantly shorter give-up times (GUTs) than poor habitats because foragers require less time within a patch before reaching the average rate of intake for the habitat as a whole. It also predicts a constant GUT within habitats regardless of patch type.

Across all trials, a rich habitat should have a significantly lower average GUT than a poor habitat. There should also be no significant difference in GUTs between high and low quality patch types within the same condition due to a higher marginal capture rate (Krebs *et al.*, 1974) where both patch type and habitat type vary by the density of food items they contain. By comparing GUT between habitat types that vary in their prey density and showing that GUT is

significantly shorter in a rich habitat, one can verify the first prediction of MVT that foragers should stay in a patch until reaching the marginal capture rate. Figure 1 shows a graph from Krebs *et al.* (1974) that demonstrates this relationship and also shows how time spent in a patch should increase in poorer habitats to compensate for energy lost during travel. Since this seminal study, most tests of MVT have measured patch residence time or food capture rates and abandoned GUT altogether (Pyke *et al.*, 1977). High quality patches should have a significantly longer residence time than low quality patches within any habitat type because more foraging time is required to reach the marginal capture rate. Poor habitats should also have significantly longer average patch residence times than rich habitats because more energy is needed to compensate for a proportionally longer travel time between patches. In the interest of testing all three predictions of MVT, this research will examine both GUT and patch residence time.

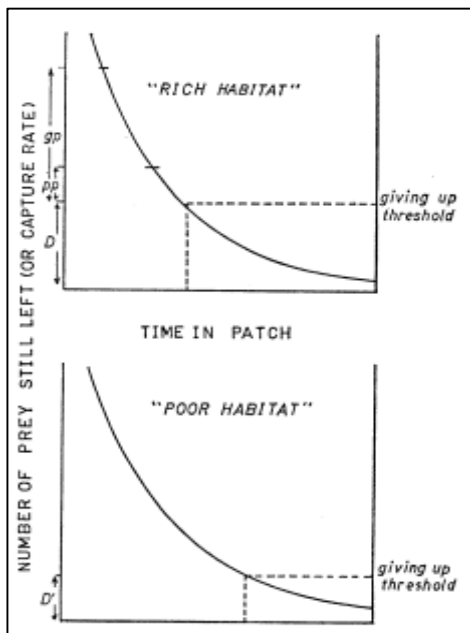


Figure 1. Compares the decrease of capture rate with time in rich and poor habitats from Krebs *et al.* (1974). The horizontal dotted line represents the giving-up threshold, which directly coincides with the marginal capture rate. The corresponding vertical line is the optimal time spent within a patch in accordance with the marginal capture rate. Because the giving-up threshold/marginal capture rate in the rich habitat is higher than in the poor habitat, the GUT should be shorter and the patch residence time should be greater.

Krebs *et al.* (1974) used the above theory to evaluate MVT by allowing black-capped chickadees (*Parus atricapillus*) to forage across a room full of tree-like apparatuses stocked with food items. Their results confirmed the predictions of MVT as translated to GUT measurements by showing that GUT was constant across patch types within a single habitat type, but was significantly shorter in rich habitats than poor ones. Though Krebs *et al.* (1974) was in many ways the foundation of this thesis in both its theory and methodology as well as a highly cited article in optimal foraging research, beyond it there is a rich literature on MVT and examining the patch model question of when to leave a patch. The only other study that used GUT studied foraging in the context of a parasitoid wasp (*Nemeritis canascens*) seeking hosts across Petri dishes that varied in their host density (Hubbard & Cook, 1978). The experiment demonstrated both constant marginal rate and GUT across patch types.

Most other non-primate research on when to leave a patch has focused on birds, including yet another highly cited paper by Cowie (1977) that tested MVT in great tits (*Parus major*) foraging on a similar series of experimental trees as in Krebs *et al.* (1974). Patches consisted of lidded dishes packed with saw dust containing some amount of mealworm pieces. Due to a lack of space, the author artificially increased travel time in different experimental manipulations by altering the difficulty of removing the lid of each patch. An optimal curve was calculated for patch residence time versus travel time between patches before comparing observed data to these expected values, which revealed that patch residence time increased with travel time, aligning with the expected values of the calculated curve as predicted by MVT. Finally, Smith & Dawkins (1971) produced a study on great tits that not only indicated that the birds spent more time in higher quality patches, but also importantly that they had the ability to distinguish between high and low quality patches (i.e., detect differences in food density) without prior

knowledge about patch quality. However, the birds had difficulty differentiating between lower food densities and were slow to change their behavior as densities increased or decreased. This shows that at least in great tits, one cannot expect to see a change in optimal foraging behavior unless densities are sufficiently different and that individuals also require time to adjust their behavior when they can perceive density changes.

As reviewed above, the most successful optimal foraging research has been largely restricted to invertebrates and birds. Given the difficulties associated with creating models for simpler organisms such as invertebrates, primate researchers have often been reluctant to apply optimal foraging models to their subjects; however, the literature includes studies that both support and reject the predictions of MVT. Agetsuma (1998) experimentally tested MVT on Japanese macaques (*Macaca fuscata*) in the lab by presenting them with a sequence of either rich or poor patches simulated by two operant conditioning schedules. For both patch types, receiving food after pressing a bar resulted in an exponentially decreasing probability of reinforcement from subsequent bar presses so as to decrease intake rate with time spent in a patch. High quality patches had a probability of reinforcement twice as high as that of low quality patches. Results showed that subjects not only had a higher response rate in high quality patches, but also more importantly stopped responding to high and low quality patches within the same habitat type at roughly the same marginal rate. A field study on Geoffroy's spider monkeys (*Ateles geoffroyi*) and mantled howler monkeys (*Alouatta palliata*) in Costa Rica also supported MVT by showing that both species increased their time spent in a patch with increasing travel time and, in many patch types, exhibited a significantly lower rate of intake before leaving a patch compared to the rate during the first half of the time spent in the patch (Chapman, 1988). This second result suggested that depletion of food density within a patch

