THE PENNSYLVANIA STATE UNIVERSITY
SCHREYER HONORS COLLEGE

DEPARTMENT OF BIOCHEMISTRY AND MOLECULAR BIOLOGY

Investigation of the Behavior of RNA G-Quadruplexes from the Human Genome under Physiological Conditions

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A thesis
submitted in partial fulfillment
of the requirements
for a baccalaureate degree
in Psychology
with honors in Biochemistry and Molecular Biology

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ABSTRACT

It has been proposed that G-quadruplexes are globally unfolded in eukaryotes but not in prokaryotes. The exact mechanism for this remains unknown. We hypothesize that G-quadruplexes are unfolded in eukaryotes due at least in part to the presence of polyamines such as spermine uniquely present in eukaryotic cells, but not prokaryotes. To test this, we utilized UV thermal denaturation of both native HeLa and HEK sequences, as well as the *E.coli* b3197 sequence to determine how G-quadruplexes behave under *in vivo*-like conditions. The difference between the prokaryotic and eukaryotic cellular conditions may affect G- quadruplex behavior. Eukaryotes have the polyamine spermine while prokaryotes do not. Additionally, prokaryotes also have a higher salt content which stabilizes the G-quadruplexes. Based on the results of my polyamine variation experiments, the presence of the polyamine spermine in the sample appears to the destabilize the G-quadruplex structure for both the HeLa and HEK samples. However, in the spermine titration experiments, the presence of the polyamine spermine in the sample correlates to the stabilization of the G-quadruplex structure in both sequences.

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ACKNOWLEDGEMENTS

The completion of this thesis would not have been possible without the guidance and support of Dr. Bevilacqua. I am so thankful for the opportunity to have worked in his lab with so many talented people. I would also like to thank my graduate student mentor, Allison Williams, for both her guidance and encouragement throughout the duration of this research project. She taught me techniques, helped to develop experiments, and interpret the experimental results. Finally, I would like to thank my parents, Don and Linda, for their support.

Chapter 1

Introduction to Nucleic Acids and G-Quadruplexes

RNA Folding

In all of the living organisms found on Earth, deoxyribonucleic acid (DNA) is the source of the organism's hereditary information. Once the DNA is replicated through the process of DNA replication, it can undergo the process of transcription. During the transcription process, ribonucleic acid (RNA) is produced which allows genetic information to be transported throughout the organism. Messenger RNA (mRNA) guides the synthesis of a protein molecule using the genetic information originating from the DNA. Ribosomal RNA (rRNA) forms the majority of the ribosome's structure and can act as a catalysis for protein synthesis. Transfer RNA (tRNA) serves as a mediator between the mRNA molecules and the amino acids required for protein synthesis. Translation can then be conducted to produce the desired protein molecule (See Figure 1).

Figure 1: A model of the central dogma of molecular biology

Although both DNA and RNA are important in the process of producing proteins, the two molecules have many structural differences. DNA is a double stranded molecule that is typically found in a double helix conformation. While some RNA molecules are double stranded, the

majority of RNA molecules are single stranded (9). RNA is also not restricted to only one structural conformation like DNA is. Some of these structures RNA can adopt are shown in Figure 2 below (8).

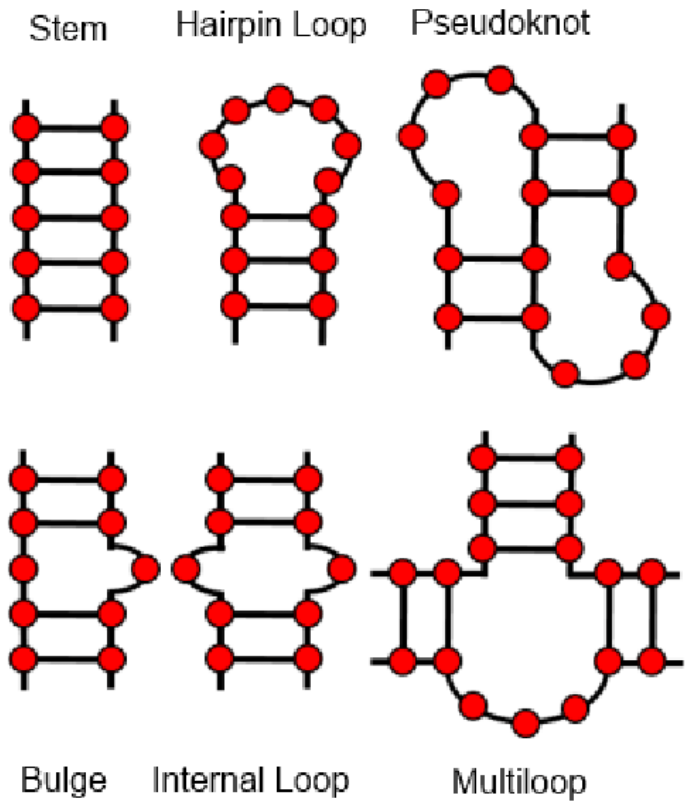

Figure 2: Models of some of the examples of RNA structure types

Another one of these structures is the G-quadruplex. G-quadruplexes are nucleic acid structures that contain two or more G-quartets where each of the four G's in a quartet bind to two neighboring G's in three-dimensional space (). There are also multiple conformations of G-quadruplexes possible, some of these conformations include a parallel and anti-parallel geometries, and can be present with either the RNA folding onto itself which is shown in Figure

