The MU McNair Journal is the official journal of the McNair Scholars Program (Ronald E. McNair Post-Baccalaureate Achievement Program) at the University of Missouri. Full funding is through a grant from the U.S. Department of Education (Grant No. P217A070148) at the amount of $252,000.

The MU McNair Journal is published annually. Manuscripts are accepted from McNair Scholars participating in the program at the University of Missouri, Columbia Missouri 65211, (573) 882-1962.

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On the Cover: McNair Scholar, Diana Ortiz
Message from the Director

It is my pleasure to introduce this outstanding collection of articles from the 2007-08 participants of the MU McNair Scholars Program. The papers presented here represent the culmination of a year’s worth of research and scholarly activity. They reflect the energy, creativity and effort of the scholars, themselves, as well as the careful guidance and diligence of their faculty mentors. Six very diverse topics are explored and reported in their entirety within this interdisciplinary journal. While their subject matter and journalistic styles may differ, they, along with the other McNair Scholars listed in this publication, are to be commended for their persistence and dedication to this rigorous undergraduate research experience.

Since 1989, the McNair Program has been a University-wide effort that continues to attract students and faculty mentors from a variety of academic departments and fields of inquiry. Students have had the opportunity to learn about the importance of earning an advanced degree, while gaining the skills and tools that will guide them through their future academic journeys. The program proudly bears the name of astronaut and scientist, Dr. Ronald E. McNair, who died in the Challenger explosion in 1986. His accomplishments and high standards set an outstanding example for these developing scholars.

As the new director of the MU McNair Scholars Program, I am truly honored to be associated with an initiative such as this. So many faculty, staff and administrative members of the MU community have worked to ensure a supportive and cohesive environment that prepares these exceptional students for graduate programs. We are proud to highlight the work of these talented young researchers, in this, the sixteenth edition of the MU McNair Journal.

Sincerely,
NaTisha Davis
Director, McNair Scholars Program

Background

College students who are considering study beyond the baccalaureate level realize their dreams through the McNair Scholars Program at the University of Missouri-Columbia (MU). MU was one of the original fourteen universities selected to develop a program established by the U.S. Department of Education and named for astronaut and Challenger crew member Ronald E. McNair. The purpose of the program is to provide enriching experiences that prepare eligible students for doctoral study.

Program Elements

One of the most exciting aspects of the McNair Scholars Program is the opportunity for junior or senior undergraduate students to participate in research experiences. McNair Scholars receive stipends to conduct research and engage in other scholarly activities with faculty mentors from the areas in which they hope to pursue graduate study. These research internships are either for the academic year or for the summer session and are under the supervision of faculty mentors. For academic year internships, students work a minimum of ten hours per week during the fall and winter semesters. Summer interns work full-time for eight weeks.

McNair Scholars also attend professional conferences with their mentors, go to graduate school fairs, prepare for graduate school entrance exams, receive guidance through the graduate school application process and obtain information on securing fellowships, graduate assistantships, and loans. Participants learn about graduate school life, advanced library skills, and effective ways to present their work. At the completion of the research internships at MU, McNair Scholars make formal presentations of their research to faculty and peers at the McNair Scholars Conference and submit papers summarizing their work. Students who participated as juniors the previous year continue in the program during their senior year for graduate school placement and to further develop their skills.

Eligibility

Participants must meet grade point average standards; be U.S. citizens or permanent residents; and qualify as either a first generation college student with an income level established by the U.S. Department of Education, or a member of a group that is underrepresented in graduate education.

All students who wish to be involved submit an application to the program. A committee composed of faculty members and representatives from both the graduate dean’s office and the McNair Scholars Program selects participants and approves faculty mentors. Research internships are offered to those students who are juniors or seniors and are identified as having the greatest potential for pursuing doctoral studies.
Within the United States the importance of human capital formation has increased substantially over the past thirty years. This has led to a dramatic upward pressure on tuition prices from both the demand and supply side. Combined with increases in the cost of higher education itself, public institutions have experienced a significant decline in state support forcing students to face a larger share of the cost of their education. Such increases in the private cost of education have raised a debate as to what are the true effects of higher education investment on economic growth, and what is the proper amount of public investment in human capital given both the public and private returns.

Specifically, this debate has focused on whether an investment in human capital through higher education leads to the substantial positive externalities as was previously expected. On one hand, some scholars argue that greater public funding on education is needed to increase labor productivity; thus, improving the efficiency of the labor force. As Gary S. Becker argues, “economic successes of individuals and even of whole economies depend on how extensively and effectively people invest in themselves” (Becker, 2002, p.3). The argument can be made that not only do individuals benefit from higher education privately, but that society benefits through positive externalities associated with increased education levels such as a lower propensity to commit crime, increase healthy behaviors, volunteer at higher rates, and become more active citizens.

On the other hand, there are arguments indicating that the cost of investing in human capital has increased so much that its returns by no means outweigh its costs; at least, not at the expected level or in the geographic regions where the investment was made. In fact, there is evidence showing that states with lower economic growth have received the greater higher education funding (Vedder, 2004b); thus, begging the question of whether this funding shall continue. Vedder (2004a) argues that the perceived positive externalities associated with higher education may be larger than the actual externalities society experiences. Such results lead some to conclude that public funding of education is not the most efficient use of public funds.

Regardless of conflicting evidence, all scholars agree on the importance of human capital investment for economic growth. Those who find negative evidence suggest that inefficient expenditure may be a potential factor driving their negative results. Hence, there is a need to address the question, not of how much is spent in higher education but rather, of how funds are allocated. Thus, this project will attempt to show that the quality of public investment forthcoming from a strategic decision process, rather than mere volume, has a higher correlation with economic growth. While our results suggest that a larger investment into research purposes yields higher rates of return, education research has shown that funds are being directed into less efficient areas of investment, as indicated by this study, such as public service, operations, and maintenance (Wellman, Desrochers, & Lenihan, 2008). Lastly, if it can be shown that a more careful investment is more likely to yield the expected positive returns at a state-level, such results would serve as evidence to help state governments efficiently allocate funds between education and other public expenditure categories.
Previous Empirical Evidence

Considering there are various public sectors across which the government must distribute its revenue, it would be inefficient for a country to publicly fund a sector that will not create sufficient returns. Previous empirical evidence suggests that investment into higher education is justified by showing that public higher education expenditure is positively related to growth. Evidence suggests that investment in human capital can promote growth through increasing productivity of people, both in present and future generations through spillover effects, and therefore the quality of goods produced (Stokey, 1991). Further, human capital accumulation is observed to positively influence growth through facilitating the absorption of new technologies within a country (Barro, 2000).

In addition to the importance of human capital accumulation for growth, the importance of expenditure on higher education relative to primary and secondary levels can be observed. Gyimah-Brempong, Paddison, and Mitiku (2006) find that higher education expenditure will generate additional positive effects on growth that are not completely mitigated by those of lower levels of education. This leads the authors to suggest that the success of promoting economic growth in Africa lies in the ability of the country to retain and employ the portion of human capital with higher levels of training. Supporting this evidence, Blankenau and Simpson (2004) finds that increases in education spending are more likely to positively affect growth if higher education receives a larger share of the total increased expenditure, thus lowering the private cost of higher education and increasing the total quantity of education attained.

Given evidence provided by economic research at a country-level, one should feel comfortable to conclude that there is a significant positive relation between public expenditures on human capital and growth. However, when such relations are analyzed across U.S. states there is still a lot of uncertainty as to what is the true effect of state-level educational spending on economic growth. Before a description of the conflicting evidence is presented, it is important to consider that a significant factor causing such different effects is the variety of methodologies used by the scholars for their analysis. Drucker and Goldstein (2007) review the empirical methodologies used in state-level economic growth literature and identify the advantages and disadvantages of each type. They argue that both cross-sectional and panel studies have the advantage of providing evidence that can be easily generalized and therefore be very useful for policy. However, significant drawbacks in using this type of analysis, such as susceptibility to sampling issues and omitted variable bias, were identified.

Davis and Wang (2005), using a panel of U.S. states, analyze the distribution of government expenditures across nine areas of public expenditure and provide evidence that suggests a negative, although insignificant, relationship between public expenditure on education and state economic growth. Specifically, they observe that increased public expenditure on higher education does not affect the quality of education, therefore, does not improve labor market efficiency. Davis and Wang form two hypotheses, both based around an inefficient allocation of resources, to explain their lack of an observed relationship between higher education spending and growth. Their first inefficiency hypothesis rests upon their observation that often increases in educational funding solely arise through the self-serving incentives faced by higher education institution administrators. Their second hypothesis is based upon the observed negative relationship between the accumulation of human capital and the accumulation of physical capital and population growth.

Similarly, Vedder (2004a) rejects the widely agreed relation between higher expenditure and college attendance. Even though he agrees that the presence of college graduates has a positive effect on growth, he finds that the influence of public higher education expenditure on college attendance is at most weakly positive, and possibly even non-existent. Therefore, he concludes that growth cannot be attributed to higher expenditure on higher education. He provides two plausible explanations for this finding. First, a self-selection bias argument, is that productivity may be determined by personal attributes of people who attend college rather than by higher expenditure levels. Second, he believes that a weak relationship between productivity and expenditure is due to an inefficient use of funds, given that a larger portion of public funds is going to the hands of college administrators and not to instructive purposes that could increase productivity of students. Alternative sources of inefficiency are found in the literature as well. For example, Aghion, Boustan, Hoxby, & Vandenbussche (2005) suggest that large investments into university research will only be favorable in economically developed states.

Single-university studies are another type of study widely used by scholars that, as suggested by Drucker and Goldstein (2007), usually find positive relationships between higher education and local economic growth. The great advantage of using single-university studies is the possibility to collect primary data, sometimes of variables or subjects that are not easy to quantify. However, these have significant limitations as well. The first problem is a problem of attribution. Results confound effects from existing relationships among organizations and ignore the characteristic of the knowledge-production of altering such relations. Other limitations are lack of geographical and time definitions, the difficulty to generalize results, their emphasis on growth effects ignoring distributional effects and finally the high costs attached to the inducement of the study. Such advantages and disadvantages should be taken into account when interpreting the evidence of the studies discussed below.

Using Xavier University as a case study, Blackwell, Cobb, and Weinberg (2002) argue that many of the studies that find the nonexistent or negative relation between public higher education expenditure and state economic growth is due to omission of important aspects in their studies such as import substitution effects. The latter being increased economic activity that results from a larger population attracted to the state by the presence of a university in the area. By adding import substitution effects in their model of analysis, they find a positive relation between state economic growth and the existence of a higher education institution in the area. These results however, as suggested by Aghion, Boustan, Hoxby, and Vandenbussche (2005), are more likely to be observed in economically developed states.

Based on the evidence presented thus far, levels of expenditure clearly are not the sole reason for previous research showing negative results with respect to growth. Alternative possible explanations as to why conflicting evidence is obtained,
are suggested by evidence of Goldstein and Renault (2004), Goldstein and Drucker (2006) and Jaffe (1989). Combined, their research suggests that the impact on local economy through different university activities varies. Specifically, the impact on economic growth arising from university research activities is shown to be more significant compared to that of other university activities. This larger significance of investment on research activities relative to other university activities has become more relevant since the move to a more knowledge based economy starting in 1986 (Goldstein & Renault, 2004). The positive effect is supported by evidence showing a positive correlation of research knowledge spillover effects and growth; a larger portion of which is captured in the local area and hence help promote local economic development (Goldstein & Drucker, 2006; Jaffe, 1989). Further, scholars find that university research boosts the positive existing effects from agglomeration economies, but that university research does not depend on agglomeration economies to generate positive contributions in the economy of small and medium size MSA’s (Goldstein & Drucker, 2006; Goldstein & Renault, 2004). Finally, Jaffe (1989) finds a distinctive relation between university research and industry research and development where university research is the factor causing industry research and development and not vice versa.

Based on this evidence, one could suggest that all universities increase research expenditures in order to improve the states economy. However, evidence provided by Aghion, Boustan, Hoxby, and Vandenbussche (2005) suggests that this would be an unsubstantiated conclusion. Making the distinction between increased research expenditures in developed states, or innovative states that need a highly educated labor force (e.g. Massachusetts), and less developed or innovative states that require more physical capital (e.g. Virginia, Alabama) differential effects were identified. Their results show that in both cases the number of degree holders increased. However, such degree holders become more mobile individuals and will be more easily retained and attracted by innovative states. For this reason, the expected positive returns were only experienced in such states. Generally speaking, the authors suggest that migration accounts for about half of the total difference in growth effects between innovative and imitative states.

Regardless of the evidence presented with respect to university research activities, Goldstein and Drucker (2006) find that educational attainment levels and the stock of business services are two factors that remain the most influential determinants of regional development across all size regions. There is also empirical evidence suggesting that quality of education will have a significantly positive effect on economic growth (Card & Krueger, 1992; Brewer, Eide, & Ehrenberg, 1999; Baryla & Dotterweich, 2001; Hill & Lendel, 2007). Positive effects from quality are mainly observed as increased returns to those who receive a better quality education; however, some studies show a positive effect on growth from induced migration that results from institutional and program reputation (Baryla & Dotterweich, 2001; Hill & Lendel 2007). Further, there is evidence showing that quantity of education will have a positive impact on growth although at a lesser degree than quality (Kane & Rouse, 1993; Barro, 2000). Therefore, it is important to consider that university activities related to factors such as education quality, educational attainment levels and others will also be important for the enhancement of economic growth. If these are observed to improve with increased funding, then efficient expenditure into these should also be considered in order to observe the expected positive returns.

Consequently, in addition to showing that there exists a strong correlation between public higher education expenditure and economic growth at the country level, there is evidence that shows that the level of impact on economic development differs depending on which university activity is being analyzed and attributes of the state were the investment is made. By creating an empirical model which differentiates based upon the allocation patterns of public funds, this study attempts to identify which university activities have a higher potential of promoting growth. Considering there are many factors that vary across states, growth maximizing policies of each state will most likely vary as well.

### Empirical Specification

A statistical analysis will be carried out through the use of economic growth models. To estimate the effect of higher education expenditure on growth at a state-level, a sample of 51 U.S. states between 1980 and 2001 is analyzed. The contribution of this research is in the treatment of the key explanatory variable higher education expenditure. Typically, previous research has investigated whether total higher education expenditure affects state level economic growth. This analysis builds on previous research by investigating whether individual components of higher education expenditure have differential effects on state economic growth. By breaking down higher education expenditure into expenditure components, we are able to better understand not just if higher education spending leads to economic growth, but which components of expenditure are better public investments.

Following previous literature (e.g. Kneller, Bleaney, & Gemmell, 1999; Davis & Wang, 2005) we begin by estimating the relationship between total public higher education institutional expenditure and economic growth using the following empirical model:

\[
(1) \quad g_{it} = \alpha_i + \beta_1 \text{PHEE}_{it} + \beta_2 \text{IGE}_{it} + \beta_3 \text{MEGE}_{it} + X_{it} + \mu_{it}
\]

Where \( g_{it} \) is the growth rate of real per-capita personal income, \( \text{PHEE}_{it} \) is public higher education institutional expenditure as a percentage of GSP, \( X_{it} \) are time-varying state-level characteristics, and \( \mu_{it} \) are state-level fixed effects.