influenced departure time. This effect could not, however, be seen in howler monkeys feeding on leaves or spider monkeys foraging in particularly large fruit trees because these patch types were so large or dense that a single group of foragers could not cause significant depletion. If reaching a marginal capture rate did not cause departure in these cases, then other factors such as meeting specific nutrient demands or predator avoidance must have played an important role. A later study similarly found that red colobus monkeys (*Ptilocolobus tephrosceles*) showed significant decreases in rate of intake throughout the time spent in a patch, but this effect was only revealed in patches of young leaves, which represented only 63% of patches (Snaith & Chapman, 2005). The remaining patch types were all affected by the size of a patch and the number of conspecifics within that patch rather than the rate of intake. By measuring feeding bouts in flowering *Acacia tortilis*, Whitten (1988) found that rate of intake predicted patch size and density, both indicators of quality, in vervet monkeys (*Cercopithecus aethiops*). This relationship held despite patch size also increasing with group size, leading to more intragroup competition. Similarly, Japanese macaques evaluated patch quality by rate of intake, but the number of conspecifics greatly influenced the distribution of the troop across patches (Nakagawa, 1990a). If one patch had much higher quality than the other, a proportional number of individuals forwent the higher quality patch for the lower because their energy gains would be higher after accounting for intra-group competition. Both this study and that of Whitten (1988) only showed that the monkeys preferred foraging in higher quality patches, which seems like an obvious conclusion.

Other studies by Nakagawa (1989; 1990b) yielded the opposite conclusion, failing to support MVT. Neither study showed that Japanese macaques have a tendency to spend more time in higher quality patches. In addition, the subjects in Nakagawa (1990b) did not exhibit a

decreasing rate of intake with residence time in a patch, suggesting that this factor did not affect an individual's decision to depart the patch. Instead, departure was most often guided by the departure of conspecifics. Grether, Palombit & Rodman (1992) also thoroughly tested the predictions of MVT on white-handed gibbons (*Hylobates lar*) and siamang (*Hylobates syndactylus*). They found that although rate of intake declined with time spent in patches, these species of gibbon did not have a constant marginal capture rate nor did they spend more time in higher quality patches. In addition, the researchers were unable to decipher whether the declining rate of intake was due to depletion or satiation, leaving even this result ambiguous. Yet another study on Japanese macaques demonstrated that rate of intake did not decrease with time spent in a patch and patch quality did not even reliably predict patch residence time (Kazahari & Agetsuma, 2008). The main determinant of patch use and foraging efficacy was the use of that patch by conspecifics. The authors propose three mechanisms for this enhancement of foraging success in the presence of conspecifics. Scramble competition, or competitive pressure from conspecifics for indefensible resources, may lead individual foragers to increase their foraging rate. Social facilitation increases the frequency or intensity of a behavior when in the presence of conspecifics engaging in the same behavior. Lastly, the chance of straying from the group decreases with group size, so larger numbers of conspecifics allow individuals to focus more on foraging (van Shaik, 1989). A review of these studies on non-human primates that utilized rate of food intake to test optimal foraging models revealed that in the studies that failed to support MVT, social factors such as the number or departure of conspecifics replaced individual foraging efficiency as the primary driver of patch residence time (Nakagawa, 2009). Most recently, a study attempted to address a classical prey model, which assumes a foraging environment of discrete items instead of heterogeneous clumps as in a patch choice model such

as MVT, in a group of wild Himalayan langurs (Sayers, Norconk & Conklin-Brittain, 2010). This study at least partially supported most of the predictions of the classical prey model, but support for this model does little to provide support for the validity of MVT. It is worth noting that not a single primate study in the literature review above used GUT as a measurement for testing MVT.

Thus far, most optimal foraging research on non-human primates has focused on Old World monkeys with only Chapman (1988) supporting MVT by studying New World monkeys. This thesis subsequently aimed to expand the MVT literature on the underrepresented taxa of New World monkeys. Given the limited diversity of model species in previous research, *Saimiri sciureus*, the common squirrel monkey, was chosen for this research testing MVT.

Saimiri sciureus is a small monkey native to the tropics of South America that lives in large egalitarian multi-male, multi-female troops. Females and their offspring form the core of the group, while males typically spend their time on the fringes of the group with the exception of breeding season. Groups spend a great deal of their time moving through the mid-canopy searching for food. A study on *Saimiri sciureus* and *Saimiri oerstedii* showed that squirrel monkeys spent more than 50% of their activity budget foraging for invertebrate prey while travelling, while only ~10% of time each day was spent foraging on fruit and nectar, which occurs in distinct patches instead of being randomly encountered like invertebrates (Mitchell, Boinski & van Shaik, 1991). One *Saimiri sciureus* population spent as much as 75% of their activity budget foraging for randomly encountered invertebrates. Another study showed that 55% of the study population's diet consisted of fruits and flowers, while only 45% consisted of arthropods; however, these numbers varied greatly throughout the six month study period due to the seasonality of the study area (Lima & Ferrari, 2002). At its peak, arthropods comprised 80%

of the diet and plant matter 20%, but by the end of the study these numbers had reversed with arthropods becoming three times more difficult to capture as availability greatly decreased. Dietary composition varied significantly across different populations, but squirrel monkeys were generally identified as insectivore-frugivores.