3 or the RNA interacting with other RNA molecules. The stability of the structure depends on the presence of potassium and to a lesser extent other salts such as Na^+ which sit between or in quartets, which is shown in Figure 4 below (2). Current algorithms predict that there are RNA quadruplexes in the human genome (1).

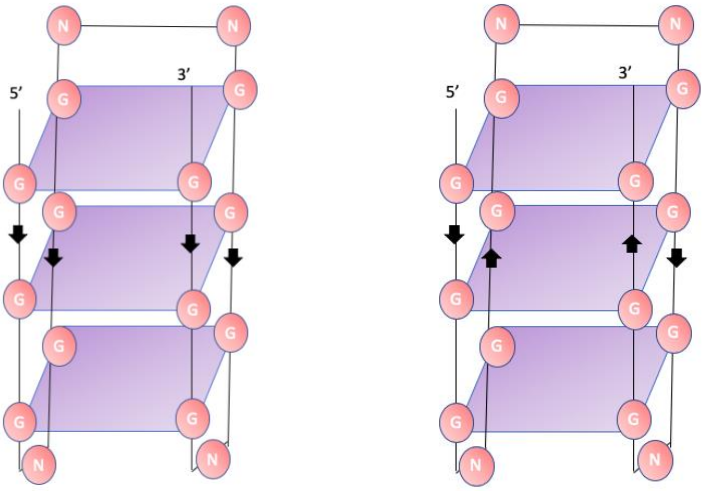

Figure 3: Model for (A) Parallel G-Quadruplex conformations and (B) Antiparallel G-Quadruplex conformations each with three quartets shaded in purple. RNA tends to adopt the parallel conformation.

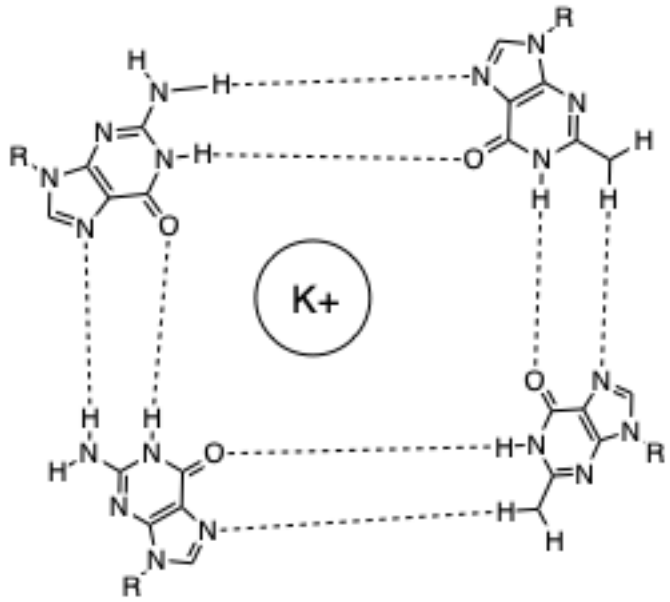

Figure 4: Model for a guanine quartet in a G-quadruplex that is surrounded by the positively charged potassium ion.

Importance of Understanding RNA Structures Inside the Cell

Recently it has been proposed that RNA G quadruplexes are globally unfolded in eukaryotes, but not in prokaryotes; however, the molecular basis for this is not fully understood (3). Bartel proposed that helicases may be responsible for unwinding quadruplexes but it seems unlikely that helicases can contend with continuously unfolding all quadruplexes. The difference between the prokaryotic and eukaryotic cellular conditions could affect G-quadruplex behavior. The structures of some of the polyamines found in eukaryotes and prokaryotes is shown in Figure 5. Eukaryotes have the polyamine spermine while prokaryotes do not, so spermine may be causing the destabilization (4). In fact, prokaryotes have a higher salt content, which stabilizes

the G-quadruplexes leading to the hypothesis that the presence of spermine in RNA samples causes the instability of G-quadruplexes (5).