To investigate whether different expenditure components have differential effects on economic growth, we alter equation (1) by breaking down PHEE into three main expenditure components – research (REGE), instruction (IGE), and miscellaneous (MEGE):

\[
(2) \quad g_{it} = \alpha_i + \beta_1 \text{REGE}_{it} + \beta_2 \text{IGE}_{it} + \beta_3 \text{MEGE}_{it} + X_{it} + \mu_{it}
\]

Typically, economists estimate economic growth equations using one of two measures. The first, Gross State Product (GSP) which is similar to the Gross Domestic Product (GDP) of a country, represents total economic output of the state (e.g. Aghion, Boustan, Hoxby, & Vandenbussche, 2005). However, GSP directly includes spending by governmental agencies, in particular all educational spending, thus any estimated relationship between
higher education spending and GSP are confounded. Thus, for this analysis we choose the second typical growth measure, real per-capita personal income (e.g. Hill & Lendel, 2007; Davis & Wang, 2005; Vedder, 2004).

Our measure of higher education spending differs from similar research as we have defined PHEE, to be expenditures at public institutions as opposed to total higher education appropriations as is traditional in this literature. We deviate from the traditional measure of public appropriations as our interest is in the allocation of money at the public higher education institutions; not simply how much is given to the institutions by the state governments. Expenditure data is gathered from the Integrated Post-Secondary Education Data System (IPEDS) for all institutions of higher education that are eligible for Federal financial aid and aggregated into statewide measures of research, instruction, and miscellaneous expenditure levels. Specifically, research expenditure includes expenses for activities organized specifically to generate research outcomes and commissioned by an agency either external to the institution or separately budgeted by the organizational unit within the institution. This expenditure category does not include expenses for training programs (Integrated Post-Secondary Education Data System [IPEDS], n.d.).

Previous literature shows that a larger investment on university research has a favorable effect on state economic growth (Goldstein & Renault, 2004; Drucker & Goldstein, 2007; Jaffe, 1999). However, as suggested by Aghion, Boustan, Hoxby, and Vandenbussche (2005), we hypothesize that the level of economic return related to investments on university research may vary depending on the state where the investment is made.

Instruction expenditure includes expenses of the colleges, schools, departments, and other instructional divisions of the institution and expenses for departmental research and public service that are not separately budgeted. This expenditure category does not include administrative expenses (e.g. academic deans) (IPEDS, n.d.).

There is some evidence suggesting that instruction expenditure increases education quality and therefore economic growth (Card & Krueger, 1992), however, there is also evidence showing the opposite (Vedder, 2004b; Davis & Wang, 2005). We therefore hypothesize that the relationship of instruction expenditure and state economic growth is ambiguous.

Miscellaneous expenditure includes expenditure in public and student services, academic support, operation and maintenance of plant and other operational services (IPEDS, n.d.). Since this spending category lumps together expenditure in various factors its relationship to state economic growth is ambiguous.

A second analysis investigates whether the channel of public investment in higher education, whether directly to institutions or directly to students, has differential effects on growth. Again, following Kneller, Bleaney, and Gemmell (1999) and Davis & Wang (2005), we begin by estimating the following baseline specification:

\[ g_{it} = \alpha_i + \beta_1 \text{GHEE}_{it} + X_{it} + \mu_i \]

Where \( g_{it} \) is the growth rate real personal income per-capita, \( \text{GHEE}_{it} \) is public higher education government expenditure as a percentage of GSP, \( X_{it} \) are time-varying state-level characteristics, and \( \alpha_i \) are state-level fixed effects. Higher education government expenditure as a percentage of GSP includes funds that are given directly to the student as well as directly to the institution. Given that it includes the funding of various factors, its relationship to growth is ambiguous. Data for \( \text{GHEE}_{it} \) is provided by Grapevine and the National Association of State Student Grant and Aid Programs (NASSGAP).

In the case for the U.S., most authors find that education has little or negative impact on state economic growth (Vedder, 2004b; Davis & Wang, 2005). Economic theory on the other side suggests education is a productive expenditure and therefore should have a positive impact on economic growth. Therefore, we hypothesize that government expenditure on higher education, may either have a positive or a negative sign.

We then extend equation (3) by breaking down government higher education expenditure into two different measures indicating the channel through which the investment is made. Specifically, we break down total government expenditure on higher education into the components - direct appropriations to institutions (AGE) and direct appropriations to students (GGE):

\[ g_{it} = \alpha_i + \beta_1 \text{AGE}_{it} + \beta_2 \text{GGE}_{it} + X_{it} + \mu_i \]

\( \text{AGE}_{it} \) includes all state government funds given to higher education that are distributed through the institution. Given that funding into various university activities and areas are lumped together in this variable, its sign is ambiguous. Data for \( \text{AGE}_{it} \) will come from Grapevine. \( \text{GGE}_{it} \) includes funds that are given directly from the state to the student which includes grants, scholarships and other such gifts. Being that the funds are going to the hands of particular individuals, its effect on growth is ambiguous.

Data for \( \text{GGE}_{it} \) is available from the National Association of State Student Grant and Aid Programs (NASSGAP).

As it can be noted, we include an identical set of control variables across all models. The reason for their inclusion is that these are factors likely to affect the economy of a state, or serve as a burden for higher education expenditure. We therefore try to control for their effects. The first three control variables represent the sectoral composition of the economy including agricultural, mining and manufacturing. We also include a set of controls related to the composition of a states’ population including state ethnic diversity, income inequality, population growth, and migration. Additionally, the models include a state budget burden and a measure of physical capital per-capita. A more complete description of the control variables and their hypothesized effects can be found in Appendix A.

**Results**

Column 1 of Table 1, reports the results of the estimation of equation 1. The first regression analyzes solely the effect of total expenditure, defined as the total amount of funds spent by public higher education institutions as a percentage of GSP on state economic growth. Holding all other variables constant, the estimated coefficient of total higher education expenditure provides evidence that an increase in total higher education expenditure has a significantly negative effect on real per-capita personal income. Specifically, a 1% increase in the change of total higher education expenditure as a percentage of GSP is observed to be related to a 3% decline in the change of real per-capita personal income. This result supports those of previous studies that find a negative correlation between public higher education expenditure...
and state economic growth (Vedder, 2004; Davis & Wang, 2005).

The estimation of equation 2 allows us to obtain evidence that can be compared with previous studies that find differential effects of higher education expenditure on state economic growth (Aghion, Bousan, Hoxby, & Vandenbussche, 2005; Goldstein & Renault, 2004; Goldstein & Drucker, 2006; Jaffe, 1989). Column 2 of Table 1 reports the results of impact from each expenditure component (i.e. research, instruction and miscellaneous) on real per-capita personal income. Holding all other variables constant, the obtained results show that an increase in research expenditure will have a significantly positive effect on real per-capita personal income. Evidence shows that a 1% increase in the change of research expenditure as a percentage of GSP is expected to be related to an 18.4% increase in the change of real per-capita personal income. On the other hand, instruction and miscellaneous expenditures are observed to be negatively related to real per-capita personal income. For comparison, the obtained estimate for instruction expenditure is statistically significant whereas that of miscellaneous expenditure is insignificantly different from zero. Specifically, a 1% increase in the change of instruction expenditure is expected to be related to a 20.8% decline in the change of per-capita personal income.

Table 2 reports the results of the estimation of equations 3 and 4. Column 1 reports the results of equation 3 where the main variable is the change in total state expenditure on higher education as a percentage of GSP. The evidence obtained shows that a 1% increase in the change of state higher education expenditure is related to a 6.9% decrease in the change of real per-capita personal income. This outcome supports that of Vedder (2004) suggesting that an increase in state higher education expenditure does not benefit the economic development of a state.

Results for the estimation of equation 4 are reported in Table 2. The first main variable in this model is change in appropriations which is defined as funds in millions of dollars given directly to the higher education institution to administrate. Results report that a 1% increase in the change of appropriations expenditure is expected to be related to a 4.9% decline in the change of real per-capita personal income. The latter estimate however, is not significantly different from zero.

The second variable entered, Grant-aid, is defined as funds in millions of dollars given directly to the students. Results show that the expected impact of increasing grant-aid expenditure on the change of real per-capita personal income is negative. The latter relation is statistically more significant than that observed between growth and appropriations, as well as evidence reports a larger magnitude of the expected effect. Specifically, a 1% increase in the change of grant-aid expenditure is observed to be related to a 42% decline in the change of real per-capita personal income whereas, a similar increase in the change of appropriations expenditure, is observed to be related to a decline in the change of real per-capita personal income of only 4.9%.

All four of the regressions estimated include the same vector of control variables. The obtained estimates for such control variables vary slightly across models but the direction

<table>
<thead>
<tr>
<th>Table 1: Impact of Investment on Research, Instruction and Other Areas of Higher Education on Economic Growth</th>
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<tr>
<td>In all specifications the dependent variable is change in real income per capita. Standard errors are in parentheses.</td>
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<tr>
<td>Independent Variable</td>
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<tr>
<td>Change in public institution total expenditure</td>
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<td>Change in public institution research expenditure</td>
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<tr>
<td>Change in public institution instruction expenditure</td>
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<tr>
<td>Change in public institution miscellaneous expenditure</td>
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<tr>
<td>Change in state agriculture expenditure</td>
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<td>Change in state mining expenditure</td>
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<td>Change in state manufacture expenditure</td>
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<td>Change in state ethnicity diversity</td>
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<td>Change in state population growth</td>
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<td>Change in state Gini coefficient</td>
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<td>Change in state education attainment</td>
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<td>Change in state tax burden</td>
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<tr>
<td>Lagged change in per-capita real income</td>
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<tr>
<td>Lagged change in per-capita real income</td>
</tr>
<tr>
<td>Year fixed effects</td>
</tr>
<tr>
<td>Constant</td>
</tr>
<tr>
<td>Constant</td>
</tr>
<tr>
<td>Observations</td>
</tr>
<tr>
<td>Number of states</td>
</tr>
<tr>
<td>R-squared</td>
</tr>
</tbody>
</table>

*Significant at 10%; **Significant at 5%; ***Significant at 1%
of the observed relationships is consistent. Based on the obtained results, only three of the included control variables are significantly different from zero at a 1% level. The first is change in state population. Using as a unit of measure the number of people residing in the state, a positive relation between changes in population and real per-capita personal income is observed. The second control variable is change in state migration. Again, a positive relation of change in migration and real per-capita personal income is observed suggesting that effects from population growth will be augmented by those of migration. Finally, the third statistically significant variable is change in state tax-burden. Evidence suggests a negative relationship between state tax-burden and real per-capita personal income.

Both tables include results of a third regression of all of our models using the Arellano Bond method. Results of these regressions are reported in Column 3 of both tables. Using the Arellano Bond method, the statistical significance of all estimates is lost. Nevertheless, the estimated direction of the effect on real per-capita personal income from the main variables of interest (i.e., expenditure variables), is consistent with the previously discussed results.

Discussion and Concluding Remarks

Previous empirical literature finds that U.S. state expenditure on higher education has a negative effect on state-level economic growth. This has the policy implication of reducing higher education funding to achieve greater economic growth. This research finds supporting evidence when analyzing the impact of total volume of higher education expenditure on state-level economic growth. However, when decomposing higher education expenditure we identify differential effects on state-level economic growth. Such differential effects suggest that higher education funds may be spent inefficiently and therefore suggest that what may be important is not the amount spent by states on higher education, but rather, the way in which funds are allocated. Specifically, evidence is found that states where universities invest relatively more in research as opposed to other areas of higher education enjoy higher rates of return. Thus, it may be in the best interest of states to provide guidance for where their money is to be spent, as opposed to blindly giving it to institutions as appropriations or to students through large scale financial aid programs.

Moreover, our results reinforce those obtained by previous country-level and some state-level studies that recognize the importance of public higher education expenditure to state economic growth. Nevertheless, our results in relation to the state-level studies of Vedder (2004b) and Davis and Wang (2005) warrant a more detailed explanation. Both Vedder (2004b) and Davis and Wang (2005) obtained results suggesting a negative or insignificant correlation between public higher education expenditure and state economic growth. In spite of the observed negative results, both consider that such investment is significantly important for the economic development of a state. For this reason, they suggest that the inefficient allocation of funds is a possible explanation of why negative outcomes are obtained. Both studies describe a potential source of inefficiency as an extensive share of funds given to school administrators rather than to students or instruction purposes, harming college attendance, productivity, quality of education, and hence reducing growth. Even though our results support the suggestion of inefficient expenditure as a potential source for negative outcomes, our results disagree with the efficiency pattern mentioned above. In contrast,

Table 2: Impact of Allocation of Public Funds across Appropriations and Grant-Aid on Economic Growth

<table>
<thead>
<tr>
<th>Independent Variable</th>
<th>(1)</th>
<th>(2)</th>
<th>(3)</th>
</tr>
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<tbody>
<tr>
<td>Change in total state expenditure</td>
<td>-0.0691*</td>
<td>-0.101</td>
<td>-0.101</td>
</tr>
<tr>
<td></td>
<td>(0.0364)</td>
<td>(0.121)</td>
<td>(0.121)</td>
</tr>
<tr>
<td>Change in public institution appropriations</td>
<td>-0.0490</td>
<td>-0.020</td>
<td>-0.747</td>
</tr>
<tr>
<td></td>
<td>(0.252)</td>
<td>(0.738)</td>
<td>(0.738)</td>
</tr>
<tr>
<td>Change in student appropriations</td>
<td>-0.0725*</td>
<td>-0.000641</td>
<td>0.0000168</td>
</tr>
<tr>
<td></td>
<td>(0.00399)</td>
<td>(0.00397)</td>
<td>(0.012)</td>
</tr>
<tr>
<td>Change in state agriculture expenditure</td>
<td>0.00729*</td>
<td>0.00725*</td>
<td>0.000168</td>
</tr>
<tr>
<td></td>
<td>(0.00236)</td>
<td>(0.00236)</td>
<td>(0.00961)</td>
</tr>
<tr>
<td>Change in state mining expenditure</td>
<td>-0.000567</td>
<td>-0.000461</td>
<td>0.0000915</td>
</tr>
<tr>
<td></td>
<td>(0.00236)</td>
<td>(0.00236)</td>
<td>(0.00961)</td>
</tr>
<tr>
<td>Change in state manufacture expenditure</td>
<td>0.00245</td>
<td>0.00249</td>
<td>0.00145</td>
</tr>
<tr>
<td></td>
<td>(0.00176)</td>
<td>(0.00175)</td>
<td>(0.00971)</td>
</tr>
<tr>
<td>Change in state ethnic diversity</td>
<td>-0.0823</td>
<td>-0.0897</td>
<td>0.184</td>
</tr>
<tr>
<td></td>
<td>(0.126)</td>
<td>(0.126)</td>
<td>(0.341)</td>
</tr>
<tr>
<td>Change in state population growth</td>
<td>0.644***</td>
<td>0.621***</td>
<td>-0.105</td>
</tr>
<tr>
<td></td>
<td>(0.119)</td>
<td>(0.120)</td>
<td>(0.159)</td>
</tr>
<tr>
<td>Change in state Gini coefficient</td>
<td>-0.0535</td>
<td>-0.0670</td>
<td>-0.0738</td>
</tr>
<tr>
<td></td>
<td>(0.0567)</td>
<td>(0.0573)</td>
<td>(0.198)</td>
</tr>
<tr>
<td>Change in state education attainment</td>
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<td>0.000160</td>
<td>0.00265</td>
</tr>
<tr>
<td></td>
<td>(0.00191)</td>
<td>(0.00190)</td>
<td>(0.00491)</td>
</tr>
<tr>
<td>Change in state tax burden</td>
<td>-2.258***</td>
<td>-2.222***</td>
<td>0.267</td>
</tr>
<tr>
<td></td>
<td>(0.516)</td>
<td>(0.515)</td>
<td>(1.561)</td>
</tr>
<tr>
<td>Change in state migration</td>
<td>0.0815***</td>
<td>0.0790***</td>
<td>0.0795</td>
</tr>
<tr>
<td></td>
<td>(0.0252)</td>
<td>(0.0252)</td>
<td>(0.0869)</td>
</tr>
<tr>
<td>Lagged change in per-capita real income</td>
<td>-0.0209</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.0798)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year fixed effects</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Constant</td>
<td>0.112***</td>
<td>0.118***</td>
<td>-0.00268</td>
</tr>
<tr>
<td></td>
<td>(0.0119)</td>
<td>(0.0125)</td>
<td>(0.0348)</td>
</tr>
<tr>
<td>Observations</td>
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<td>200</td>
<td>150</td>
</tr>
<tr>
<td>Number of states</td>
<td>50</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>R-squared</td>
<td>0.727</td>
<td>0.731</td>
<td></td>
</tr>
</tbody>
</table>

*Significant at 10%; **Significant at 5%; ***Significant at 1%
the evidence obtained in this research suggests that a larger share of funds invested into research activities rather than instruction purposes would yield higher rates of return at a state level.