Squirrel monkeys were well suited to this experiment because their small size and dexterity allowed them to interact effectively with the tree-like apparatus that contained evenly distributed platforms representing food patches. These platforms varied in the food density they contained allowing for high and low quality patches in each trial and rich and poor habitat trials based on the overall quality of the high and low quality patches therein. Using this method allowed the comparison of data within and between habitat types. The size and mild temperament of the monkeys also allowed the researcher to be close enough to accurately collect data. Using this apparatus, I tested the three main predictions of MVT:

1. Marginal capture rate (based on GUT) will be constant across patch types in the same habitat type, but will be higher in poor habitats due to a lower marginal capture rate.
2. Average residence time will be longer in high quality patches than low quality patches in the same habitat type.
3. Average residence time will be longer in poor habitats than rich ones.

For each of these predictions, I hypothesized the following:

1. Marginal capture rate, as measured in GUT, would not appear constant across patch types within a habitat type, but would be longer in poor habitats than rich ones.
2. Patch residence time will be longer in high quality patches than low quality patches within the same habitat type.
3. Patch residence time will be larger in poor habitats than rich ones.

Methods

Subjects

The Bucknell Primate Lab *Saimiri sciureus* colony consists of 11 individuals raised in captivity including nine females and two males. Ten monkeys were born at Stanford University between 1992 and 2007 making them between eight and 23. One of unknown age arrived at Stanford in 2000 from Osage Primates. Bucknell acquired the monkeys from shipments in 2008 and 2012. All individuals were used in preliminary testing and two main females were used for data collection. Many of the subjects including the two main females had some experience with cognitive tasks, but none of them had any prior experience with foraging tasks or experimental tree apparatuses. The two individuals used in primary testing were chosen based on their ability to consistently and successfully operate on the foraging apparatus.

Housing

A cylindrical outdoor corn crib enclosure constructed of wire measuring at 12m high and 5m in diameter was connected by two tunnels to an indoor enclosure measuring 5.3m × 5.8m × 2.3m, which was further divided into three chambers. While weather permitted, the monkeys had free movement between all areas in their habitat, but were restricted to the indoor rooms during colder months. The indoor enclosure contained numerous climbing structures in addition to toys and other objects for enrichment spread across the three chambers, each connected by vertically swinging doors that could be opened and closed by rotating a handle outside of the junction between chambers. The floor was covered in wood-shaving bedding. Here, the

monkeys also had *ad libitum* access to vegetables and standard monkey chow from trays and water from bottles fixed to the outside of each chamber. They also received a daily snack of peanuts, cereal, and raisins, occasionally also receiving mealworms as a treat. The indoor chambers also contained various enrichment objects such as plastic children's toys, swinging perches suspended from the ceiling, and other climbing structures. The tunnels between the indoor and outdoor areas could be opened and closed by horizontally swinging wooden doors from the inside and metal guillotine doors from the outside. In the outdoor enclosure, climbing structures made of tree branches or PVC were arranged arbitrarily at varying heights and locations. The ground of the corn crib enclosure was regular earth populated by numerous types of local, low-lying plants.

Apparatus

The climbing structures typically present in the outdoor cylindrical corn crib enclosure were replaced with an experimental tree built by the experimenter. Constructed from PVC pipe, the tree was 1.2m in height and consisted of eight branches each 2.5m in length and extending to the edge of the enclosure (Figure 2). The branches were stratified into two layers of four branches each, with the layers set 45 degrees askew from one another, so as to not be directly above one another. Modelled after the apparatus used in Voelk & Huber (2000), there was a feeding platform at the end of each branch constructed of a 0.61m x 0.18m wooden board covered in gray acrylic paint to facilitate cleaning and reduce porosity (Figure 3). Two hooks drilled into the corners of each platform allowed them to hang from the wall of the corn crib above the end of each branch. Each platform also had six black plastic film canisters bolted down with screws and in evenly spaced rows with caps attached with zip-ties. Non-toxic clay

was molded into the bottom of each canister to cover each screw, preventing any food reward from getting stuck between the screw and the inside edge of the canister.

Replacing the metal guillotine doors for this experiment, transparent acrylic doors were placed at the end of each tunnel nearest to the outdoor enclosure so that individuals isolated outside for testing could still see their conspecifics in the tunnels, thereby lessening their anxiety. In addition, plants were cut as needed to prevent them from becoming obstacles to the lowest feeding platforms.



Figure 2. Shows the experimental tree with platforms.



Figure 3. Shows one of eight feeding platforms

Procedure

After the construction of the experimental tree, all individuals were given a week to explore their redesigned outdoor enclosure and could move freely between the indoor and outdoor areas. During this time, all film canisters contained a single mealworm, which were a normal part of their diet, to encourage individuals to interact with the apparatus and allow the experimenter to assess their ability to open canisters and learn that a food reward lay within. The number of individuals allowed outside at a time was gradually reduced until the experimenter completed a roster of which individuals were able to learn how to consistently open canisters. At this stage of preliminary testing, subjects exhibited anxiety if isolated in the corn crib enclosure alone, typically pacing and vocalizing alarm calls instead of interacting with feeding platforms. Consequently, these individuals were paired up with a monkey that failed to learn how to open canisters to access mealworms in order to mitigate anxiety while foraging on the experimental tree. It was also at this point that the metal guillotine doors that blocked off the tunnels were replaced with transparent acrylic, so that subjects could maintain visual contact with conspecifics inside the tunnels during testing. After a few weeks of this preliminary testing, two individuals, Gwen and Arlene, were selected as experimental subjects due to their high performance in opening canisters and ability to remain in the outdoor enclosure alone for the duration of a trial without becoming stressed.