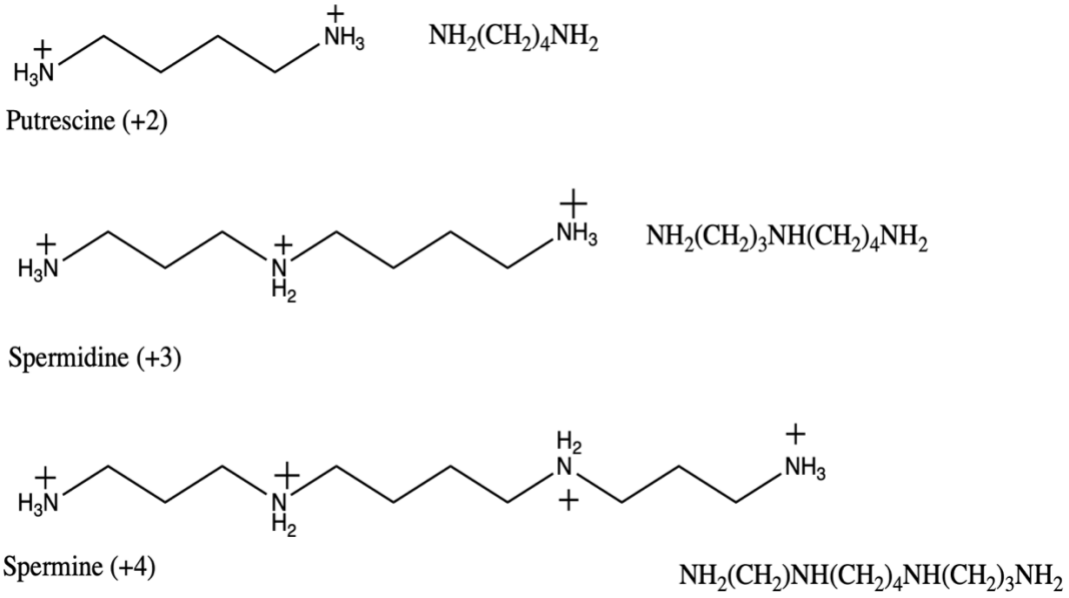

Figure 5: Model of polyamines with major charge state at physiological pH for (A) putrescine (+2), (B) spermidine (+3), and (C) spermine (+4).

It has also been proposed that G-quadruplexes are linked to gene regulation as well as cancer; making this work of potential medical relevance (7). There is currently a lack of evidence for *in vivo* condition behavior, but there is evidence of high stability *in vitro* (3).

Picking Biological Sequences

The process of selecting which biological sequences are used in RNA experiments is extremely important. Most of my experiments with RNA either take place in *in vitro* conditions or in *in vivo*-like conditions so highly symmetric RNA sequences are preferred. However, this type of biological sequence is rarely found in nature.

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Chapter 2

UV Thermal Denaturation of Native RNA Sequences

Abstract

Many organisms in both the eukaryotic and prokaryotic domains contain RNA sequences that have the potential to form stable G-quadruplexes (1). Therefore, my first task was to identify RNA sequences in multiple organisms that had a high probability to form a stable G-quadruplex confirmation. In this process, we used the supplementary data compiled from Bartel and Guo's publication to evaluate the RNA sequences that they used. From the data, sequences were determined based on high average reverse transcription stop frequency as well as a high probability to form a G-quadruplex structure. In this study, the native RNA sequences previously selected were analyzed by thermal denaturation to understand the folding and the thermodynamics of the G-quadruplexes present in the sequence.

Introduction

Before experiments were conducted, I evaluated potential sequences in both prokaryotic and eukaryotic organisms to find the optimal organisms to represent each domain. There are many organisms that contain RNA sequences that have the potential to form a G-quadruplex (5). Using the transcriptomes that Guo and Bartel analyzed, I found the optimal sequences for UV thermal denaturation experiments. To do this, the average reverse transcription stop time frequency and the enrichment of potassium by the sequence was analyzed for the HEK293T and HeLa transcriptomes. Once potential sequences were filtered out of both transcriptomes, they

were ran in the NCBI Basic Local Alignment Search Tool, or BLAST, in order to obtain the full nucleotide sequence. Using the reverse transcription stop sequence number, the G quadruplex sequence was determined from within the full nucleotide sequence. The collection of sequences from each transcriptome based on the highest average reverse transcription stop frequencies were then evaluated to determine the sequence with the highest probability of forming a G-quadruplex conformation.

G-quadruplexes vary in structure and stability in a laboratory setting outside of biological condition, but little is known about what happens inside the cell in biological conditions (8). The behavior of G quadruplexes also has a significant biological importance. G quadruplexes have been implicated in both mRNA processing and translation. This has led to the proposition that G quadruplexes can play a role in cancer and other diseases (7). Recently, it has been proposed that G-quadruplexes are globally unfolded in eukaryotes but not in prokaryotes (5). However, the exact reason and the mechanism remains unknown. We hypothesize that G-quadruplex unfolding in eukaryotes is due at least in part to the presence of spermine in eukaryotic cells (6). We are utilizing UV thermal denaturation on HEK and HeLa RNA sequences to investigate how G quadruplexes behave under controlled conditions and we compare their thermodynamic stability. It has been shown that G-quadruplexes have unusually high stability when they are tested outside of biological conditions (3). The behavior of G quadruplexes under controlled conditions may offer an insight into the mechanism behind this stability.