Additionally, we observed that when controlling for migration, the effects observed from research expenditures were not affected. Nevertheless, one should be careful when interpreting such results given that, in order to obtain the potential positive returns from university research investments, the efficient level of the investment will vary across states. The latter is more thoroughly analyzed by the study of Aghion, Boustan, Hoxby, and Vandenbussche (2005) that suggests that states that are more economically developed will benefit more from larger investments into research activities than less developed states.

Further, our second set of findings reinforces the suggestion of research investments as a more efficient investment. For instance, if one considers the potential positive results from research investments and combines this with the outcome of negative correlations of appropriations and student-aid with growth, the case of inefficient expenditure becomes more plausible. Recall that the negative correlation between student-aid and growth is more significant than that of growth and appropriations. States that are currently spending more in grant-aid are driving funds away from more efficient areas of investment (university research) and therefore yield the observed negative results on growth. When states provide student assistance through grant-aid institutions are forced to attract more students to the institution in order to generate the funds necessary to support such a large aid system. To attract this large number of students the institution starts to invest in areas that will serve as student magnets such as recreation centers and improved infrastructure, which are not necessarily efficient areas of investment if state economic growth is the goal.

Based on our findings, if higher education expenditure is intended to produce higher rates of return within the state where the investment is made, we consider that it is not a matter of solely increasing the volume of the investment but rather strategically distributing the funds to produce higher rates of return. We consider that instead of blindly giving aid to students or merely increasing the amount of institution appropriations, states and higher education institutions should invest a larger share of funds into university research activities at a level which is efficient to the specific state where the investment is made. Moreover, considering our results on the particular significance of university research to growth and the significance of factors such as quality and quantity of education observed by Card and Krueger (1992) and Kane and Rouse (1993) respectively, further research could be carried out to analyze the relation between these three factors to see if an alternative allocation pattern, that would yield even higher rates of return, can be detected.

References


Footnotes
1. The analysis of Equations 3 and 4 exclude the District of Columbia given that there are no direct appropriations into higher education in this state.
2. A detailed list of control variables, their sources, and hypothesized effects can be found in Appendix A.

### Appendix A: Data dictionary

<table>
<thead>
<tr>
<th>Variable</th>
<th>Source/Definition</th>
<th>Hypothesized sign</th>
</tr>
</thead>
<tbody>
<tr>
<td>AGR</td>
<td>Bureau of Economic Analysis Gross State Product from Agriculture/GSP*100</td>
<td>Positive effect given that an increase in the share of agricultural product is expected to increase GSP.</td>
</tr>
<tr>
<td>MAN</td>
<td>Bureau of Economic Analysis Gross State Product from Manufacture/GSP100</td>
<td>Positive effect given that an increase in the share of manufacture product is expected to increase GSP.</td>
</tr>
<tr>
<td>MIN</td>
<td>Bureau of Economic Analysis Gross State Product from Mining/GSP100</td>
<td>Ambiguous impact given to a low or declining mining GSP share as economic basis diversifies.</td>
</tr>
<tr>
<td>ETHNIC</td>
<td>U.S. Census [\text{ethnic} = 1 - \sum_{i=1}^{n} (\text{Race}_i)^2] (i \in {\text{White, Black, Asian, Pacific Islander, American Indian and Other}})</td>
<td>Ambiguous effect of ethnic diversity on growth given to uncertain empirical evidence (e.g. Easterly and Levine, 1997; Rupasingha, Goetz &amp; Freshwater, 2002; Teitz &amp; Chapple, 1998).</td>
</tr>
<tr>
<td>POP</td>
<td>Bureau of Economic Analysis ((\text{Population} - \text{Population}<em>{t-1})/\text{Population}</em>{t-1})*100</td>
<td>Positive effect based on the resulting larger labor force and larger market of consumption (e.g. Becker, Glaeser &amp; Murphy, 1999).</td>
</tr>
<tr>
<td>GINI</td>
<td>U.S. Census A measure of income inequality</td>
<td>Ambiguous effect given to uncertain empirical evidence since income inequality and growth may cause each other (e.g. Persson &amp; Tabellini, 1994; Aghion, Caroli &amp; Garcia-Penalosa, 1999; Barro, 2000; Panizza, 2002).</td>
</tr>
<tr>
<td>EDUC</td>
<td>U.S. Census Percentage of 25 year old with a High School Diploma or greater</td>
<td>Negative effect based on evidence suggesting a positive effect on growth from higher education attainment (e.g. Barro, 2000; Gyimah-Brempong, Paddison and Mitiku, 2006).</td>
</tr>
<tr>
<td>TAX</td>
<td>U.S. Census State government tax revenues</td>
<td>Ambiguous effect given that the study does not differentiate between distortionary and non-distortionary taxation, which according to literature have opposite effects (e.g. Kneller, Bleaney &amp; Gemmell 1999; Barro, 1990).</td>
</tr>
<tr>
<td>MIG</td>
<td>National Center of Health Statistics (NCHS) Total change of state population - (births + deaths)</td>
<td>Positive effect as suggested by previous evidence (Aghion, Boustan, Hoxby &amp; Vandenbussche, 2005; Baryla &amp; Dotterweich, 2001).</td>
</tr>
<tr>
<td>RPKPC</td>
<td>Brown, Hayes &amp; Taylor (2003) Real growth rate of real per capita physical capital ((\text{RPKPC}<em>{t-1} - \text{RPKPC}</em>{t-1})/\text{RPKPC}_{t-1})*100</td>
<td>Positive effect given that physical capital leads to higher economic growth as per Solow (1956).</td>
</tr>
</tbody>
</table>
Adults experience significant declines in memory as they get older. For this reason, psychology researchers attempt to understand the possible causes for such declines. Specifically, we see that older adults experience declines in episodic memory. Episodic memory involves a particular memory linked to a specific context, or memory of events (as opposed to factual memory). Episodic memory is important for everyday functioning. It can include remembering a person’s name when you see their face or recalling what specifically happened during an event for eyewitness testimony. Older adults have a much harder time remembering such events than do younger adults.

Naveh-Benjamin (2000) suggested an associative deficit hypothesis (ADH) to explain the decline in episodic memory in older adults. The ADH states that older adults have poorer episodic memory because they have a more difficult time binding items together in order to remember the associations. Naveh-Benjamin explains that an episode consists of both individual units of information, as well as the relationship between the individual components (i.e., associations). An interesting empirical result about memory in older adults is that their memory for individual components of an episode is relatively similar to that of younger adults. However, older adults’ performance in remembering the associations between the components is significantly lower than younger adults (Naveh-Benjamin, 2000).

In the past, perception and cognition were viewed as somewhat separate areas. Recently, however, the processes underlying these two aspects of behavior have been claimed to be related to one another (Schneider, 2002). According to Schneider, perceptual or sensory processes take place early on in the processing sequence, while cognitive processes can be thought of as an expansion of what occurred before it. From this premise, he postulated that age-related declines in cognitive processing could be attributed to the sensory declines we see with aging.

To explain the high positive correlations in performance of sensory/perceptual tasks and cognitive tasks, especially found in older adults, Baltes and Lindenberger (1997) suggested a “common cause” hypothesis of the relationship between sensory and cognitive processing. The “common cause” hypothesis suggests that deterioration of the brain leads to both intellectual and perceptual declines.

A different suggestion, the permeation hypothesis, suggests that the high correlation between sensory and cognitive performance is due to the fact that putting more effort into sensory processing leaves fewer resources for performing the cognitive processes necessary to adequately encode and retrieve information (Lindenberger, Marsiske, & Baltes, 2000; Rabbit, 1968; 1991). Several studies support this notion by trying to assess whether younger adults under degraded sensory information conditions behave like older ones. For example, younger adults’ performance on a paired-associates task in the presence of background noise mirrors the performance of older adults when there is no background noise (Murphy, Craik, Li & Schneider, 2000). These results suggest that one reason for age-related declines in associative memory could be a decline in sensory functioning.

Specifically, as there is a decline in sensory processing in old age, more effort is put into seeing or hearing the stimuli. That is, if people cannot see stimuli very well, for example, they put
more resources into trying to see the individual components. This leaves fewer resources for binding information together. Subsequently, associative memory will be significantly worse than component memory. Component memory should not be reduced despite any sensory declines because of the increased effort in deciphering them.

One way to test whether there is a relationship between sensory acuity and cognitive processing is to simulate the sensory functioning of older adults in younger adults by degrading, or blurring the stimuli presented. If the substantial declines in associative memory in older adults are at least partially due to declines in sensory processing, we expected to find an associative deficit in younger adults when using degraded stimuli. The more degraded the stimuli are, the more of a decline in associative memory in younger adults. In this case, memory performance in younger adults should model the associative deficit of older adults when the stimuli are moderately degraded. In addition, when older adults study non-degraded stimuli, their memory should show an associative deficit as in previous studies. Finally, the more degraded the stimuli, the more of an associative deficit should occur in older adults, as well. Component memory may be enhanced by the level of degradation since increased degradation leads to an increased effort in seeing the individual stimuli.

To assess the above suggestions, this study looked at issues not fully addressed in previous studies. In particular, past studies that did use degraded stimuli tested the effects of degrading stimuli at study alone (e.g., Naveh-Benjamin, Kilb, & Hara, 2007). Because the current study aimed to simulate the sensory processing of older adults, it seemed more valid to simulate declines in visual acuity both at study and test, since older adults also experience sensory declines at encoding and retrieval.

It was originally suggested that older adults remember information obtained from pictures as well as younger adults (Park, Puglisi, & Smith, 1986). However, results from later experiments demonstrated that the associative deficit seen in relation to item memory occurs with pictorial information as well as verbal information (Naveh-Benjamin, M., Hussain, Z., Guez, J., & Bar-On, M., 2003). There are not many other studies that also look at pictorial information, as most studies focus primarily on the verbal domain, whether auditory words or visual words. However, it is important to apply the ADH to both verbal and visuospatial realms. Previous studies have applied the ADH to face-name associations (Naveh-Benjamin, Guez, Kilb, & Reedy, 2004), but they have not manipulated degradation levels. Also, older adults had intact item memory, suggesting that they could distinguish among the faces. However, when looking at face-name associations, it cannot be determined if the participants could actually identify the faces at study. By using nameable objects, we will be able to assess the degree to which they are identified during encoding, as this is especially important when manipulating degradation levels.

To summarize, this study aimed at assessing whether the associative deficit shown for older adults is mediated by a decline in sensory processing in old age. We tested this assertion by presenting both younger and older adults with non-degraded or degraded pictures of pairs of objects and later asked them to recognize the individual objects as well as their associations to each other.

**Method**

**Participants**

Eighteen younger adults and 16 older adults participated in the study (see Table 1). The younger adults were students at the University of Missouri who received course credit for their participation in the experiment. The older adults were local Columbia, Missouri residents who received monetary compensation for their time. The mean age for the younger adult group was 19 (SD=1.0) and the mean age for the older adult group was 74 (SD=5.0). The mean years of education for younger adults was 13.5 (SD=0.8) and for older adults was 14.5 (SD=1.7). Also, the older adults selected for the experiment reported being in good health and had good vision (measured by a Snellen® eye chart).

**Table 1**

<table>
<thead>
<tr>
<th>Demographic Information</th>
<th>Younger adults</th>
<th>Older Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (years)</td>
<td>19</td>
<td>74</td>
</tr>
<tr>
<td>Years Education</td>
<td>13.5</td>
<td>14.5</td>
</tr>
<tr>
<td>Men</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>Women</td>
<td>10</td>
<td>13</td>
</tr>
</tbody>
</table>

**Design and Materials**

Five variables were used: between-subjects group (young vs. old adults), within-subjects test (individual pictures vs. their associations), a within-subjects degradation level at study (none, slight, moderate), between-lists degradation at test (within-subjects: none, slight, moderate), and between-lists picture type (within-subjects: black/white and color). The level of degradation was manipulated using the “Gaussian Blur” feature of Adobe Photoshop. Pictures under no degradation were perfectly clear, those under slight degradation were somewhat blurry, and those under moderate degradation were very blurry (see Figure 1)

A total of 432 pictures were used in the actual experiment. Of the 432 pictures, half were black and white and half were colored pictures. The experiment included 6 lists of picture pairs (3 color and 3 black and white). Each list consisted of 30 picture pairs, as well as 12 distracter pictures (did not appear at study). A practice trial included 10 picture pairs at study, with 4 distracters at test. All trials were counterbalanced with the list order, stimuli order, test order, degradation at study, and degradation at test. Each list contained 10 pairs of pictures at each degradation level (none, slight, severe), and each test contained 4 targets and 4 distracters for each degradation level. All picture pairs underwent all degradation levels in the different configurations, and each picture pair appeared in only one of the study lists.

**Figure 1**

**Presented stimuli: Levels of degradation**
Procedure
Each participant was tested individually and saw 30 picture pairs in each list at a rate of one pair every 3 seconds. The studying of the pictures was intentional, where participants were told to try to remember each individual picture, as well as which picture they appeared with to prepare for the subsequent tests. A 60-second filler task of counting backwards occurred between each of the study and test phases. After the filler task, each list was followed by two recognition tests—item and associative.