During the data collection period that followed, the two subjects received equal numbers of tests in two different experimental manipulations. Both “rich” and “poor” manipulations contained four high quality patches and four low quality patches with each feeding platform representing a patch. Each subject received equal numbers of trials in each manipulation. In the rich habitat, all six canisters in high quality patches contained a mealworm and three out of six

canisters contained a mealworm in low quality patches. In the poor habitat, four out of six canisters in high quality patches contained a mealworm and two out of six canisters contained a mealworm in low quality patches. For each trial, the order that subjects tested and whether they received rich or poor manipulations was randomized. The locations of high and low quality patches as well as which canisters contained mealworms within each patch were also randomized. Randomization eliminated placement biases from the experimenter as well as the possibility of subjects memorizing the distribution of mealworms across the experimental tree.

Before the beginning of each trial all individuals were brought inside and distributed across the three indoor chambers in a way that allowed the experimenter to easily alternate testing of the two subjects by lifting the exterior guillotine doors. The experimenter began a stopwatch during each trial when the subject crossed the threshold of the tunnel into the corn crib and recorded the elapsed time at the following events: arrival at a patch, opening a canister, ingesting a mealworm, and departing a patch. Once a subject had opened all of the canisters in the habitat, or if two minutes had elapsed without opening a canister, they were allowed back inside through the same door they had exited. Each trial typically lasted between five and ten minutes and each subject completed no more than two trials, one per habitat type, per day.

Data Analysis

Subtracting the time at the final ingest of a mealworm within a patch from the time of departure yields the give-up time (GUT) of that patch, which was the key information extrapolated from each trial. After acquiring GUTs from the raw data, the experimenter modified the averages from each trial. Using the definition of GUT given by marginal value theorem (Charnov, 1976) of the time between last prey capture in a patch and departure from that

patch, the experimental setup predetermines some of the predictions of optimal foraging theory and therefore the hypotheses of the study. A smaller number of filled canisters per patch is more likely to increase the GUT of that patch because the subjects have a greater chance of opening empty canisters after their final prey capture, which is included in GUT. Given that empty canisters were overall more likely to remain toward the end of a platform in the poor condition, this would skew the data towards longer GUTs in poor habitats due to the experimental setup. Furthermore, the same confound occurred between high and low quality patches of a given condition producing artificial differences in GUT values. Correction factors were therefore necessary to ensure the validity of the data in the context of this experimental setup.

To calculate the correction factors, the experimenter compiled all possible permutations of filled and empty canisters in a patch type to determine the average number of empty unopened canisters remaining after the capture of the final mealworm in the patch. This number was then divided by six (the total number of canisters) to give a percentage, which was subtracted from one to yield the average percent of the patch utilized up to and including the final canister to contain a mealworm. For example, high quality patches in the poor habitat had an average of 0.4 empty canisters remaining after the final mealworm capture, translating to 6.7%, which means that on average 93.3% of each patch was “active.” Because the order that subjects opened canisters in each patch was not feasible to record, this .933 correction was applied to all GUT values for high quality patches in the poor condition by multiplying the GUT values by .933 before using the data for statistical testing. No correction was applied to GUT data from patch type A in the rich habitat because all six canisters contained mealworms, ensuring that an ingestion always occurred on the final canister opening. All of the values for these corrections are shown in Table 1.

Table 1. Shows the steps used to modify GUT values for each patch type. The final row contains the final correction factors applied to the data.

Patch type	Rich, High	Rich, Low	Poor, High	Poor, Low
Mean number of canisters remaining	0	0.75	0.4	1.333
% of canisters remaining	0	12.5	6.7	22.2
% of platform “active”	100	87.5	93.3	77.8

The experimenter conducted 12 trials per rich and poor condition per subject, totaling 48 trials. Data were arranged such that for both subjects every rich condition trial was paired with a poor condition trial (Table 2). Data were analyzed using a two-way repeated measures ANOVA to compare average GUTs of rich and poor habitat types and high and low quality patch types. A rich or poor habitat type by high or low quality patch type interaction was also tested in the original ANOVA. In addition, two post-hoc paired t tests were used to compare average GUTs of high and low quality patches within rich and poor habitat types. To account for multiple comparisons in the post-hoc tests, a Bonferroni correction for two tests was used, changing α from .05 to .025. The same statistical methods as above were used to analyze residence time data. Measuring patch residence time was not subject to the same methodological confound as GUT and so did not require the use of any correction factors to modify the data. Each trial pair was treated as an independent data point in the ANOVA, which violated the independence assumptions of the ANOVA. Due to the small sample size, this was the only recourse for analysis; however, a three-way ANOVA with subject as a factor did not change the conclusions