Since thermal denaturation is difficult to perform under *in vivo* conditions, we studied stability under *in vivo-like* conditions that mimic ionic concentrations within the cell. The sample was slowly heated to unfold the RNA, and the absorbance at 294 nm was measured at each temperature since melting of G-quadruplexes can be uniquely observed at this wavelength (4).

The data were then plotted to observe the thermodynamic stability under each condition. Typically, a hypochromic transition in the RNA sequence represents a decrease in thermodynamic stability since the sequence is melting at a specific temperature. A relatively stable absorbance level at 294 nm throughout the temperature range suggests that there is little to no change in the thermodynamic stability.

Results and Discussion

Selection of Biological Sequences

Using the above protocol, one sequence from each transcriptome contained both a high reverse transcription-stop time frequency as well as a high probability of forming a G-quadruplex. Sequences from both the HEK293T and HeLa transcriptomes were selected because these sequences are commonly found in human cell lines associated with the kidneys and cancer (2).

Table 1: List of the Selected RNA Sequences

Sequence Name	Nucleotide Sequence
HEK	5' GGGUGGGAGGGCUGGGACAGUUUUU 3'
HeLa	5' GGGGGCCCUGGUGGCCCUGGGAUGGG 3'
E. coli - b3197	5' GGGGAUGGGAAAAUCGGGGCAUAUUGGGCG 3

UV Thermal Denaturation of a Native HeLa Sequence

The sequence was subjected to UV thermal denaturation under five variations of eukaryotic polyamine conditions. All five of these conditions were in the presence of 1M KCl, 1 M NaCl, and 0.25 M $MgCl_2$ conditions, which mimicked cellular conditions in eukaryotes. Solutions contained both spermidine and spermine and the positive control contained no polyamines in the solution. There was also a spermidine-only condition, a spermine-only condition, and a putrescine-only condition.

The RNA sequences appear to some G-quadruplex conformation. Based off of the eukaryotic samples, it appears that the G-quadruplex, (Figure 6, red), is thermodynamically stable in the absence of the polyamine spermine. When spermine is present, the G-quadruplex structure substantially loses its stability (Figure 6, dark green), but once the spermine is eliminated, the stability recovers when in the presence of the polyamines spermidine (Figure 6, black), and putrescine alone (Figure 6, light blue).

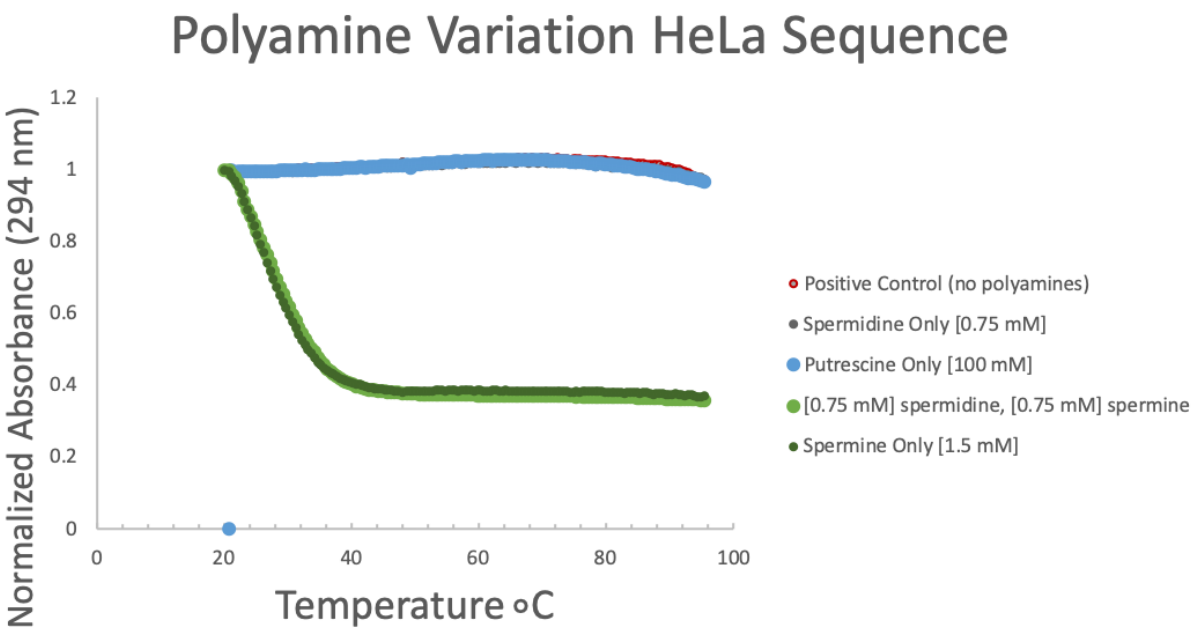

Figure 6: Polyamine Variation HeLa Sequence

UV thermal denaturation reaction at 294 nm wavelength conditions. Normalized absorbance versus temperature is shown. The red circles show the positive control with no polyamines, green circles show the experiment with 0.75 mM of both spermidine and spermine, grey circles show 0.75 mM spermidine, purple circles show 0.75 mM spermine only, and blue circles show 0.2 mM putrescine only.