The tests were experimenter-paced, with stimuli being presented every 5 seconds. The item test measured the participants’ memory for individual pictures. Participants saw 12 individual pictures that appeared at study and 12 individual pictures that did not (e.g., distractors). They were asked to indicate whether each picture appeared at study. The associative test measured the participants’ memory for which pictures appeared together (e.g., associations). Participants saw 24 picture pairs, with 12 of them being intact (appeared together at study) and 12 of them being recombined (appeared at study, but not together). Participants were asked to indicate whether each picture pair appeared together at study or not. Both tests were equally distributed in terms of how many pictures from each degradation level at study were represented.

Results
We calculated the proportion of ‘hits’ (e.g., a correct response of ‘yes’ to a target) minus the proportion of ‘false alarms’ (e.g., an incorrect response of ‘yes’ to a distractor). Means were calculated for both tests for each degradation level and picture type (e.g., color or black/white) in both younger and older adults. We tested our hypotheses, using a between-subjects factor of age (young vs. old) and within-subjects factor of test (item vs. associative), degradation at study (none, slight, moderate), degradation at test (test, none, slight, moderate), and picture type (black/white versus color). The .05 significance level was used to interpret all statistical comparisons. Results can be seen in Table 2 and 3.

The 5-way interaction of picture type, test type, degradation at study, degradation at study, and age was not significant, F(1,108)=.493, MSE=.086, p>.05, but was significant when gender was considered as well in the interaction, F(1,108)=2.978, MSE=.086, p>.05. The main effect of age was not significant, F(1,29)=2.108, MSE=.289, p>.05. Where younger adults showed better performance (M=.57) than older adults (M=.48). There was a significant effect of picture type, F(1,27)=4.509, MSE=.188, p<.05, where participants showed better performance with color pictures (M=.54) than with black/white (M=.47). There was also a significant effect of test type, F(1,27)=76.046, MSE=.289, p<.01, where participants performed better with the item test (M=.67) than with the associative test (M=.34). The effect of degradation at study was also significant, F(1,54)=6.362, MSE=.106, p<.01, where participants showed better memory performance for non-degraded pictures (M=.52) than for pictures that were moderately degraded at study (M=.45). We were unable to find an interaction between age and test type, F(1,27)=1.402, MSE=.289, p>.05. We did not find an interaction of test type, age, and degradation at study and test, F(1,108)=.626, MSE=.064, p>.05. The interaction of test type, degradation at study, and age was not significant, F(1,54)=.89, MSE=.09, p>.05, but was significant when gender was a factor in the interaction, F(1,54)=3.801, MSE=.09, p<.05. There was an interaction of picture type and age, F(1,27)=4.856, MSE=.188, p<.05, with older adults not differing significantly between color and black/white pictures, while younger adults showing better performance with the color pictures than with the black/white pictures.

Table 2
Memory Performance: Degradation at study

<table>
<thead>
<tr>
<th></th>
<th>No degradation</th>
<th>Slight degradation</th>
<th>Moderate degradation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Item</td>
<td>Associative</td>
<td>Item</td>
<td>Associative</td>
</tr>
<tr>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td>Color</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young</td>
<td>.77</td>
<td>.28</td>
<td>.98</td>
</tr>
<tr>
<td>Old</td>
<td>.79</td>
<td>.22</td>
<td>.34</td>
</tr>
<tr>
<td>B/W</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young</td>
<td>.68</td>
<td>.32</td>
<td>.33</td>
</tr>
<tr>
<td>Old</td>
<td>.65</td>
<td>.28</td>
<td>.31</td>
</tr>
</tbody>
</table>

Table 3
Memory Performance: Degradation at test

<table>
<thead>
<tr>
<th></th>
<th>No degradation</th>
<th>Slight degradation</th>
<th>Moderate degradation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Item</td>
<td>Associative</td>
<td>Item</td>
<td>Associative</td>
</tr>
<tr>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td>Color</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young</td>
<td>.75</td>
<td>.29</td>
<td>.37</td>
</tr>
<tr>
<td>Old</td>
<td>.72</td>
<td>.27</td>
<td>.34</td>
</tr>
<tr>
<td>B/W</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young</td>
<td>.65</td>
<td>.29</td>
<td>.39</td>
</tr>
<tr>
<td>Old</td>
<td>.61</td>
<td>.33</td>
<td>.38</td>
</tr>
</tbody>
</table>

Discussion
The goal of this study was to extend the ADH to the visuospatial realm. More specifically, we wanted to assess whether the associative deficit seen in older adults is mediated by a decline in sensory processing. We expected that younger adults would show an associative deficit like older adults when using moderately degraded stimuli. Also, we predicted that the associative deficit of older adults would become larger as stimuli were degraded. The results did not support such predictions.

When looking at how degrading stimuli at study affects memory performance, we found that item memory decreased for both younger and older adults with degradation, but the decline was larger for older adults. Older adults did show an associative deficit compared to younger adults in no degradation conditions, but the deficit was not affected by degradation level. Also, degrading stimuli at study did not result in an associative deficit in younger adults. This finding could be due to the decline in item memory for younger adults as stimuli were more degraded. No associative deficit can be found if there is a decrease in both item and associative memory. This decrease in item memory for older adults can also be an explanation as to why the associative deficit of older adults was not affected by degradation. When looking at how degradation at test affects memory performance, we found that item memory did not decrease for either younger or older adults with degradation, as was found for degrading stimuli at study. Older adults showed an associative deficit under non-degraded conditions, with the deficit getting larger across degradation conditions at test. Younger adults, however, did not
show an associative deficit as stimuli became more degraded.

The decrease in item memory performance could be due to the possible difference between the visuo-spatial realm (i.e., picture pairs) and past research involving the verbal realm with word pairs (Naveh-Benjamin, personal communication). When studying word pairs, no matter how degraded the stimuli, it requires some effort to decipher what the word is (e.g., “that word says ‘dog’”). On the other hand, it is possible that picture pairs require an extra step to identify compared to word pairs, even with pictures that are not degraded, as they needed to be named (e.g., “What is that a picture of...That looks like a dog”). If pictures do take longer to identify, that would be at the expense of the item memory, due to less time to encode the information as the stimuli become more degraded. In order to assess whether the difference in the visuo-spatial realm can account for the decline in item memory for both younger and older adults, future research can use a control group to obtain identification ratings and reaction times.

Another possibility of why the results did not fall in line with the predictions could be due to the participant composition of older adults. Older adults had a significantly larger proportion of females to males compared to that of younger adults. As the results suggested, there was a significant effect of gender, with males in both groups performing significantly poorer than that of the females. It is possible that the larger number of males in the younger adults group brought down the means. As well, the older adults’ means may have been higher than what would normally be expected, due to the shortage of male participants. It is predicted that had there been a larger number of older adult males, that the results would have more closely mirrored that of past studies (i.e., Naveh-Benjamin, 2000; Naveh-Benjamin, Guez, Kilb, & Reedy, 2004; Naveh-Benjamin, Hussain, Guez, & Bar-On, 2003). Future research should aim to address all such limitations.

References
Parent-child communication is essential in order to foster healthy development among children. More specifically, it is crucial for minimizing problem behavior among adolescents, such as misconduct, psychological issues, etc. (Hartos & Power, 2000; Patrick, Snyder, Schrepfeman & Synder, 2005; Yu, Clemens, Yang, Li Stanton, Deveaux, et al., 2006). However, parent-child communication is not the only predictor of problem behavior. Many may underestimate the importance of siblings. Several studies support the finding that an older sibling’s display of risky behaviors increases the probability that their younger sibling will display the same problem behavior (Ardelt & Day, 2002; East & Jacobson, 2001; Slomkowski, Rende, Conger, Simons, & Conger, 2001). Yet while many accept this finding, researchers are still investigating the reasons for this occurrence. One factor reverts back to exploring influences of parent-child communication. Researchers found that parent-child communication can be influenced by an infinite number of factors, such as trust, marital status, (Tucker, Barber & Eccles, 2001), sibling presence (Cicirelli, 1978), and gender (Cicirelli, 1978; Tucker et al., 2001). Nevertheless, few studies have explored sibling ordinal status as a factor in relationship quality and its relation to internalizing and externalizing behaviors.

Focusing on problem behaviors, depression, and communication, Yu and colleagues found that adolescents were more likely to engage in risky behaviors and have higher levels of depression with poor communication among parents and reduced parental supervision (2006). Magoon & Ingersoll displayed a similar negative correlation to Yu et. al with communication, trust and gambling (2006). Adolescents were less likely to gamble on games that require skill (e.g. betting on sports, playing cards) if they reported higher levels of trust, communication and affiliation with their parents. In addition, the likelihood of classification as a problem gambler displayed the same pattern of a negative correlation with trust and communication as gambling on games that require skill (Magoon & Ingersoll, 2006). With these findings, however, the sample was atypical. Using 116 students, between the ages 14-19, 73% of these students were eligible to receive free or reduced lunch and free textbooks. Furthermore, the study used only one method of data collection (self-report questionnaire). Research with multiple measures and more typically-developing samples is necessary for future research to further develop understanding the interaction of trust and communication and problem behavior.

Although Yu and colleagues’ findings illustrate the negative relationship between depression and poor communication, the study is limited to a small subset of depressed youth within the larger sample (2006). Despite this, other studies support the significance between the quality of communication and psychological issues. Houck, Rodrigue, and Lobato investigated how the quality of parent-child communication between pairs of healthy and ill parents influences psychological symptoms of children. They found that higher levels of parent-adolescent communication were associated with lower depressive symptoms (2007). Father-adolescent communication was significantly related to depressive symptoms as well. Nonetheless, these results are limited to pairs of healthy and ill parents, which showed no moderator effects with depression, and a small sample size. A larger sample size is needed without limiting parental conditions.

Parent-adolescent communication has such a large effect on
adolescents, yet studies have found that it varies with gender (Bumpus, Crouter, & McHale, 2001; Campione-Barr & Smetana, under review; Cicirelli, 1978). During Cicirelli’s study, mothers provided different verbal interactions for the tasks depending on the sex of the sibling. There were no differences for the same-sex female siblings; however, mothers increased verbal interaction for same-sex male siblings (Cicirelli, 1978). The effects of these gender differences may be shown in the parent-child decision making process. Bumpus, Crouter, & McHale looked at adolescent gender differences with decision making and parental monitoring (2001). The greatest difference with decision making input was found between first-born females and second-born males, followed by the same-sex female sibling dyad (Bumpus, Crouter, & McHale, 2001). Campione-Barr & Smetana found that later-born females reported more decision-making input than first-born females within certain domains (under review).

Differences in adolescent decision-making influence the level of problem behavior of adolescents. Testing healthy autonomy in African American adolescents, Smetana, Campione-Barr, and Daddis (2004) looked at four different aspects involving autonomy three times over the course of five years: conventional issues (social norms), personal issues (personal choices, privacy, etc.), prudential issues (safety, potential harm to self, etc), and multifaceted issues (issues involving cleaning one’s bedroom, music choice, time with friends, etc.). With this longitudinal data, they found significant correlations between problem behavior and autonomy for each time. Early adolescents with more control over multifaceted issues reported more deviance, lower self-worth, and decreased academic performance. Two years later, middle adolescents were more deviant when they reported more decision-making over conventional and prudential issues. The following three years, adolescents still showed greater deviance with more control over multifaceted issues, in addition to reporting more depressed mood (2004). However, although too much autonomy during adolescence can be deleterious to child development, parents should caution with limiting adolescent autonomy, as it also can influence negative internalizing symptoms (Hasabe, Nucci and Nucci, 2004).

Finding the balance of the right amount of autonomy is crucial with adolescent development, yet autonomy varies within families. Campione-Barr & Smetana studied how sibling ordinal status affects behavioral autonomy, family decision making and conflict. They found that later-born adolescents (in 10th grade) provided more input when making family decisions than first-born adolescents (in 10th grade), specifically with decisions involving conventional and prudential issues (under review). Later-borns in early and middle adolescents also expected autonomy sooner than first-born adolescents and classified more as being under their personal control than first-born adolescents (Campione-Barr & Smetana, under review). With greater expectations for autonomy, later-born adolescents had more conflict when compared at the same age, which is opposite of Whitman, McHale, and Crouter’s study of parenting behavior differences between first- and later-born children. According to Whitman, McHale, & Crouter, second-born adolescents experienced less conflict than first-born adolescents. Additionally, conflict with parents began at an earlier age for the second-born sibling than the first-born siblings and decreased sooner as well (2003). Although the findings from the two studies clash, both show differences between the first-born and later-born adolescents' communication with parents. These differences may lead to more problem behavior among later-born adolescents, which increases the need for research with sibling ordinal status and communication.

Sulloway explored the variance between first- and later-born siblings and behavior. His research showed that first-borns display more conservative behaviors than later born siblings (1997). Testing these findings, Zweigenhaft & Von Ammon examined the sibling ordinal status of U.S. college students arrested during Kmart protests. They found that later-born college students were arrested more than first-born college students (2000). The study, however, is limited to those arrested during the protests. Furthermore, while the control and experimental groups were asked questions about birth order, the experimental group took part in a telephone interview, but the control group completed a questionnaire (Zweigenhaft & Von Ammon 2000). This inconsistency could have influenced the participants’ responses. Moreover, the researchers obtained birth order data of the friends of those arrested in order to increase the population of the study. This data may be inaccurate because the participants may not have known all of the information about their friends. Thus, more reliable research on sibling ordinal status and problem behavior is necessary for the future.

With studies showing sibling ordinal status differences with behavior, researchers have looked for factors that influence these variations. Exploring parental differential treatment effects on child adjustment, Richmond, Stocker & Rienks found that when parents treated the older siblings more favorably, the older siblings had fewer externalizing problems than the younger siblings (2005). As time increased with this treatment toward the older siblings, the externalizing problems increased for the younger siblings, but decreased for older siblings (Richmond, Stocker & Rienks, 2005). This study illustrates that child behavior is dependent on many factors other than parenting styles like parental differential treatment. Yet the parental differences with children may stem deeper than treatment. Further research is necessary to learn more about specific factors that influence child behavior.

In attempts to identify specific factors that influence adolescent behavior, this study investigated how parent-child communication and trust were affected by sibling ordinal status, gender, and age. More specifically, this study was interested in how parent-child communication and trust may differ for groups of first-born and later-born children and how those differences may influence child problem behavior and depression. This study hypothesized the following:

1. Greater communication and trust with parents than later-born siblings.
2. First-born adolescents will have higher levels of trust and communication with parents than later-born siblings.
3. Later born adolescents will be more likely to exhibit problem behaviors than first-born adolescents.
4. Sibling-ordinal status will act as a moderator in the relationship between trust and communication and child problem behavior and depression.