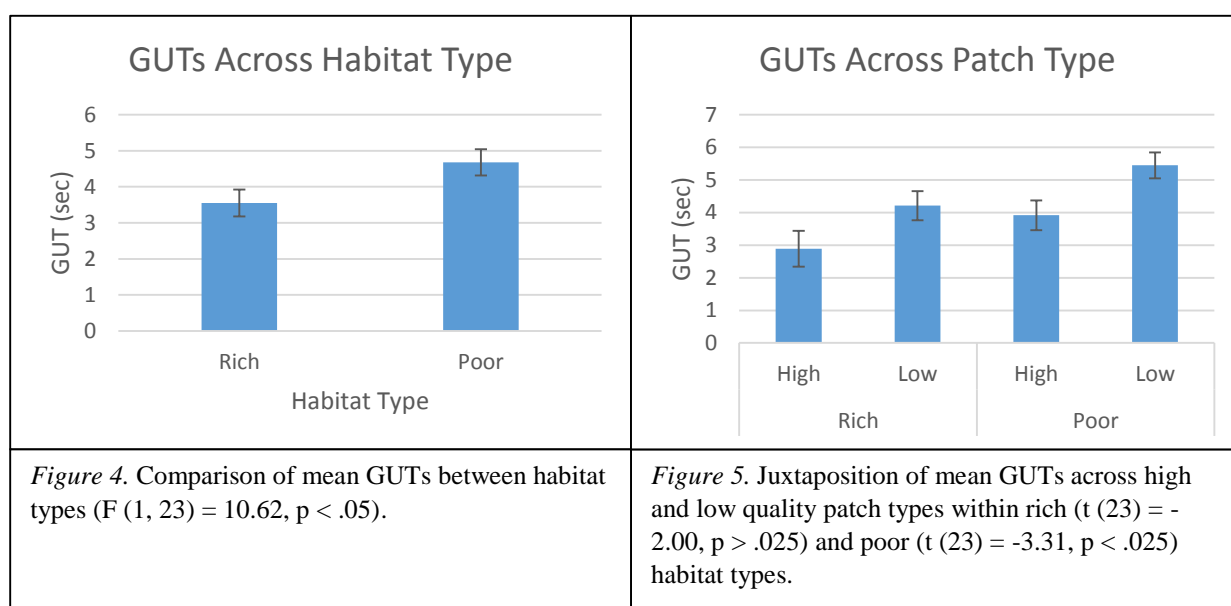
drawn from the analysis, showing that the two subjects exhibited sufficiently similar behavior to have little effect on the analysis.

Table 2. Example of data arrangement.

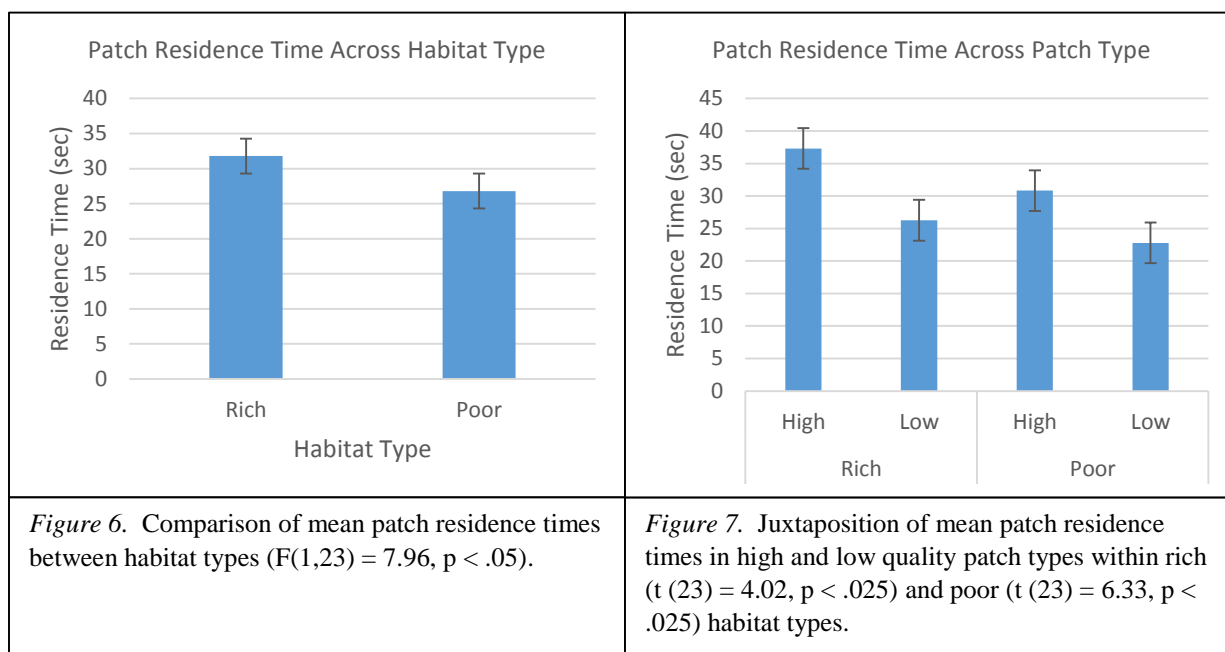
	Rich		Poor	
subject	High	Low	High	Low

Results

A two-way repeated measures ANOVA showed that the rich habitat produced significantly shorter GUTs than the poor habitat ($F(1, 23) = 10.62, p < .05$) as predicted by marginal value theorem (Figure 4). Post-hoc tests demonstrated no significant difference in GUTs between patch types in the rich manipulation ($t(23) = -2.00, p > .025$), but a significant difference between patch types in the poor manipulation ($t(23) = -3.31, p < .025$; Figure 5). There was no significant interaction between patch type and habitat type ($F(1, 23) = .063, p > .05$).



For patch residence time, the ANOVA failed to support the prediction that poor habitats would produce significantly longer overall residence times than rich habitats, instead showing the opposite ($F(1,23) = 7.96, p < .05$; Figure 6). Post-hoc tests showed that residence time was significantly higher in high quality than low quality patches in both the rich habitat ($t(23) = 4.02, p < .025$) and the poor habitat ($t(23) = 6.33, p < .025$) as predicted by MVT (Figure 7). There was no significant interaction between patch type and habitat type ($F(1, 23) = 1.48, p > .05$).



Discussion

Ultimately, this study found largely ambiguous results for the predictions of MVT measured in either GUT or patch residence time. MVT successfully predicted that residence time was significantly longer in high quality patches than low quality patches in any habitat type, but failed to show that it would be significantly higher in poor habitats than rich ones. The result indicated that high quality patches took longer than low quality ones to deplete to the marginal capture rate in either habitat, but that the energy cost of travel was not sufficient to necessitate longer patch residence times in the poor habitat than the rich one. As predicted, GUT was significantly shorter in the rich habitat compared to the poor, but GUT was not constant across patch types within the same habitat type. If GUT was in fact the inverse of marginal capture rate, which was dubious as discussed below, these results suggested that marginal capture rate was significantly higher in rich habitats due to a higher food density.