UV Thermal Denaturation of a Native HEK Sequence

These experiments were conducted identically to the Native HeLa Sequence. The sequence was subjected to the process of UV thermal denaturation under five variations of eukaryotic polyamine conditions. All five of these conditions were in the presence of KCl, NaCl, and $MgCl_2$ conditions that replicated cellular conditions in eukaryotes. The solutions contained both spermidine and spermine and the positive control contained no polyamines in the solution.

There was also a spermidine-only condition, a spermine-only condition, and a putrescine-only condition.

The RNA sample appears to form stable G-quadruplexes in the absence of the polyamine spermine (+4). For the sample that contained both spermine (+4) and spermidine (+3)m the G-quadruplexes were much less stable at a melting temperature $\leq$ 70 °C. The positive control, which contained no polyamines, and the sample with only spermidine (+3) and putrescine (+2) formed stable G-quadruplexes (Figure 7). Based on the data, there appears to be an absence of a hypochromic transition which is significant since all unfolding of G-quadruplexes occurs through a hypochromic transition. This absence can mean one of two things: there is either no G-quadruplexes present in the samples or the G-quadruplexes present in the sample are so stable

that they melt outside the range of the experiment.

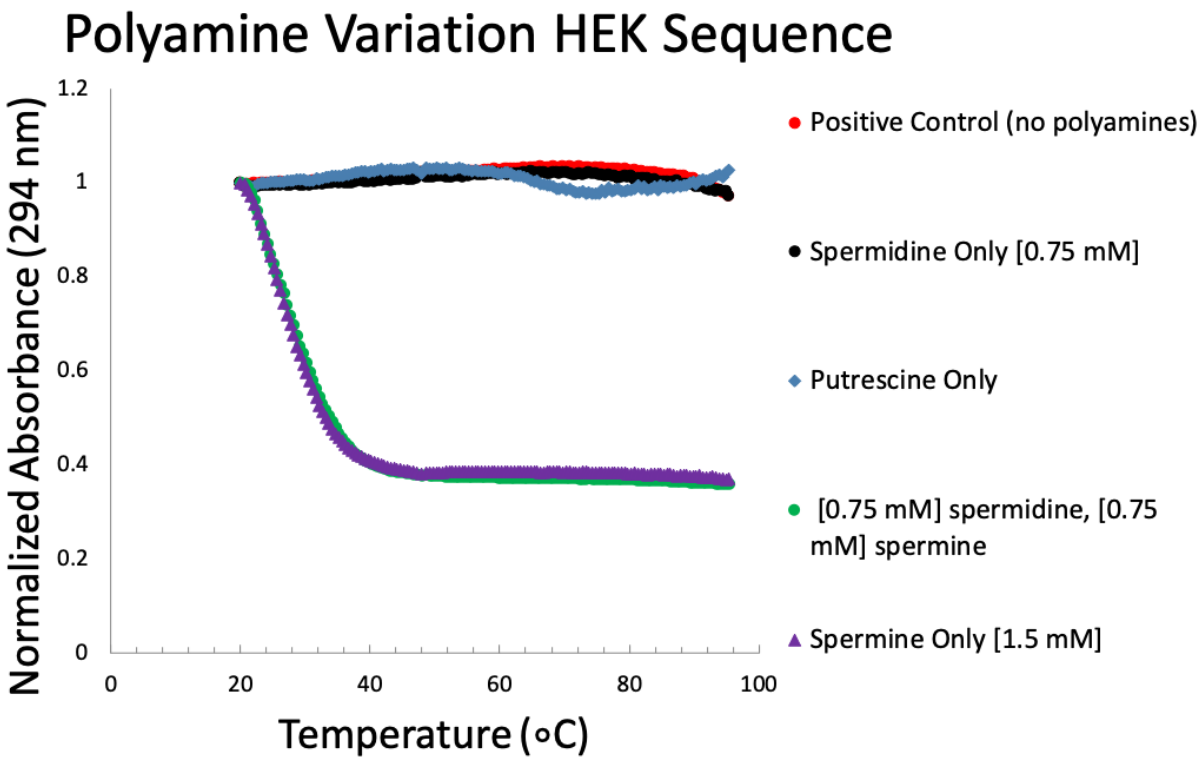

Figure 7: Polyamine Variation HEK Sequence

UV thermal denaturation reaction at 294 nm wavelength conditions. Normalized absorbance versus temperature is shown. Red circles show the positive control with no polyamines, green circles show the sample with 0.75 mM of both spermidine and spermine, black circles shows 0.75 mM spermidine, purple circles show 0.75 mM spermine, and blue circles show 0.2 mM putrescine.