**Method**

**Participants**
The sample consisted of 118 adolescents and one of their parents. Fifty-seven of the adolescents were in the 7th grade (25 first-
Measures

Trust and communication. The subscales of trust and communication were taken from the Armsden and Greenberg (1987) Parent and Peer Attachment Inventory. Previous research using the trust and communication subscales (Campione-Barr & Smetana, 2004) has shown that the two subscales are highly correlated. The scale consisted of 18 items rated on a 5-point scale, ranging from 1 (almost never or never true) to 5 (almost always or always true). Adolescents completed the questionnaire separately for mothers and fathers. Alphas were .80 and .88 for adolescents’ ratings of trust with mothers and fathers, respectively, and .77 and .84 for adolescents’ communication with mothers and fathers. Adolescents’ ratings of trust and communication were highly correlated for ratings of mothers, r(117) = .7, p<.001 and fathers, r(117) = .76, p<.001. Therefore, mean ratings of trust and communication for each parent were obtained. Adolescents’ ratings of mothers and fathers were significantly but moderately correlated, r(117) = .35, p<.001.

The 18 items were also worded to obtain parents’ ratings of trust and communication with their adolescent. Alphas were .80 and .77, respectively. Parent ratings of trust and communication likewise were highly correlated, r(118) = .71, p<.001, and thus, the two scales were combined to form a mean parental relationship quality scale.

Problem behavior. The Problem Behavior Survey (PBS; Mason, Cauce, Gonzales, & Hiraga, 1996), a 19-item report of problem behavior adapted from Jessor and Jessor (1977) was given to participants. Adolescents rated items focusing on drug and alcohol use, gang activity, vandalism, stealing, truancy, precocious sexual activity, and fighting with or without a weapon on a 7-point scale ranging from 1 (never happens) to 7 (happens very often).

Depressed mood. The Center for Disease Control – Depression Scale (CES-D; Radloff, 1977), a well-known 20-item measure of depressed mood, was used for the first-born and later-born adolescents. For each item, participants responded about how they felt during the past week on a four-point scale ranging from 1 (rarely or none) to 4 (most or all of the time). Cronbach alpha was .84.

Procedures

Participants were recruited from two middle schools and one high school in a suburban school district near a mid-sized Northeastern city as part of a larger study. Letters describing the study were sent to the parents of all 7th and 10th grade students, and interested parents mailed responses back to the investigators. Inclusion criteria for the larger study were that students had to have a sibling within one to four years of the target child. Older sibling 7th or 10th graders had to be the first-born in their family and younger sibling 7th or 10th graders could be any later-born status (but the participating sibling participating had to be the first-born). Families were paid honoraria for their participation.

Families participated in a two-hour visit at a university lab. During the family visit, all family members individually completed questionnaires administered online. Family members also completed additional questionnaire measures, interviews, and family interaction tasks as part of the larger study on family relationships during adolescence.

Results

Table 1

<table>
<thead>
<tr>
<th>Mean</th>
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<td>T Prob</td>
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Note: T= Teen, P= Parent, M= Mother, F= Father, Cesd= Depressed mood, Prob= Problem behavior, Educ= Education

Table 2

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<td>5.</td>
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<td>-.21**</td>
<td>-.17*</td>
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<td>-.05</td>
<td>-.39**</td>
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<td>-.01</td>
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<td>-.24**</td>
<td>.22*</td>
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</table>

Note: + p<.10, * p<.05, ** p<.01, Ordinal status = First- v. Later-born, T= Teen, P= Parent, M= Mother, F= Father, Cesd= Depressed mood, Prob= Problem behavior, Intact v. all Else = Married families v. Single, divorced, etc. families, Educ=Education

Descriptive Statistics

Correlations among the demographic and study variables are presented in Table 2. There was a significant association between depressed mood and problem behavior, as well as an
association with age and problem behavior, such that older teens reported more problem behavior than younger teens. As predicted, all reports of depressed mood and problem behavior produced significant, negative correlations with relationship quality for both mother and father individually. Mother and father relationship quality were also significantly associated with each other, showing that the higher levels of relationship quality with father, the better quality of relationship with mother. Relationship quality was also shown to be significantly correlated with mother’s education, indicating that the more education of mothers, the lower relationship quality with mother.

Table 3
Parent moderation analyses for assessments of depressed mood and problem behavior

<table>
<thead>
<tr>
<th></th>
<th>Depressed Mood with Mother</th>
<th>Depressed Mood with Father</th>
<th>Problem Behavior with Mother</th>
<th>Problem Behavior with Father</th>
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<td>Step 1</td>
<td>Step 2</td>
<td>Step 3</td>
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<td>10.01 (.15)</td>
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<td>T Age</td>
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<td>Ordinal Status</td>
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<td>F∆  R²∆  β</td>
<td>F∆  R²∆  β</td>
<td>F∆  R²∆  β</td>
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<tr>
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<td>4.16 (.07)</td>
<td>4.39 (.07)</td>
<td></td>
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<tr>
<td>Step 2</td>
<td>3.90 (.06)</td>
<td>2.07 (.03)</td>
<td>2.84 (.05)</td>
<td></td>
</tr>
<tr>
<td>Step 3</td>
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<td>0.00 (.00)</td>
<td>8.36 (.06)</td>
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</tbody>
</table>

Note: + p < .10, * p < .05, ** p < .01. All β are from the final step of the analysis. Ordinal status (OS) = First- v. Later-born, T = Teen, Relate Quality = Relationship Quality

Association with Relationship Quality and Depressed mood

Two hierarchical regression analyses were performed to test the relationship between depressed mood and mother-adolescent relationship quality and father-adolescent relationship quality. Depressed mood was the dependent variable; adolescent age and sex were entered as controls in the first step of the analyses. In the second step, main effects of relationship quality and sibling ordinal status were entered, and in the final step, the interaction of relationship quality and sibling ordinal status was entered to test moderating effects (see Table 3).

The analysis for mothers yielded a significant main effect of sex, such that females reported more depressed mood, and marginally significant main effects of age and ordinal status. This analysis also found a main effect of relationship quality, showing the lower relationship quality with mothers, the more depressed mood in teens. The analysis with father yielded similar results, such that teen relationship quality with father and depressed mood show a trend toward significance.

Association with Relationship Quality and Problem Behavior

Two hierarchical regression analyses were performed to test the relationship between problem behavior and mother-adolescent relationship quality and father-adolescent relationship quality. Problem behavior was the dependent variable; adolescent age and gender were entered as controls in the first step of the analyses. In the second step, main effects of relationship quality and sibling ordinal status were entered, and in the final step, the interaction of relationship quality and sibling ordinal status was entered to test moderating effects.

Main effects of age were found in both analyses with mother and father, revealing that the older the teen, the more problem behavior reported (age was only significant effect within the mother analysis). There was a main effect of ordinal status for analysis with father; contrary to the hypothesis however, later-born adolescents reported less problem behavior, instead of more problem behavior. As expected, there was a main effect of relationship quality, such that the higher relationship quality with fathers, the less problem behavior in teens. The analysis also shows a significant ordinal status x relationship quality with father interaction, which indicates a moderating effect (see Figure 1). For first-borns adolescents, a better relationship with father was associated with less problem behavior, however for later-born adolescents, there was no difference based on relationship quality.

Figure 1:
Interaction of Ordinal Status and Relationship Quality with Father

The graph indicates a moderating effect. For first-born adolescents, a better relationship with father was associated with less problem behavior. For later-born adolescents, there was no difference (β = 1.17, p<.01).

Discussion

In response to the need for the advancement of sibling effects on child development, the current study examined how differences in parent-child relationship quality between groups of first-born and later-born children influence adolescent depressed mood and problem behavior, as well as differences in problem behavior with first-born and later-born adolescents. Using a large, predominately European-American sample, confirmation of our hypothesis lead us to conclude that parental relationship quality positively influences problem behavior and depressed mood. This confirms previous research about impact of the parent-adolescent relationship quality on adjustment (Yu, Clemens, Yang, Li, Stanton, Deveaux, et al., 2006; Magoon & Ingersoll 2006; Patrick, Snyder, Schrepelman & Synder, 2005), as well as the impact of mothers on internalizing behaviors (Hartos & Power, 2000). Also consistent with previous findings, females reported more depressed mood than males (Hankin & Ambramson, 2001).
While sibling ordinal status did not appear to impact depressed mood, there were ordinal status effects on problem behavior. Contrary to our hypothesis, when examining the impact of father-child relationship quality, later-born adolescents were less likely to exhibit problem behaviors that first-born adolescents. This decrease in deviant behavior may depend on first-borns’ conduct, rather than classification as a later-born sibling. Additionally, younger teens reported significantly less problem behavior than older teens. This may be attributed to older adolescents gaining more freedoms and privileges than younger adolescents (Tucker, McHale & Crouter, 2003), thus increasing the opportunity to engage in risky behaviors.

Findings of the present study seem to suggest that the quality of relationships with fathers appears to have an impact on deviant behavior, while the quality of relationships with mothers appears to have an impact on adolescent depressive behaviors. These differences may be attributed to the basis of the relationship, such that communication with mothers may emphasize peer and romantic relationships, while fathers may handle more general concerns, like academics, careers, and money (Youniss & Smollar, 1985). Research has shown that mothers tend to focus on emotional development and family unity, whereas fathers accentuate their child’s independence and acquaint their child with the outside world (Collins & Russell, 1991; Youniss & Smollar, 1985). These differences may account for lack of mother-relationship quality effects on problem behavior, yet may fuel the effects of father-relationship quality on problem behavior, e.g. the unique interaction. The interaction of ordinal status and father-child relationship quality for problem behavior is distinctive because fathers may spend less time with children than mothers, so any increase or decrease in relationship quality may have a more substantial impact.

Although these findings further increase knowledge about the influences of parent-child relationship quality, a few limitations of the study should be noted. With a predominantly ethnically homogeneous and middle-class sample, it is difficult to generalize results to varying ethnic groups or social classes. Future research should explore more diverse samples. Since a small portion of the participating families included step-parents (9%) or single-parents (21%), future research should examine how this may modify the moderating effects. Furthermore, participants were concentrated in one geographic region; future investigations should test these results in varying locations. In addition, another limitation of the present study was using a between-subjects design, instead of a within-subjects design. A between-subjects design allows comparisons between different groups of first-born and later-born adolescents, but a within-subjects design would allow us to investigate older and younger siblings within the same families. However, in order to maximize results and investigate the direction of effects, a within family design that was also longitudinal (i.e., following families until the second-born child becomes the same age as the first-born child at the time of first assessment) would account for all of the limitations of both the between families design and the cross-sectional within families design. Future investigations should also explore the moderating effects of sibling ordinal status on other variables, such as aggression, anxiety, or educational outcome. Internalizing symptoms, such as anxiety, may produce interactions with mother-adolescent relationship quality, whereas externalizing behaviors, such as aggression, may elicit similar interactions as did this study with father-adolescent relationship quality. Moderating influences may be found for educational outcome with both mother-adolescent and father-adolescent relationship quality.

In conclusion, this study allowed us to identify father-adolescent relationship quality as an influencing factor of deviant behavior for first-born adolescents. Fathers should improve efforts to deter first born siblings from engaging in risky behaviors as the relationships with fathers may serve as a protective factor in keeping first-born children out of trouble. This may be especially important for this group and later-born adolescents, as previous research has shown that younger siblings are more likely to engage in risky behaviors when their older siblings do the same (Ardelt & Day 2002; East & Jacobson, 2001).

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Introduction

Global demand for protein is increasing rapidly because of an exponentially growing human population, coupled with an increasing tendency for people to feed high on the food chain, preferring to eat beef, pork and salmon, for example, rather than to consume grains directly (Brown 2004). Capacity to substantially increase protein production beyond current levels through standard agricultural methods is thought to be reaching upper limits, owing to factors including global warming, overuse of irrigation waters and overgrazing (Brown 2004). Similarly, capacity to harvest fish from the oceans has reached or surpassed sustainable limits (FAO 2007), and is unlikely to increase in the future. Consequently, concern over food security in the near future is high.

Aquaculture, the rearing of fish and other aquatic organisms in ponds, tanks, and cages, is currently undergoing rapid growth, having increased at an annual rate of ~10% since 1984 (FAO 2007). Aquaculture is among but a few food-production systems believed to be capable of significantly closing the gap between the increasing demand for protein and available supply, with production levels having reached ~40 million metric tones annually (FAO 2006).

The United States is lagging in fish production levels through aquaculture, producing far fewer metric tons annually than China and other Asian countries, and being ranked outside of the top 10 fish-producing countries worldwide. Consequently, the U.S. suffers from a multi-billion dollar international trade deficit for fish and fishery products (FAO 2007). The Regional Aquaculture Center program was established by the federal government about 20 years ago to promote fish production through aquaculture in the U.S. The research project proposed herein is related to an initiative through the North Central Regional Aquaculture Center (NCRAC) to develop capacity to efficiently rear sunfishes (Lepomis spp.) to large sizes (> 227 g; 0.5 lbs) as food fish (NCRAC 1999).

Background

Recent studies have demonstrated that male bluegill possess the highest growth capacity among Lepomis sunfishes (Hayward and Wang 2002; 2006), indicating that this fish in particular should be reared for the sunfish food market. Fast-growing sunfish are required for this market because desired sizes must be reached within two years of rearing; this requirement relates to fish producer’s unwillingness to accept high risks of loss that are associated with longer rearing periods (Loveshin and Matthews 2003). However, accompanying the male BGs rapid growth capacity is an inherently high level of aggressiveness (Hayward and Doerhoff, in preparation). This characteristic leads to the formation of social hierarchies within reared groups that can result in reduced food consumption and slowing of growth rates, if not properly managed. Consequently, when rearing fast-growing male BG, it will be necessary to disrupt the formation of social hierarchies so that these fishes’ inherently high growth capacity can be realized.
Study Objectives
1. Determine whether rearing MM (≥ 70 % male) BG groups in intensively-managed standard production ponds results in higher fish growth rates and production of higher numbers of large, food-size sunfish (≥ 227 g; 0.5 lb), compared to MS (~ 50:50) groups that are reared over a two-year period.
2. Determine whether application of a cull-harvesting, or topping-off approach increases the growth of food-size sunfish produced in the MS and MM groups.

Hypothesis
The topping-off harvest approach will control the presence of social hierarchies which will improve the rearing efficiency of BG for the purpose of marketable sized food fish. Rearing MM, BG groups will lead to larger mean sizes due to the higher growth capacity of male versus female BGs.

Literature Review
Aquaculture, the rearing of fish and other aquatic organisms in ponds, tanks, and cages, is currently undergoing rapid growth, having increased at an annual rate of ~10% since 1984 (FAO 2007). Aquaculture is among a few food-production systems believed to be capable of significantly closing the gap between the increasing demand for protein and available supply, with production levels having reached ~40 million metric tonnes annually (FAO 2006).

The United States is lagging in fish production levels through aquaculture, producing far fewer metric tons annually than China and other Asian countries, and being ranked outside of the top 10 fish-producing countries worldwide. Consequently, the U.S. suffers from a multi-billion dollar international trade deficit for fish and fishery products (FAO 2007). The Regional Aquaculture Center program was established by the federal government about 20 years ago to promote fish production through aquaculture in the U.S. The research project proposed herein is related to an initiative through the North Central Regional Aquaculture Center (NCRAC) to develop capacity to efficiently rear sunfishes (Lepomis spp.) to large sizes (≥ 227 g; 0.5 lbs) as food fish (NCRAC 1999). Sunfish have been identified as an emerging major fish group for food market aquaculture in the north central region (NCR).