Several studies have argued that GUT may not always be the best approximation of marginal capture rate or may be entirely invalid for the purposes of marginal value theorem. Iwasa, Higashi & Yamamura (1981) argue that optimal rules for patch use depend on the spatial distribution of patches in an environment. When patches are distributed uniformly, as in this experiment, constant GUT will not produce optimal foraging. So long as patch quality is unknown to the forager, instead measuring a fixed amount of food taken from a patch or fixed time in a patch are more accurate because these variables have a more direct effect on changing the rate of capture within a patch. According to this paper, GUT should only be the most accurate of the three strategies discussed if variance in patch quality is very high. McNair (1982)

goes further to plainly state that GUT is an invalid measurement to use for testing predictions in MVT. If, as written in the introduction, GUT is a measurement of persistence, one would think that it would differ by patch type. For a forager to persist equal lengths of time in patches that vary greatly in their quality would seem in opposition to optimal foraging. McNair goes further to criticize any use of GUT because it was never a feature of the model used in MVT. He and others (Pyke *et al.*, 1977) claim that Krebs *et al.* (1974) had little theoretical basis for the conjecture that GUT is the inverse of the marginal capture rate, which calls into question the relationship upon which their whole study is based. GUT was used in this study because it was the only possibility for accurately approximating marginal capture rate and therefore testing the first prediction of MVT. If critics are correct, then the first prediction may have proven false simply because measuring GUT was not a valid test of the prediction.

The calculations in McNair's (1982) paper made an entirely different GUT prediction; high quality patches should have had longer GUTs, as foragers should be more persistent in areas they know contain more food. Ultimately, McNair demonstrated that MVT was meant to make predictions based on the time spent in a patch and not the GUT associated with that patch, after which he developed an analogous mathematical model to make similar predictions using GUT (that clearly were not validated by the results of this study). His GUT model did not always produce the same conclusions as the corresponding patch time model of MVT; however, the important conclusion for this thesis is that GUTs have differed between patch types in the same habitat. If this was true, then Krebs *et al.* (1974) instead provided evidence for non-optimal foraging in their chickadee subjects. Krebs later went on to state that GUT was not a good measure of optimal foraging theory for the same reason that correction factors were included in this data analysis; the experimental design promoted the intended predictions occurring in the

results (Cowie & Krebs, 1979). Because of the higher density of rich patches versus poor, the GUT will be smaller due to fewer empty canisters at the end.

As shown above, there is considerable disagreement on how to go about testing optimal foraging models such as MVT, which may largely explain why researchers, and especially primatologists, have been reluctant to use optimal foraging theory. With that said, a meta-analysis (Sih & Christensen, 2001) showed that only 11.4% of quantitative and 41.4% of qualitative studies disagreed with the premises of optimal foraging theory that they tested. Prey mobility negatively correlated with the success of studies, so only looking at those with immobile or near immobile prey conducted in non-herbivores corroborated predicted results in 82.1% of studies. It is worth noting, however, that the date of publication had borderline significant influence on the success of a study with earlier studies more likely to confirm optimal foraging than others. Despite this meta-analysis, the harsh criticisms of Krebs *et al.* (1974) by the aforementioned studies throw into question the validity of at least this single study, which was included as a success in Sih & Christensen (2001). It raises the question of how many other such studies may not be methodologically sound.

One of the most difficult aspects of testing optimal foraging theory in the lab is adequately simulating the model organism's natural foraging environment and without meeting this criteria, a study hardly reveals any useful information (Pyke, 1984). Squirrel monkeys may not be suitable candidates for this type of experiment because it fails to closely replicate their naturalistic foraging behavior. As mentioned in Mitchell *et al.* (1991), wild squirrel monkeys spent only 10% of their active hours feeding on patchily distributed resources such as fruit. They foraged on the invertebrate prey that compose the majority of their diet concurrently with travelling. Yet even when the majority of their diet is fruit, as in Lima & Ferrari (2002), this

may not mean that squirrel monkeys typically forage in a patchy environment. As little as 3% of foraging occurs in large patches such as tree crowns with other food items, including fruits and flowers, occurring in a more dispersed and unpredictable manner (Boinski, 1988). It may therefore be unrealistic to expect squirrel monkeys to engage in optimal foraging behavior in the scenarios presented to them in this study.

Alternatively, testing MVT in the field comes with its own difficulties as it may be challenging to satisfy all of the assumptions of MVT. In the lab, the locations of patches can be randomized to meet the necessary criteria; however, the role of spatial memory in foraging may have a large effect on how foragers navigate between patches in a naturalistic environment. Studies on moustached (*Sanguinus mystax*) and saddle-back tamarins (*Sanguinus fuscicollis*) and brown capuchins (*Cebus apella*) indicate that spatial memory plays a role in how these monkeys exploit a patchy environment (Garber, 1989; Janson, 1998). The results of the field study on tamarins was later corroborated with computer models further demonstrating the importance of prior knowledge of patch locations to optimal foraging (Garber & Hannon, 1993). With that said, several experiments in which squirrel monkeys completed a number of foraging tasks revealed that they have only limited spatial memory (Roberts, Mitchell & Phelps, 1993). Though these results should only be generalized with caution due to the researchers use of only two subjects, squirrel monkey behavioral ecology may not necessitate well developed spatial memory given their particularly kinetic style of foraging in the wild. More recent research, however, has shown results to the contrary, providing evidence that squirrel monkeys are quite capable of successfully completing spatial memory tasks (Ludvig, Tang, Eichenbaum & Gohil, 2003). With this study and evidence for spatial memory in other New World monkeys, it seems probable that squirrel monkeys have significant spatial memory capabilities. Should this be the

case, the randomization of high and low quality patches during each trial may have made this task much more difficult given the likely important role of spatial memory in optimizing food intake.