Spermine Titration of a Native HEK Sequence

The sequence was tested under four different spermine levels in order to test the sensitivity to polyamines and to help determine the eukaryotic baseline for future experiments.

All four of these conditions were in the presence of KCl, NaCl, and $MgCl_2$ conditions that replicated cellular conditions in eukaryotes. Samples were in the presence of 0.2 mM, 0.5 mM spermine, 0.7 mM and 1.5 mM spermine.

All four samples effectively maintained the same stability when tested.

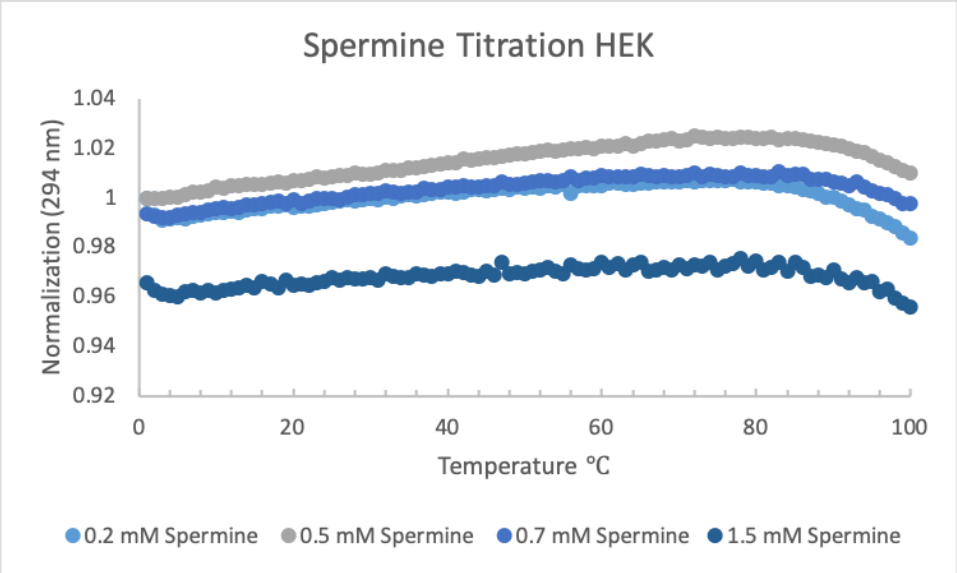

Figure 8: Spermine Titration HEK

Spermine Titration of a Native HeLa Sequence

The HeLa sequence, which has a G3 rather than the HEK G2 sequence, was tested under four different spermine levels in order to see the effects of these spermine levels and to help determine the eukaryotic baseline for future experiments. All four of these conditions were in the presence of KCl, NaCl, and $MgCl_2$ conditions that replicated cellular conditions in eukaryotes. The first sample was in the presence of 0.2 mM spermine, the second sample was in the presence of 0.5 mM spermine, the third sample was in the presence of 0.7 mM spermine and the fourth sample was in the presence of 1.5 mM spermine. All of the spermine concentrations seemed to

maintain a similar stability rate except the 1.5 mM concentration. That sample remained relatively stable until the G-quadruplex approached the approximate melting temperature.