Bluegill production in the U.S. was historically conducted extensively in ponds to produce small fish for pond stocking (Swingle 1946). Bluegill production has recently become more intensive with the use of prepared feeds in part due to the demand for larger food fish. Currently, production of high densities of bluegills or B × G hybrids to large sizes in ponds has been widely unsuccessful. Historically, age-1 BGs of 3-4 inch size were stocked in ponds during early spring, while the spawn produced by the stocked fish is controlled by adding predator fish (usually largemouth bass, Micropterus salmoides), stocked during fall. However, this general culture technique has not proven effective for many producers because it takes more than two growing seasons to produce food-size fish.

There are about 250 sunfish producers in NCR; bluegill (Lepomis macrochirus) is the most commonly produced sunfish, being raised by approximately 45% of NCR fish producers (Morris and Mischke, 2003). Bluegills grow well in warm water such as ponds, lakes, and slow-moving streams. Their geographical distribution covers North America, Europe, South Africa and Asia (Pflieger, 1975; Carlander, 1977; Avault 1996). Bluegills have been reared mainly as a forage fish for largemouth bass (Micropterus salmoides) and as a sport fish in the U.S. (Swingle, 1946). They have been introduced from the U.S. to other parts of the world for the purpose of sport fishing or aquaculture, or as a forage fish (Brunson and Morris 2000). However, there are no data available on sunfish aquaculture production outside the U.S. Schmittou (1965) reported a mean size of 200 g reared from 2-g bluegill for 19 months at a low stocking density (5,000/ha), by feeding them a protein-rich (45% crude protein) sinking pellet. Largemouth bass (1 g) were stocked at 375/ha to control BG offspring. Low stocking density, a protein rich diet, favorable southern temperature, and better control of offspring may have accounted for the high mean size of bluegills that resulted. Production was 757 kg/ha, which is lower than expected in this study probably because of low stocking density. These results influenced other studies to determine the efficiency of BG as a profitable aquaculture species.

Recent research has demonstrated that male BG possess the highest growth capacity among Lepomis sunfishes (Hayward and Wang 2002; 2006), indicating that this fish should be reared for the sunfish food market. Fast-growing sunfish are required for this market because desired sizes must be reached within two years of rearing; this requirement relates to fish producer’s unwillingness to accept high risks of loss that are associated with longer rearing periods (Loveshin and Matthews 2003). However, accompanying the male BGs rapid growth capacity is an inherently high level of aggressiveness (Hayward and Doerhoff 2007). This characteristic leads to the formation of social hierarchies within reared groups that can result in reduced food consumption and slowing of growth rates, if not properly managed. Consequently, when rearing fast-growing male BG, it will be necessary to disrupt the formation of social hierarchies so that these fish’s inherently high growth capacity can be realized.

In addition to monitoring and controlling the social hierarchies, MS and MM BG populations are also being evaluated to determine if the presence or absence of female BG inhibit or initiate the development of social hierarchies. Doerhoff (2006) applied a size-grading approach to produce predominantly male BG populations. A study comparing growth performance of MM (68% males) versus MS BGs (54% males) in indoor rearing systems showed significantly higher mean-weight and growth rate in the MM groups. On average, males gained 48.6 g more than females. This study also revealed that BGs of greatest length (predominantly males) maintained better condition (Wr>100), while fish of lesser lengths were in poorer conditions. Although male BGs have greater potential growth rate than females, no substantial difference was noticed between the MM and MS groups in their overall growth performance. Comparing plots of relative weight versus length indicate that the presence of strong social hierarchies restricted growth of BGs. Thus, this study suggests that topping-off higher weight percentiles in tanks might reduce social hierarchies and increase the growth of BGs in the lower weight percentiles, assisted by compensatory growth. While size grading was adopted by Lane and Morris (2002), selecting the upper 70% produced only 53% of males, which did not differ from MS group in sex-ratio, and so did not have any influence on final fish production.
Lane and Morris (2002) evaluated the growth performance of upper-70%, size-graded BGs in 0.15-ha earthen ponds, at a rearing density of 12,000/ha, in the Midwest U.S.. Growing BGs for 384 days with a catfish feed with 36% crude protein, at a feeding rate of 1.5% of body weight, yielded only 250 kg/ha with a final weight of 33 ± 13.8 g and a survival rate of 62 %. Unfavorable winter temperatures, uncontrolled offspring populations, a low-protein diet, and poor survival likely contributed to the reduced low individual weights and overall yield of BGs.

Recent attempts to standardize stocking density and increase production for intensive BG culture in earthen ponds have been made. Loveshinv and Matthews (2003) evaluated stocking densities of 25,000, 50,000, and 75,000 fish/ha of 6.5-g BGs. Rearing BGs for 346 days by feeding to satiation on a floating catfish diet (36% protein) produced final mean weights ranging from 83-104 g, and total yields ranging from 2080-2,973 kg/ha for the three different stocking densities. Feed conversion ratios increased progressively with stocking density; the lowest value (2.7) was recorded at 25,000/ha and the highest value (3.6) was recorded at 75,000/ha. However, no statistical difference was found either in total yields or final mean weights among treatments. Poor growth of BGs was caused by sub-optimal winter temperature, decreased supplemental feeding due to freezing water, ineffective control of offspring and high stocking densities (Loveshinv and Matthews, 2003). Evaluations of past studies such as this one indicate that rearing BGs at high stocking densities may involve increased social costs and reduce growth efficiency in ponds. Past studies reveal that more efficient methods of topping-off need to be explored and applied more systematically to determine the overall production benefits of reducing social costs.

Ultimately, the goal of this study is to improve the use of a “topping-off” strategy for pond-raised BGs, while providing insight on possible farming methods for other aquaculture species. As the need for new sources of protein increases with the diminishing supply of wild-caught fish, other alternatives must be considered. As aquaculture technology advances, methods of fish production will continually improve to supply the on-going demand for protein. Past studies of BG have been few in number and limited information has resulted, specifically regarding the costs of production at different life stages and the application of more intensive methods for grow-out. Therefore, much research is still needed in relation to sunfish culture (Brunson and Morris 2000).

**Methods**

**Experimental Design**

In March 2006, bluegill were randomly selected from a nursery pond stocked into three 0.33-acre fish production ponds (2000 fish per pond) at the Harrison Fish Farm in Hurdland, MO. These stocked fish represent the balanced sex-ratio (control) populations. A recently developed approach for size-selecting male bluegills from mixed-sex (MS) groups (Hayward and Doerhoff 2007) was applied to the nursery pond, with 2000 of the selected fish being stocked into the remaining three production ponds (treatment populations). Post-stocking evaluations indicated averages of 57 and 73% male fish in control and treatment ponds, respectively. Control ponds reflect the MS ratios of fish from the original pond, whereas the treatment ponds have more skewed sex ratios involving MM.

Fish in all ponds were fed ‘Aquamax grower-400’ feed (45% crude protein; 16% crude fat) at daily rates 1.5-2.0% of estimated total fish biomass per pond five days weekly (Lane and Morris 2002). Fish were not fed during ice-cover periods, which is standard practice in the aquaculture industry. Approximately 70 BGs selected at random were marked with individually numbered tags in each pond to increase statistical power for determining differences in fish growth rates among the ponds.

Lengths (nearest 1 mm) and weights (nearest g) were measured and documented for 100 fish per pond, collected by seineing every 3 to 4 weeks, except during ice-over months, from March 2006 through December 2007 (Masagounder, in preparation). Population sex ratios were later estimated upon the final harvest. The sex of individual fish was determined by identifying reproductive organs of 100 bluegills from each control and treatment pond.

Reproduction was another aspect of this study that had to be assessed (Loveshinv and Matthews 2003). This is not a positive occurrence as the production of offspring requires energy for reproductive organ formation and maturation, which would preferably be directed towards somatic growth to increase fish flesh. Offspring also decrease parental growth by competing with the larger fish for both natural and added food sources in the ponds. To reduce numbers of spawned BG, large-mouth bass were stocked in each of the ponds, at a ratio of 67:1 (prey: predator) to reduce the negative growth effects of juvenile BG on overall fish growth.

**Procedure and Measurements**

The presence of social hierarchies in each pond was assessed by regressions of fish condition index (Wr) versus fish length. Significant positive regression relationships indicate the presence of social hierarchies (Hayward and Doerhoff 2007). Under the assumption that social hierarchies were present in ponds, a “topping-off” harvesting approach was applied to one control pond and one treatment pond in an attempt to reduce the effects of social hierarchies. Topping-off involves harvesting of only the largest fish (upper 10% by weight) in a pond. By removing the largest fish, it was expected that the next-largest size group (and to an extent, lower size groups also) would rapidly move up in weight as a result of being released from the competitive effects on food access, that were exerted by the largest, dominant fish in the social hierarchy. Topping-off was implemented twice between May and November 2007. The large fish removed were placed and maintained within cement raceways for further analysis. In addition to measuring the larger BG, 30 spawn (> 3 inches) were monitored from each pond to track the amount of growth, and determine if this affected measurements of adult sizes. Numbers of large, food-size fish harvested from ponds receiving the topping-off approach were compared to numbers of large fish produced in ponds not subjected to topping-off, among the treatment and control ponds. Following each topping-off effort, fish in the lower weight percentile were stocked in the ponds from which larger fish had been removed, in order to maintain a balanced fish density among all six ponds.

**Statistical Analysis**

Bluegill growth rates were compared among the six ponds using one-way ANOVA with within-pond growth
variance provided by individually marked fish (Masagounder, in preparation). Differences in numbers of large, food-size fish produced between control and treatment ponds (only for ponds that were not topped-off) were assessed by t-tests, or a nonparametric analog, and likewise for coefficients of weight variation. Effects of the topping-off harvest approach were assessed within control and treatment groups by simply comparing numbers of large fish produced.

Significance levels of positive linear regressions of fish’s Wr values versus their lengths will indicate the presence of social hierarchy in ponds. Furthermore, steeper regressions of Wr will indicate stronger hierarchies. Results will be compared to other studies, including an indoor tank study that focused on BG social hierarchies. The Wilcoxin Rank Sum Test (one sample t-test) will also be used to evaluate the benefit of topping off within MS and MM groups (Masagounder, in preparation). Specific growth rate (SGR) is another important fish production parameters that estimates growth capacity by, and will be compared between treatment groups in this study. Data have been compiled in Microsoft Excel to evaluate the rate of hierarchy development, fish growth in MM versus MS (control) ponds, and overall fish production rates.

**Results**

No significant differences between MS and MM overall production could be detected. Mostly-male and control MS groups were obscured by low percentage survival (25% for treatment (MM) vs. 41% for control (MS)). Topping off did not increase overall production for treatment ponds. Noticeable reduction of survival rates were observed across all 6 ponds. Treatment pond production resulted with an average of 421 kg/ha in treatment ponds and the control ponds resulted with 558.2 kg/ha. Mean weight was greater for treatment ponds (104 g) compared to the control ponds (82 g). Specific growth rate percentages were also greater for control ponds, 0.27% (treatment) and 0.36% (control). Tracking the ponds over several months led to the conclusion that while social hierarchy became established in RAS tanks within 3 months, it takes about 7 months for these to be established in ponds.

Figure 1 expresses the differences in SGR, or the differences between the ideal weight and lengths for fish between ponds. The SGR declined for smaller fish, as the larger fish continued to dominate food intake, thus influencing the SGR for all fish. Figure 2 represents overall fish condition declines as social hierarchy developed over time. Larger BG apparently dominated the smaller fish and controlled the food intake, which results in variable sizes across all ponds.
Production in the top-off ponds was slightly greater than in those that were not topped off (Figure 3), but these results were not significantly different. Figure 4 shows that SGR was greater in those ponds that were not topped-off. The opposite results were achieved when comparing MS and MM ponds that were topped off. Figure 5 shows that growth in MS ponds was only 20 g less than in the MM ponds.

**Discussion**

Treatment ponds were not significantly different from control ponds when assessing specific growth rate (SGR), production (kg/ha), and mean weight (g). This study provided results that suggest social hierarchy effects are currently the most critical impediment to efficient rearing of large sunfish – which has shown to occur in both ponds and tanks. Combined rearing strategies for sunfish (e.g., pond rearing followed by tank rearing) may be most beneficial when trying to improve the rearing efficiency of any food fish. Currently, researchers are evaluating approaches to reduce social effects on BG growth in tanks and ponds, e.g., cull harvesting and application of a physical structure.

This study provided insight on efficient ways to improve the rearing efficiency of BG. Decreasing fish condition is a negative affect that can reduce the overall size and vitality of all fish. Social hierarchy reduces growth rate and feed efficiency, and so, raises questions the economic viability of BG culture in tanks and small impoundments. Further research is needed to assess the conditions under which growth rates improve, compared to those conditions under which growth rates actually decrease. In addition, increasing the number of ponds to study will likely increase the percent of survival rates, which would provide statistically significant results. Close monitoring of pond environments will decrease the affects of predation by birds, which could overall increase the survival rates. Pheromones should also be studied to determine their affects on fish behavior and the cues that cause BG to become dominating over other individuals. Continual research is needed to determine an efficient technique for reducing social costs in ponds.

The proposed research has been supported by the federal government to be an important future aspect of mainland aquaculture. The information gained from this study will further support the need for improved rearing techniques, as the need for innovative food production becomes greater. As the United States starts becoming more reliant on aquaculture, the support and demand for related research will become more widely accepted and encouraged. In addition, the ability to improve the rearing efficiency of BG will ultimately be applied to many other species of aquaculture food-fish.

**References**


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Introduction

Population genetics research has typically focused on neutral genetic variation. The increasing availability of highly variable molecular markers and sequence data allows analyses of neutral variance to be direct and informative (Hedrick 2004, Holderegger et al. 2006). While neutral variants can provide information about population structures across landscapes, relatedness of individuals, and evolutionary processes, e.g., gene flow, migration or dispersal (Holderegger et al. 2006), the limitations of these variants are important considerations with regard to conservation research. Neutral genes are assumed to have no effect on fitness and are not acted upon by natural selection, and therefore provide no information about whether a gene has adaptive value (Holderegger et al. 2006). Investigation of genetic variation underlying adaptive traits is of great importance. Patterns of adaptive variation may help predict future effects of natural selection in threatened and endangered species (Hedrick 2004). Adaptive genetic variation is difficult to identify without extensive sequence data and genomic resources (Vasemagi 2005). Furthermore, there is little knowledge of what genes are involved in adaptation; there is no apparent way to differentiate between genes that are adaptive or neutral (Hedrick 2004), and a single trait could be affected by multiple genes or alleles.

Despite difficulties, links between adaptive traits and genes have been successfully identified. Variation in the Mc1r allele has been shown to contribute to adaptive color patterning in the beach mouse, a subspecies of *Peromyscus polionotus* (Hoekstra et al., 2006). The approach to determine the relationship between Mc1r and the cryptic coloration involved sequencing of the McR1 coding region and genetic crosses of *Peromyscus polionotus* subspecies (Hoekstra et al. 2006). Several other approaches may be useful to investigate the relationships between genotypes and adaptive phenotypes. One approach uses DNA polymorphisms to determine whether variation at loci have been affected by evolutionary forces. If the patterns of variation suggest that the trait has been acted on by evolutionary forces, it is considered non-neutral and hence assumed to be adaptive. Another approach focuses on phenotypic variation that is known to be adaptive, and aims to identify loci involved in producing the phenotype (Vasemagi 2005).