More generally, primates are difficult candidates for testing optimal foraging models due to the typical complexity of their diets. Many of the studies, both in the lab and in the field, that support MVT do so using a very limited number of patch types or even a single patch type. The results of these studies are certainly valuable in their own way, but they can only reveal so much regarding how wild primates engage in optimal foraging. Primates are particularly omnivorous animals, which compounded with the high biodiversity of their often tropical habitats, would require accounting for a huge number of patch types. Furthermore, the predictable growth patterns of many patchy resources such as fruit trees encourage nonrandom and goal-directed foraging patterns (Garber, 1987), which is out of line with optimal foraging models. Given the intricacy of primate sociality, it also comes as no surprise that this factor would impact their individual foraging success. Kazahari & Agetsuma (2008) showed that the presence of conspecifics had a great effect on enhancing foraging success through mechanisms such as scramble competition and social facilitation. Once again, these are respectively competitive pressure from conspecifics for indefensible resources and increases in the frequency or intensity of a behavior when in the presence of conspecifics engaging in the same behavior. This may be especially relevant in species such as squirrel monkeys that engage in such heavy scramble competition due to their highly dispersed food sources (Koenig, 2002). Within-group scramble competition varies individual foraging efficiency inversely with group size (Janson & van Shaik, 1988), yet the pressure of competition from conspecifics may stimulate individual foraging effort (Kazahari & Agetsuma, 2008) through social foraging mechanisms such as social facilitation and

local enhancement, which is the tendency to go to locations where they have observed conspecifics. It would seem then that modeling optimal foraging would have to take into account at least group size if not other factors to remain accurate. Ultimately, individual testing may not truly reflect optimal foraging behavior because socially foraging animals may do so less-than-optimally without the presence of their group.

Results in this study were probably also affected by aspects of the testing situation and procedures. The study used only two subjects; however, primate studies are known for using a small sample size and one this low is certainly not exceptional. In addition, the season highly limited the amount of data collected. Because trials were run in an outdoor enclosure and the squirrel monkeys were not allowed outside in cold weather, data collection only occurred from September to November. There were also simply a large number of mealworms per trial, so satiety could have an effect even without food deprivation, but a change rate of intake throughout each trial would have to be calculated to investigate this possibility. In addition, there was no food deprivation before trials, which is a common strategy in these types of experiments to prevent satiety. Nonetheless, foragers reduced the food density within a patch to zero the majority of the time. In some other experimental setup where prey within a patch are more difficult to find than checking six film canisters, the GUT and residence time values may have been different. Here a patch design such as that in Cowie (1977) may have been better because the process of finding mealworms buried in saw dust would likely have given rise to a decreasing average rate and marginal rate better suited to testing the predictions. The patch design of this experiment may have prevented the patch residence time prediction for habitat type because it violated the MVT assumption that travel time between patches exceeds the time between prey captures within a patch. Looking at the raw data at least anecdotally suggested that travel time

between patches was frequently comparable to the inter-capture interval. Though a more detailed analysis is needed to confirm this conclusion, this seems like a probable and parsimonious explanation for the failure to fully confirm the patch residence time predictions.

The ability to make accurate predictions about different aspects of foraging behavior has far-reaching applications, making optimal foraging theory a fascinating and worthy research area, but nonetheless the validity of many optimal foraging models including marginal value theorem remains in debate. As shown by the optimal foraging literature reviewed in this thesis, the soundness of these models becomes even more uncertain when applied to primates. At least some primatologists such as Garber (1987) believe that the present utility of applying optimal foraging models to primates is limited because the assumptions are difficult to apply to foragers that rely so heavily on complex cognition and experience with particular resources. For example, consuming difficult-to-access resources often forms an important part of primate diets and allows them to meet specific nutrient needs, but maximizing the efficiency at accessing such resources may take many years. It is worth noting that MVT does not attempt to address other aspects of optimal foraging theory such as specific nutrient constraints, risk of predation, and other factors important to foraging in a naturalistic environment. These limitations may, however, play a role in why primates often appear to fit poorly into the model given Garber's points. As Iwasa, Higashi & Yamamura (1981) and McNair (1982) made clear, patch residence time models (such as MVT), GUT models, or ones using other parameters may be the best to use in different scenarios. With such a lack of generalizability it seems unlikely that any of these options are the actual foraging strategy used across all taxa. This leaves us to wonder not just what measurement makes for the most accurate models, but what cognitive process goes on in an organism to allow optimal foraging to occur. Further research should address this question

of how animals cognitively make these types of foraging decisions in addition to refining existing models to permit their accurate use in broader scenarios. This study in particular would benefit from being redone after taking into account some of the criticisms elaborated upon earlier in the preceding paragraphs. Upon doing so, the experimenter would have a much greater capacity to draw more reliable conclusions about supporting or rejecting marginal value theorem in squirrel monkeys and primates in general.