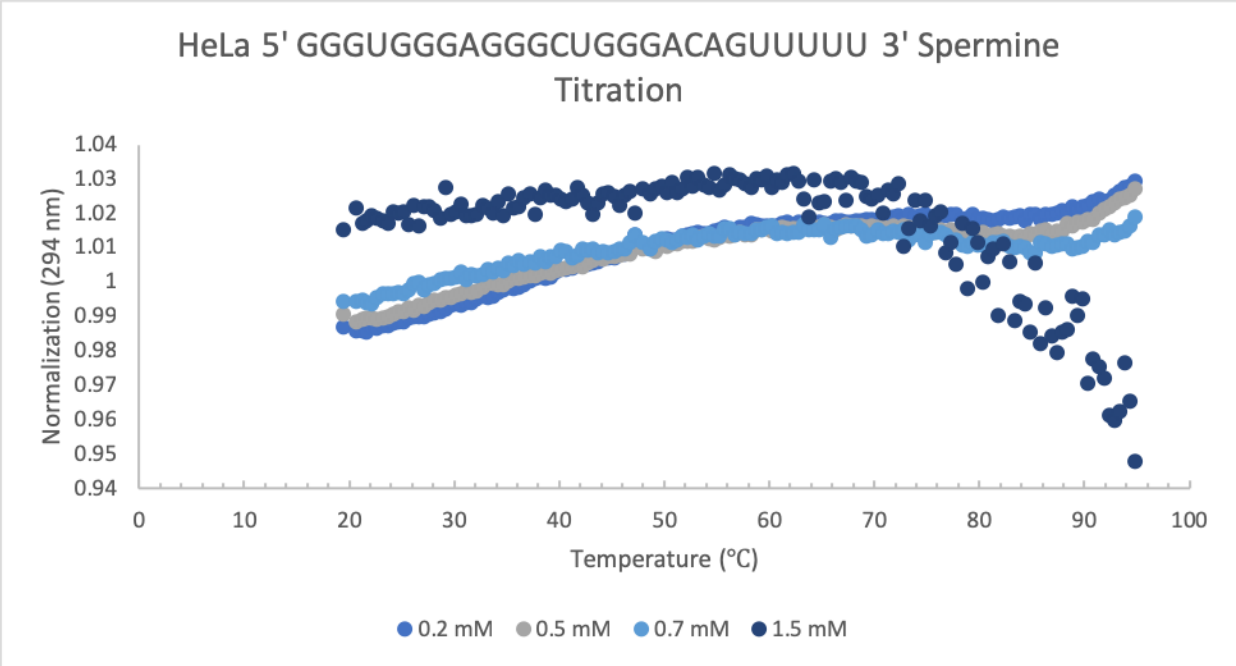

Figure 9: HeLa Spermine Titration

Spermine titration reaction at 294 nm wavelength conditions. Normalized absorbance versus temperature is shown. Blue circles show the 0.2 mM spermine concentration, grey circles show the 0.5 mM spermine concentration, light blue circles shows 0.7 mM spermine concentration, and dark blue circles show 1.5 mM spermine concentration.

Materials and Methods

Selection of Biological Sequences

Potentially stable G-quadruplexes were determined from the table in the Bartel paper using the average RT-stop time frequency and the enrichment of potassium by the particular sequence. Once the stable sequences were determined, they were run in BLAST to obtain the full nucleotide sequence. Using the RT stop sequence number from the table obtained from the Bartel paper, the G quadruplex was determined from within the full nucleotide sequence.

UV Thermal Denaturation

The UV thermal denaturation samples were prepared with 1 M KCl, 1 M NaCl, 0.25 M $MgCl_2$, and 0.2 mM, 0.5 mM, 0.7 mM, and 1.5 mM spermine. Samples were boiled for two minutes at 80°C and were cooled in ice for 1 minute. Samples then went into the MyBlock for 5 minutes on 37°C. Samples were then vortexed and spun down for thirty seconds. Samples were then added to 330 µL 1 cm pathlength cuvettes and were run on the OLIS HP 8452 Diode Array Spectrophotometer for approximately two hours on a wavelength range of 200-600 nm.

Polyamine Variation

Table 2: Polyamine Variation Conditions for the HeLa Sequence

HeLa Polyamine Variations in µL								
	RNA (193 mM)	KCl in 10 mM HEPES (1M)	NaCl in 10 mM HEPES (1 M)	$MgCl_2$ in 10 mM HEPES (0.25 M)	Spermidine in 10 mM HEPEs (20 mM)	Spermine in 10 mM HEPES (10 mM)	10 mM HEPES	Total Volume
Spermine and Spermidine	18.1	52.5	3.5	0.7	31.5	26.25	233.74	350
Positive Control	18.1	52.5	3.5	0.7	0	0	291.49	350
Spermidine Only	18.1	52.5	3.5	0.7	31.5	0	265.24	350
Spermine Only	18.1	52.5	3.5	0.7	0	26.25	259.99	350
Putrescine Only	18.1	52.5	3.5	0.7	0	0	255.2	350

Table 3: Polyamine Variation Conditions for the HEK Sequence

	HEK Polyamine Variations in µL							
	RNA (244.5 mM)	KCl in 10 mM HEPES (1M)	NaCl in 10 mM HEPES (1 M)	$MgCl_2$ in 10 mM HEPES (0.25 M)	Spermidine in 10 mM HEPEs (20 mM)	Spermine in 10 mM HEPES (10 mM)	10 mM HEPES	Total Volume
Positive Control	14.3	52.5	3.5	0.7	31.5	26.25	221.25	350
Negative Control	14.3	52.5	3.5	0.7	0	0	279	350
Spermidine Only	14.3	52.5	3.5	0.7	31.5	0	247.5	350
Spermine Only	14.3	52.5	3.5	0.7	0	26.25	259.75	350
Putrescine Only	14.3	52.5	3.5	0.7	0	0	259	350