The African forest (*Loxodonta cyclotis*) and savanna elephants (*L. africana*) are potential candidates for the above mentioned approach to study genes involved in adaptation. The African savanna elephant is believed to have diverged from the forest species during the Pleistocene epoch, approximately 2.6 million years ago (Roca et al. 2001). Both species have been affected by selective processes unique to their savanna and forest habitats. Adaptive variations in these species will have allowed survival in their distinct environments (Hedrick 2004).

Predictions for adaptive variation can be made from an investigation of important differences in forest and savanna ecology. Light exposure is considerably greater in the savanna than in the forest. Excessive exposure to light can result in damage to the retina, causing reduced visual acuity and impairments of dark adaptation and night vision (Rózanowska et al. 2005). Important long-term adaptations to higher light intensities involve the down-regulation of rhodopsin synthesis (Schremser 1995). Regeneration of rhodopsin is supported by IRBP-mediated transfer of 11-cis-retinal (Okajima 1990).
Interphotoreceptor binding protein (IRBP) is involved in the transfer of retinoids through the aqueous compartment between the retina and pigment epithelium during light and dark adaptation (Pepperberg 1993), and is found in most vertebrates (Stanhope 1995). Variations in this gene sequence could potentially result in adaptive variations to increased light exposure.

Other important adaptations are those that relate to differences in diet between savanna and forest habitats. Forest vegetation is a poor source of iron, while savanna grasses are richer in iron (Smith et al. 1995). Without sufficient adaptation, savanna elephants would be greatly susceptible to hemochromatosis, a condition resulting from too much iron (Fairbanks 1971). In the African black and Sumatran rhinoceros it is believed the HFE gene is part of an adaptive mechanism involved in the increased assimilation of iron (Beutler et al. 2001). Variation in HFE and IRBP could potentially result in adaptive phenotypes in African forest and savanna species.

In this study I compared sequences from African forest and savanna elephants at the HFE and IRBP loci. Species level differences at these loci may be indicative of genetic adaptations to savanna and forest habitat. Genetic changes were examined to determine whether they affect the nature of the amino acids.

**Materials and Methods**

**Field Sample and DNA extraction**

Dung piles were sampled for populations of *L. cyclosis* at the Gamba Complex, Gabon, Africa, and at Parc National de la Marahové, Côte d’Ivoire, Africa. Fecal samples for a population of *L. africana* were collected at Saburu National Park, Kenya, Africa. The Toledo Zoo, Toledo, OH, provided blood samples from *L. africana* that were used for the positive control.

DNA was extracted from fecal samples according to the protocol and reagents of Eggert et al. (2005). DNA extraction procedure was performed on blood samples according to manufacturer’s protocol of DNeasy® Blood and Tissue Kit (Qiagen).

**DNA Amplification and Sequencing**

I screened primers used in other species for Interphotoreceptor binding protein (IRBP) (Rózanowska 2005) and the first and sixth exons of Hemochromatosis (HFE1 and HFE6 respectively) (Beutler et al. 2001). To determine the correct annealing temperatures for each locus, I amplified DNA extract from *L. africana* using a temperature gradient. The amplifications were performed in a 25 μl volume containing: 12.8 μl H2O, 2.5 μl of reaction buffer (Promega, Madison, WI, USA), 2.5 μl of 2 μM dNTP mix, 1.0 μl of forward primer at 2 μM, 1.0 μl of reverse primer at 2 μM, 2.0 μl of MgCl2, 2.0 μl BSA and 0.2 μl of Taq gold® DNA polymerase (Promega, Madison, WI, USA). The PCR temperature profile consisted of denaturation at 95°C for 10 min, followed by 45 cycles of: 1 min denaturation at 95°C, 1 min of primer annealing at a gradient of 50°C to 60°C and 1 min of 72°C, and a final cycle of primer extension at 72°C. After viewing PCR products in an agarose gel, products that were successfully amplified and appeared to be at the optimal temperature were sequenced. Products from HFE1 and IRBP were chosen for sequencing for *L. africana* and *L. cyclosis*. I used the sequences to confirm amplification of the correct loci by comparing with published sequences in GenBank.

The loci HFE1 and IRBP were selected for amplification and sequencing in sampled populations of *L. cyclosis* (n=15) and *L. africana* (n=15). PCR amplification for these populations were carried out using the same combination of 25 μl mixture used to amplify HFE-1 in the positive controls. The temperature profile remained the same with the exception of primer annealing at a temperature of 55°C instead of the gradient of 50°C to 60°C. The sequenced products were compared using Sequencher 4.5 (Gene Codes, Inc.) to assess variation at the HFE1 and IRBP loci between individuals and populations. Finally, sequences with genetic changes were translated to determine whether the changes affect the gene products.

**Results**

The HFE6 primers that were developed in African rhinos failed to amplify in both elephant species, and no comparisons could be made between the species. The IRBP primers that were developed for numerous species, amplified and sequenced a 307 bp fragment in both forest and savanna elephants. A comparison of the sequences showed no polymorphisms between individuals or species. The HFE1 primers, also developed in African rhinos, amplified a 284 bp fragment in both species. All savanna elephant samples were amplified and sequenced and three forest elephant
samples were amplified and sequenced. When I compared the sequences I found a total of six polymorphisms. Four of the polymorphic bases differed among savanna elephant individuals. There were two base pairs at which forest and savanna elephants consistently differed (Fig. 1). Translation of the sequence in the most likely reading frame indicates the two species level sequence differences are in the second codon position and would result in amino acid changes.

**Discussion**

HFE codes for a protein similar to an MHC class I-type protein, hence there is high variability between species. The HFE sequences from elephants could not be aligned with any other species at either the base pair or amino acid level. This research is part of an ongoing study and the next step is to establish homology between the elephant sequence and rhino and horse HFE using RNA sequences. Once homology is established, the nature of the amino acid changes will be investigated to determine whether they are likely to affect the function of the protein in iron regulation.

The HFE gene has been linked to human hemochromatosis, though the mechanism is not yet clear (Fairbanks 1971). Other species, e.g. the African cape buffalo (*Syncerus caffer*) and African forest buffalo (*S. c. nanus*), have changed from a browsing diet that is poor in iron to a grazing diet that is rich in iron as populations became adapted to a more open environment. Forest and savanna elephants may help us understand the genetic changes that accompany this adaptation.

**Literature Cited**


Introduction

Approximately 20,000 new cases of Lyme disease are reported each year, making it the most common vector-borne disease in the US (7). Lyme disease is caused by an infection from a tick-transmitted spirochete, *Borrelia burgdorferi* (1, 5). One of the most commonly seen clinical signs of Lyme disease infection is an oval shaped rash at the site of the tick bite called erythema migrans. The erythema migrans is thought to signify the dissemination of the bacteria through the skin from the initial infection site into various tissues, resulting in neurological abnormalities, myocarditis, and arthritis (8, 2). About 60% of humans will develop a transient arthritis from untreated *Borrelia burgdorferi* infection and 10-20% of untreated people will go on to develop chronic arthritis (5, 8). The presence of *B. burgdorferi* in joint tissues causes an area of inflammation that leads to increased production of proinflammatory cytokines, which may play a role in the development of pathology in arthritis (6).

The mechanisms responsible for the development of pathology are presently unknown, and thus a murine model is used to study Lyme disease pathogenesis. Lyme arthritis is studied in mouse models, where susceptible animals will have peak arthritis about 21 days post infection (1, 5). Various mouse strains used for these studies include arthritis susceptible strains such as C3H/HeJ, resistant DBA/2, or relatively resistant BALB/c (1, 5). The purpose of using several mouse strains is to have an observable range in the severity of contracted arthritis; since arthritis in mice is genetically determined (5). For this reason, mice are a good model to use in studying the Lyme disease pathogenesis and immunoregulation of subacute Lyme arthritis, which is most commonly seen in humans (5).

Lyme disease pathology is due to infection with *B. burgdorferi* and the spirochete’s ability to invade various tissues and evade the host’s immune defense (1, 5). Once *B. burgdorferi* infiltrates host tissues, an infection occurs and can persist for several months or years (5). Even though antibodies from the host play a role in regulating the bacteria load, the host is still unable to completely clear away the infection, and spirochetes can be found in mainly in the joints, heart, and skin (5, 6). The inflammatory response is due to the bacteria possessing pathogen-associated molecular patterns (PAMPs) such as lipopolysaccharides (LPS), lipoproteins, and flagellin, which are recognized by the host’s innate immune system and especially by toll-like receptors (TLR) (6). The interaction of PAMPs and host’s immune system leads to the production of proinflammatory products. *B. burgdorferi* do not produce LPS, so the main contributor to pro-inflammation is lipoprotein. Lipoprotein activates the inflammation signaling pathway by interacting with CD14, which facilitates the recognition of lipoprotein by Toll-like receptor 2 (TLR-2) (5, 6). TLR-2 interaction with bacteria lipoprotein results in production of pro-inflammatory cytokines, such as IL-1β, IL-6, TNF-α, and IFN-γ (5, 6, 8).

Previous studies have shown a correlation between arthritis development and immune responses by depleting specific cell types, cytokines, and antibodies in mice through disruptions of specific genes. Regulation of the inflammatory response is a balance between pro-inflammatory and anti-inflammatory cytokines. One specific anti-inflammatory cytokine is interleukin-10 (IL-10), which regulates lipoprotein-mediated cytokine production and IL-10 can be induced by lipoprotein.
Previous studies using mice on a C57Bl/6 background and lacking IL-10 showed that these mice developed mild arthritis, whereas littermate wild type mice did not develop arthritis. The IL-10 knockout mice also had tenfold less bacteria in their joints compared to littermate wild type mice, which indicates the IL-10 knockout mice were more efficient at clearing the infection (5).

Cyclooxygenase (Cox) enzymes play a role in the inflammatory response during an infection. The main role of the Cox enzyme is to convert arachidonic acid into prostaglandins (PG) (4, 9). The isoenzymes Cox-1 and Cox-2 play specific roles in mammalian cells. Cox-2 is an inducible enzyme, which is an enzyme expressed under adaptive value, that is activated at the site of infection and mediates the inflammation and pain response by production of pro-inflammatory prostaglandins (4). Cox-1 is a constitutive enzyme, which is an enzyme produced all the time, that synthesizes prostaglandins thought mainly to protect and maintain the gastrointestinal tract (4). The discovery of Cox-2 led to the development of Cox-2 inhibitory drugs that block pain and swelling associated with inflammatory responses, while avoiding the gastrointestinal side effects associated with long-term use of non-steroidal anti-inflammatory drugs (NSAIDs).

Chemokines and Cox enzymes play specific roles in the inflammatory response pathway. The connection for an inflammatory agent in the pathway begins with the release of arachidonic acid from the phospholipid membrane, and this process goes through the Cox or leukotriene (LT) pathways, which are multi-step enzymatic reactions (11). Arachidonic acid is released from the phospholipid membrane in response to infection or trauma by the enzyme, cytoplasmic phospholipase A2 (cPLA2), which is involved in the tissue-selective production of eicosanoids that signal inflammation (11, 12). The arachidonic acid is converted to 5 (S)-hydroperoxy-6-trans-8,11,14-cis eicosate transonic acid (HpETE) by the 5-lipoxygenase (LO) pathway (11, 12). The HpETE is converted to LTA4 and this can be converted to hydroxyl LT, LTB4, epoxide hydrolase by neutrophils and other inflammatory cells (11, 12). LTA4, LTBP, and LTC4 [known as cysteinyl leukotriene (CysLT)] are important in mediating inflammation induced by mast cells, eosinophils, and alveolar macrophages. LTC4 is a neutrophil chemoattractant and induces their release of the antimicrobial peptide α-defensin. The inhibition of receptor 1 of CysLT by MK-571 induces increased production of cytokines IL-5 and TNF-α by mast cells. TNF-α production is also associated with LTC4 (12).

The transcellular eicosanoid biosynthesis and induction of cytokines with enzymes from the 5-LO pathway to PMN create intermediate sources for epithelial leukotriene and cyclooxygenase products (12). The pathway starts with arachidonic acid being released from the lipophsid membrane by cPLA2 once arachidonic acid is released into cytoplasm of the cell the Cox-1 and Cox-2 enzymes are able utilize arachidonic acid and make products (12). Some end products are thromboxane, which is a vasoconstrictor, from Cox-1 and prostaglandin PGD2, which is an anti-inflammatory mediator, and prostaglandin PGE2, which causes vasodilatation, pain, fever, and induction of pro and anti inflammatory mediators (12).

Most research into the roles of the Cox enzymes during inflammation have focused on the role of Cox-2 while neglecting a possible role for Cox-1. This study seeks to determine if Cox-1 also plays a role in regulating inflammatory responses in response to B. burgdorferi infection.

Materials and Methods:

Mice and Infection: Male and female wild type C3H/HeJ and Cox-1 knockout mice that have been backcrossed ten generations on to a C3H/HeJ genetic background were used for experiments (1, 13, 14). The mice were purchased from Jackson Laboratories (Bar Harbor, Maine) and housed in microisolator cages under specific-pathogen-free conditions (13). The age and sex of mice were kept constant throughout the experimental groups. All mice were between 4 to 6 weeks of age at time of infection (13, 14, 15). B. burgdorferi was cultivated from frozen stocks placed in BSK II medium (Sigma Chemical Co., St. Louis, MO) then grown to log phase (13, 14, 15). The spirochetes were incubated for 5 days at 32°C and enumerated using darkfield microscopy (13, 14, 15). The mice were infected with 1x10⁵ of B. burgdorferi strain N40 in 50 μL BSK II in both hind foot pads.

Assessment of Pathology: On days 7, 14, and 21 post infection ankle swelling was measured at the tibiotarsal joint’s thickest anteroposterior diameter of the ankle, using a metric caliper (Ralmike’s Tool-A-Rama, South Plainfield, NJ) (13, 14, 15). Ankle measurements were determined by baseline measurements before infection and weekly measurements thereafter. Ankle diameter increases were determined by subtracting the baseline measurement from the weekly experimental measurements (13, 14).

On day 21 post infection the mice were sacrificed by CO₂ asphyxiation (13, 14). Ankles, knees, ear, heart, and blood were collected from each mouse. The left tibiotarsal joints were sent to RADIL histology services for mounting and staining. The joints were removed by cutting above and below the tibiotarsal joint, and the excised tissue were fixed in 10% buffered zinc-formalin (Anatech LTD, Battle Creek, MI) and embedded in paraffin (13, 14, 15). Sections 5-μm thick were stained with hematoxylin and eosin (H&E) and assessed for arthritis severity on a scale of 0 to 3 by two experienced independent observers (1, 13, 14, 15). The arthritis scores indicate grade zero to have no inflammation, grades 1 and 2 to represent mild-to-moderate inflammation, and grade 3 to represent severe inflammation (13, 14, 15).