References

- Agetsuma, N. (1998). Simulation of patch use by monkeys using operant conditioning. *Journal of Ethology*, 16(2), 49-55.
- Boinski, S. (1988). Sex differences in the foraging behavior of squirrel monkeys in a seasonal habitat. *Behavioral Ecology and Sociobiology*, 23(3), 177-186.
- Chapman, C. (1988). Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. *Behaviour*, 105(1), 99-116.
- Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical population biology*, 9(2), 129-136.
- Cowie, R. J. (1977). Optimal foraging in great tits (*Parus major*). *Nature*, 268(5616), 137-139.
- Cowie, R. J., & Krebs, J. R. (1979). Optimal foraging in patchy environments. In Anderson, R.M., Turner, B.D. & Taylor, L.R. (Eds.), *Population dynamics* (183-205). London: Blackwell Scientific.
- Croze, H. (1970). Searching image in carrion crows: hunting strategy in a predator and some anti-predator devices in camouflaged prey. *Zeitschrift fuer Tierpsychologie*, 5, 85.
- Garber, P. A. (1987). Foraging strategies among living primates. *Annual review of Anthropology*, 16, 339-364.
- Garber, P. A. (1989). Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. *American Journal of Primatology*, 19(4), 203-216.

- Garber, P. A., & Hannon, B. (1993). Modeling monkeys: a comparison of computer-generated and naturally occurring foraging patterns in two species of neotropical primates. *International Journal of Primatology*, *14*(6), 827-852.
- Grether, G. F., Palombit, R. A., & Rodman, P. S. (1992). Gibbon foraging decisions and the marginal value model. *International Journal of Primatology*, *13*(1), 1-17.
- Hill, K., Kaplan, H., Hawkes, K., & Hurtado, A. M. (1987). Foraging decisions among Ache hunter-gatherers: new data and implications for optimal foraging models. *Ethology and Sociobiology*, *8*(1), 1-36.
- Hubbard, S. F., & Cook, R. M. (1978). Optimal foraging by parasitoid wasps. *The Journal of Animal Ecology*, *47*(2), 593-604.
- Iwasa, Y., Higashi, M., & Yamamura, N. (1981). Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist*, 710-723.
- Janson, C. H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. *Animal Behaviour*, *55*(5), 1229-1243.
- Janson, C. H., & Van Schaik, C. P. (1988). Recognizing the many faces of primate food competition: methods. *Behaviour*, *105*, 165-186.
- Kazahari, N., & Agetsuma, N. (2008). Social factors enhancing foraging success of a wild group of Japanese macaques (*Macaca fuscata*) in a patchy food environment. *Behaviour*, *145*(6), 843-860.
- Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, *23*(4), 759-783.

- Krebs, J. R., Ryan, J. C., & Charnov, E. L. (1974). Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Animal Behaviour*, 22(4), 953-964.
- Kurland, J. A., & Beckerman, S. J. (1985). Optimal foraging and hominid evolution: labor and reciprocity. *American Anthropologist*, 87(1), 73-93.
- Lima, E. M., & Ferrari, S. F. (2003). Diet of a free-ranging group of squirrel monkeys (*Saimiri sciureus*) in eastern Brazilian Amazonia. *Folia Primatologica*, 74(3), 150-158.
- Ludvig, N., Tang, H. M., Eichenbaum, H., & Gohil, B. C. (2003). Spatial memory performance of freely-moving squirrel monkeys. *Behavioural brain research*, 140(1), 175-183.
- MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *American Naturalist*, 100, 603-609.
- McNair, J. N. (1982). Optimal giving-up times and the marginal value theorem. *American Naturalist*, 119(4), 511-529.
- Mitchell, C. L., Boinski, S., & Van Schaik, C. P. (1991). Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedii* and *S. sciureus*). *Behavioral Ecology and Sociobiology*, 28(1), 55-60.
- Nakagawa, N. (1989). Foraging behavior of Japanese monkeys: a viewpoint of optimal foraging strategy. *Primate Research*, 5(1), 1-13.
- Nakagawa, N. (1990a). Choice of food patches by Japanese monkeys (*Macaca fuscata*). *American Journal of Primatology*, 21(1), 17-29.
- Nakagawa, N. (1990b). Decisions on time allocation to different food patches by Japanese monkeys (*Macaca fuscata*). *Primates*, 31(4), 459-468.

- Nakagawa, N. (2009). Feeding rate as valuable information in primate feeding ecology. *Primates*, 50(2), 131-141.
- Pyke, G. H. (1984). Optimal foraging theory: a critical review. *Annual review of ecology and systematics*, 15, 523-575.
- Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, 52(2), 137-154.
- Roberts, W. A., Mitchell, S., & Phelps, M. T. (1993). Foraging in laboratory trees: Spatial memory in squirrel monkeys. In Zentall, T.R. (Ed.), *Animal Cognition. A Tribute to Donald A. Riley* (131-151). New York: Psychology Press.
- Sayers, K., Norconk, M. A., & Conklin-Brittain, N. L. (2010). Optimal foraging on the roof of the world: Himalayan langurs and the classical prey model. *American journal of physical anthropology*, 141(3), 337-357.
- Schoener, T. W. (1971). Theory of feeding strategies. *Annual review of ecology and systematics*, 2, 369-404.
- Sih, A., & Christensen, B. (2001). Optimal diet theory: when does it work, and when and why does it fail?. *Animal behaviour*, 61(2), 379-390.
- Smith, J. N., & Dawkins, R. (1971). The hunting behaviour of individual great tits in relation to spatial variations in their food density. *Animal Behaviour*, 19(4), 695-706.
- Snaith, T. V., & Chapman, C. A. (2005). Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Ptilocolobus tephrosceles*). *Behavioral Ecology and Sociobiology*, 59(2), 185-190.

Stephens, D. W., & J. R. Krebs. (1986). *Foraging theory*. Princeton: Princeton University Press.

van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In Standen, V. & Foley, R.A. (Eds.), *Comparative socioecology: The behavioural ecology of humans and other mammals* (195-218). Oxford: Blackwell Scientific.

Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, 60(2), 195-202.

Whitten, P. L. (1988). Effects of patch quality and feeding subgroup size on feeding success in vervet monkeys (*Cercopithecus aethiops*). *Behaviour*, 105(1), 35-52.