Spermine Titration

Table 4: Spermine Titration Conditions for the HeLa Sequence

HeLa Spermine Titration in µL							
	RNA (500 mM)	KCl in 10 mM HEPES (1M)	NaCl in 10 mM HEPES (1M)	$MgCl_2$ in 10 mM HEPES (0.25 mM)	Spermidine in 10 mM HEPES (20 mM)	Spermine in 10 mM HEPES (20 mM)	10 mM HEPES
0.2 mM	6.7	52.5	3.5	0.7	0	7	261.7
0.5 mM	6.7	52.5	3.5	0.7	0	17	251.2
0.7 mM	6.7	52.5	3.5	0.7	0	24.5	244.2
1.5 mM	6.7	52.5	3.5	0.7	0	52.5	216.2

Table 5: Spermine Titration Conditions for the HEK Sequence

HEK Spermine Titration in µL							
	RNA (223.6 mM)	KCl in 10 mM HEPES (1M)	NaCl in 10 mM HEPES (1M)	$MgCl_2$ in 10 mM HEPES (0.25 mM)	Spermidine in 10 mM HEPES (20 mM)	Spermine in 10 mM HEPES (20 mM)	10 mM HEPES
0.2 mM	15.67	52.5	3.5	0.7	0	7	270.63
0.5 mM	15.67	52.5	3.5	0.7	0	17	260.13
0.7 mM	15.67	52.5	3.5	0.7	0	24.5	253.13
1.5 mM	15.67	52.5	3.5	0.7	0	52.5	225.13

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Chapter 3

Future Directions

This work identified stability trends of RNA G-quadruplexes under conditions where polyamines were varied and under conditions where the concentration of spermine (+4) was varied. Particularly, it was discovered that the stability of RNA G-quadruplexes decreases when spermine (+4) is present in the sample. We hypothesize that the presence of spermine (+4) in eukaryotic organisms may contribute to why RNA G-quadruplexes appear unfolded in this domain. Based on the results of the data described above, there are several experiments that can be conducted in the future such as size exclusion chromatography and CD spectroscopy. Other organisms in the eukaryotic domain can be analyzed to determine if the stability trends remain the same throughout other species.

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Education

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Presentations

Poster Presentations

1. **Veglia K.,** Yamaguchi-Pedroza, K., Loviscky, A., Vescio, T. (February 2022). Gender Threats and Anti-Female Sentiments To be Presented at SPSP 2022
2. **Veglia, K.,** Loviscky, A., Vescio, T., Schermerhorn, N (April, 2021). The Effects of Masculinity Threats on Anti-Fat Attitudes Pennsylvania State University Psi Chi Exposition
3. Loviscky, A., **Veglia, K.,** Vescio T., Schermerhorn, N. (April, 2021) Threats to Masculinity are Associated with Increases in Racism. Pennsylvania State University Undergraduate Psi Chi Exposition
4. **Veglia, K.,** Loviscky, A., Vescio, T., Schermerhorn, N (April, 2021). The Effects of Masculinity Threats on Anti-Fat Attitudes Pennsylvania State University Undergraduate Research Exposition

5. **Veglia, K.,** Loviscky, A., Vescio, T., Schermerhorn, N (March, 2021). The Effects of Masculinity Threats on Anti-Fat Attitudes" To be Presented at the Psi Chi session of the Annual Meeting of the Mid-Western Psychological Association.
6. **Veglia K.,** Vescio, T., "Extreme Attitudes of Female Body Proportions" Pennsylvania State University Undergraduate Research Exposition
7. **Veglia K.,** Williams A**.,** Bevilacqua, P. "Investigation of the Behavior of RNA G-quadruplexes from the Human Genome under Physiological Conditions" Eberly College of Science Poster Conference 2017

Publications

Publications in Preparation

1. **Veglia K.,** Yamaguchi-Pedroza, K., Loviscky, A., Vescio, T. (February 2022). Gender Threats and Anti-Female Sentiments
2. Loviscky, A., **Veglia, K.,** Vescio T., Schermerhorn, N. Threats to Masculinity are Associated with Increases in Racism.

Research Experience

Undergraduate Research Assistant, Pennsylvania State University Spring 2019-present

Advisor: Theresa Vescio, Department of Psychology

Role of masculinity threat on victim blaming, racist attitudes, and support for status quo maintaining decision makers and policies

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Survey construction and online programming

Data coding and Data Analysis

Report Writing: Posters and Manuscript Preparation

Undergraduate Research Assistant, Pennsylvania State University 2017-2018

Department of Molecular Biology

Advisor: Philip Bevilacqua

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Data Analysis

Report Writing: Posters and Manuscript Preparation

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Conduct Poster Creation Workshop

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Participate in Weekly Pedagogy Seminar

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Pennsylvania State University

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Research Grants

Contributions to Prior Funded Research January 2017-May 2018

Investigation of the Behavior of RNA G-quadruplexes from the Human Genome under Physiological Conditions

Principlal Investigator: Philip Bevilacqua, PhD

Eberly College of Science, $1,500

Role: Co-author, My role on RNA G-quadruplex research was part of the basis for this award. I provided preliminary data and wrote the application with Dr. Bevilacqua