Quantification of cytokine levels in joint extracts: The knee joint was removed and immediately frozen in liquid nitrogen and pulverized with a hammer. Pulverized joints were sent to RADIL histology services for mounting and staining. The joints were removed by cutting above and below the tibiotarsal joint, and the excised tissue were fixed in 10% buffered zinc-formalin (Anatech LTD, Battle Creek, MI) and embedded in paraffin (13, 14, 15). The homogenized knee tissues were centrifuged at 2,000 x g for 0.2% protease inhibitor cocktail [Sigma] and 0.5% NP-40) using a tissue homogenizer (IKA Works, Wilmington, N.C.) (13, 14). The homogenized knee tissues were centrifuged at 2,000 x g for 10 min at 4°C, and supernatants were filtered through a 0.45-mm-pore-size filter (13). The filtrates were diluted to 1.5 ml using lysis buffer, split into aliquots, and stored at -80°C until analyzed (13). Several murine cytokines and chemokines were then quantified using enzyme-linked immunosorbent assays (ELISA) (13, 14). The pro-inflammatory cytokines, interleukin 18 (IL-18), interferon gamma (IFN-γ), anti-inflammatory cytokines IL-4, and IL-10 were quantified by OptEIA ELISA sets (BD Pharmerge, San Diego, Calif.) (13).

Assessment of B. burgdorferi loads: The right ankle was used to determine levels of B. burgdorferi DNA by quantitative real-time PCR. The right ankle samples were collected after the mice were...
sacrificed, snap frozen in liquid N₂ and stored at -80°C until processed (13, 14, 16). DNA and RNA were extracted from the ankle samples using TRizol and resuspended in 200 μL DEPC-H₂O. The quantification of B. burgdorferi DNA in ankle samples was estimated to contain 1,000 copies of the mouse Nidogen gene in one microliter of a diluted sample used in PCR reactions (13, 14). The mouse Nidogen gene was used as an endogenous control and Flagellin gene of B. burgdorferi was used to determine the number of spirochete genome equivalents. The TAQ-man Real Time PCR kit was used according to the manufacturer’s instructions (Life Technologies, Gaithersburg, MD). The ABI Prism 7700 Sequence Detection System was used in amplification of DNA (PE Applied Biosystems, Foster City, Ca) (13, 14). Amplification of DNA starts at 50°C for 2 min, 95°C for 10 min, and then 45 cycles of 95°C for 15 s and 60°C for 1 min (13, 14). The copy numbers for B. burgdorferi and mouse genomes were collected. Quantitative real-time PCR was performed for each sample in duplicates and analyzed for flagellin and normalized to copies of nidogen DNA from the same tube (13, 14). B. burgdorferi’s DNA within each sample was quantified by comparing to a standard curve consisting of known numbers of B. burgdorferi genomes (13, 14). The normalization of mouse DNA for each sample was completed by comparing it to a standard curve of dilutions of mouse DNA from the same tissue (ear, heart, or ankle) (13, 14).

**B. burgdorferi specific antibodies:** Whole blood was collected from mice at time of sacrifice and serum isolated. The serum was tested for percentage levels of B. burgdorferi specific antibody IgM (14). Serum was stored at 4°C until processed. The antibodies were analyzed using Immulon plates (96-well) that were coated overnight at 4°C with 400 ng sonicated B. burgdorferi antigen (BbAg) (14). Nonspecific binding was blocked with 3% bovine serum albumin (BSA) in phosphate-buffered saline (PBS)/0.05% Tween (PBST) by incubating at ambient temperature for 2 hours (14). For individual mouse plasma, dilutions of 1:100 in 3% BSA were added in duplicate, and then incubated for 2 hours at room temperature (14). After washing, the plates were incubated with alkaline phosphatase-conjugated rat anti-mouse antibodies (Abs) to IgM, (all from Jackson ImmunoResearch Laboratories, West Grove, PA) diluted 1:1000 and incubated for 45 min at ambient temperature (14). Plates were developed using Sigma 104 reagent (Sigma) and read at 405 nm on a spectrophotometer.

**Statistical Analysis:** Results were expressed as means plus/minus standard deviation. Statistical analysis was completed using SigmaStat software (SPSS Inc., Chicago, IL). Critical values for statistical significance were set at α = 0.05.

**Results**

The deletion of Cox-1 gene results in a variation of Lyme arthritis pathology. To examine the possible role of Cox-1 in the inflammatory response to a B. burgdorferi infection we infected arthritis-susceptible C3H/HeJ mice and C3H Cox-1 knockout mice, and followed the course of arthritis development. Figure 1 shows measurements for ankle diameter for mouse strains wildtype C3H and Cox-1 knockout.
Also the Cox-1 knockout mice had fewer copies of \textit{B. burgdorferi} DNA gene flagellin in ankle joints (Figure 3). Samples were normalized to copies of mouse nidogen gene (Figure 3). Although there was no statistical significance ($P = 0.261$) when compared wild-type to knockout animals (Figure 3).

Ankle swelling does not always correlate with underlying arthritis development and thus we turn to the more accurate histological slides (15, 17). The histological slides indicated the cellular infiltration in the joint and surrounding tissues (Figures 4a, 4b). Infiltration of neutrophils, macrophages, and other leukocytes represent inflammation, and the amounts of cells present in the joint determined the arthritis severity in the joint. A severity scale was used by two independent examiners, who scored the severity of the inflammation in the ankles in a blinded manner. This suggests that Cox-1 might limit the development of severe inflammation by acting as an anti-inflammatory agent.

Antibody levels for the Borrelia-specific IgG were assessed from whole blood. Previous experiments in our lab have shown that Cox-1 deficient mice had a deficit production of Borrelia-specific IgG responses. Our current data showed no differences in IgM levels with a $p = 0.865$ when comparing wild-type to knockout mice, however as suggests that Cox-1 may play a role in antibody class-switching (Figure 5).

Cytokine production in the knee joints were also similar in both strains of mice (Figure 6); however, there was a trend for higher levels of the pro-inflammatory cytokines IFN-$\gamma$ and IL-12, again suggesting that Cox-1 might play an anti-inflammatory role during infections.
Discussion:

*B. burgdorferi* infection results in Lyme disease and includes joint inflammatory arthritis. In the present study we used C3H/HeJ mice, which are known to develop Lyme disease symptoms similar to those observed in humans and are an arthritis-susceptible murine strain (6, 15). Arthritis-susceptible and -resistant mice can harbor similar loads of spirochetes in tissues, but each strain of mouse retains its distinct disease phenotype (6, 15). The specific genotype regulates the host’s response to the infection that results in the development of disease. Susceptible murine strains produce chemokines in response of *B. burgdorferi* infection that elicit inflammatory cells to the infected site (13, 19). Inflammatory cells amplify the response by production of both pro-inflammatory and anti-inflammatory cytokines that will activate more inflammatory cells to aide in clearing the spirochetes (13, 19).

In the current study, we examined the role Cox-1 plays in the development of Lyme arthritis. Lyme arthritis consists of infiltration of neutrophils and other inflammatory cells into the joint and surrounding tissue. The cellular infiltration can be correlated to the severity of inflammation. Cox-1 knockout mice were shown to have more severe inflammation in tibiotarsal (ankle) joints when compared to wild-type mice (Figure 2). Histological analyses confirmed cellular infiltration in both wild-type and Cox-1 knockout mice, and that joints from Cox-1 knockout mice had more cellular infiltration and cellular degradation when compared to wild-type (Figure 2a, 2b). The Cox-1 knockout mice had more severe inflammation with fewer copies of *B. burgdorferi* DNA in the joint (Figure 3). This suggests that Cox-1 might limit the development of severe inflammation by acting as an anti-inflammatory agent. Also in this study, the Cox-1 knockout mice have shown pro-inflammatory cytokines to be elevated when compared to wild-type counterparts. This data again suggests that Cox-1 might play an anti-inflammatory role during infection.

These results are similar to a new report in the field on possibilities of Cox-1 immunological role in inflammation (18). In that study, Chen et al found the enzyme Cox-1 to directly affect disease pathogenesis by specific prostaglandin PGI2, however in this study they were inconclusive in regard to Cox-1 end products may or may not mediate anti-inflammatory response (18). In the current study we have not determined how the anti-inflammatory products from Cox-1 enzyme aid in the inflammatory response. Further experiments are planned to repeat the experiment with more mice per group. Also in future experiments we will determine the anti-inflammatory products responsible for mediating the pro-resolution response in a *B. burgdorferi* infection. Further studies are required to determine if this occurs.

References:

Marcia Chatelain, PhD  
Reach for Excellence Assistant Professor of African-American Studies and Honors  
University of Oklahoma-Norman Honors College

Although I have lived in Washington, D.C., Providence, RI, Chicago, Santa Barbara, and now Oklahoma City, Columbia and the University of Missouri campus has always felt like home to me. When I first came to MU to study journalism and religious studies in 1997, I had no idea that I would discover a passion for teaching and research. When I first heard about the McNair Scholars Program, I thought it was a good opportunity to learn more about a topic I was interested in (African-Americans in the Catholic Church) and get an opportunity to get to know my faculty mentor, Dr. Jill Raitt, better. I had no idea that the McNair program would introduce me to the career that I now have and love. The two most valuable McNair experiences I had included attending the American Academy of Religion’s annual conference in Boston, where I first met a critical mass of African-American female professors, and the great relationship I forged with Dr. Raitt. When I decided to blend my love of writing with my curiosity of religion and culture, I discovered the field of American Studies. After spending a year working in Washington, D.C. I returned to school at Brown University. In 2008, I earned my Ph.D. in American Civilization. My dissertation examined African-American girls’ lives in Chicago during the Great Migration era, with a focus on how women shaped girls’ leadership programs. Without my McNair research and presentation experiences, I would have had a tough time developing and committing to a research agenda.

I am now an assistant professor at the University of Oklahoma’s Honors College. The McNair program not only guided me through the stresses of applying to graduate school and supported my many campus visits, the program taught me how to be an effective mentor for future students. Dr. Raitt’s encouragement coupled with Dr. Vicki Curby’s commitment to the program helped launch me from an interested student to a truly engaged scholar. It was a pleasure to include Dr. Raitt when I celebrated my wedding in Oklahoma City last year. The McNair program has allowed me to maintain important ties to MU, develop deep friendships and feel like I always had a home back in Columbia. The road to the Ph.D. is not easy, but with the McNair community at your disposable, the process is a lot easier.

Melissa J. Herzog, PhD  
Research Specialist, Behavior & Education Division, Thompson Center for Autism & Neurodevelopmental Disorders  
Adjunct Faculty, Department of Human Development & Family Studies  
University of Missouri

Prior to becoming a McNair Scholar in 1999, I was unsure how to make the degrees I was earning in Psychology and in Human Development and Family Studies translate into a career that would keep me fulfilled for years to come. The answer came through my participation in McNair. The objectives of the McNair Program – to prepare students for graduate school by offering experiences in research activities, mentoring relationships, teaching preparation, and the details of navigating the graduate climate – were accomplished, and then some, in my time as a McNair Scholar. Most importantly though, was the time spent with my faculty mentor, Dr. Teresa Cooney.

With Dr. Cooney’s guidance and encouragement, I found the entire research process enthralling. I took delight in finding that “perfect citation” for a concept I was trying to convey. I was excited to collect the completed surveys that I had created. I enjoyed learning a new statistical technique to answer my research questions. I loved weaving together theory, method, and analysis into a cohesive written product. Through all these experiences, I realized that this was something that I could do really well, and I wanted to keep doing more of it – the grad school bug had bitten me.

McNair served me well in my graduate career. The opportunity to showcase a finished research product that was nearing publication in a peer-reviewed journal was an invaluable asset in my graduate application, as it demonstrated my capacity to be a successful researcher in my field. I found myself at a distinct advantage compared to my graduate cohorts as I was able to draw upon the many skills I had begun to hone during my McNair experience. The program also provided a financial advantage in the form of a McNair Graduate Fellowship.

In the summer of 2007, I earned a Ph.D. in Family and Human Development at Arizona State University. Three years earlier, I also earned my M.S. in Family and Human Development with a specialty in Marriage and Family Therapy at ASU. At the beginning of 2008, my McNair experience came full circle – I accepted a research position right back here at MU. I will also be teaching graduate and undergraduate courses in the MU HDFS department – the academic home of my McNair mentor. Thanks in large part to the skills and life lessons I learned through McNair, I can now call my mentor a colleague.
## 2007-2008 Research Topics

<table>
<thead>
<tr>
<th>Scholar</th>
<th>Major</th>
<th>Title</th>
<th>Mentor</th>
</tr>
</thead>
<tbody>
<tr>
<td>David Aguayo</td>
<td>Secondary Education</td>
<td>“Latino Newcomers in Missouri: Cultural Adaptation and Ethnic Identity”</td>
<td>Lisa Flores</td>
</tr>
<tr>
<td>Valeska Araujo</td>
<td>Philosophy &amp; Economics</td>
<td>“Differential Effects of the Components of Higher Education Expenditure on U.S. State Economic Growth”</td>
<td>Bradley Curs</td>
</tr>
<tr>
<td>Brittani Brown</td>
<td>Psychology</td>
<td>“Parent Communication with Teacher and Child Involvement”</td>
<td>Michael Lambert</td>
</tr>
<tr>
<td>Michelle Clark</td>
<td>Communication Science</td>
<td>“The Salience of Nouns and Verbs in Speech to Toddlers”</td>
<td>Judith Goodman</td>
</tr>
<tr>
<td>Sean Crockett</td>
<td>Chemical Engineering</td>
<td>“Use of Highly Nanoporous Carbon in Batteries and Supercapacitors”</td>
<td>Galen Suppes</td>
</tr>
<tr>
<td>Miriam Galenas</td>
<td>Geological Sciences</td>
<td>“Transport Properties of Mid-Ocean Ridge Basalt from the East Pacific Rise”</td>
<td>Alan Whittington</td>
</tr>
<tr>
<td>Danielle Graef</td>
<td>Psychology</td>
<td>“Sensory Decline as a Mediating Factor in Age-Related Differences in Associative Memory”</td>
<td>Moshe Naveh-Benjamin</td>
</tr>
<tr>
<td>Kamara Jones</td>
<td>Journalism</td>
<td>“Media Lynching On the Campaign Trail: The Use of Race in Political Ads, 1988-2006”</td>
<td>Carol Anderson</td>
</tr>
<tr>
<td>Jimmie Jones</td>
<td>Business</td>
<td>“Student-Athlete or Athlete Student: Role Identity Crisis of College Athletes”</td>
<td>Lori Franz</td>
</tr>
<tr>
<td>Lindsey Lanfersieck</td>
<td>English</td>
<td>“The Manifestation of Death in Nathaniel Hawthorne’s Gothic Fiction”</td>
<td>John Evelev</td>
</tr>
<tr>
<td>Tracey Latimore</td>
<td>Psychology</td>
<td>“Parent-Adolescent Relationships, Sibling Ordinal Status, and Adolescent Adjustment”</td>
<td>Nicole Campione-Barr</td>
</tr>
<tr>
<td>Olga Mafotsing Fopoussi</td>
<td>Biological Sciences</td>
<td>“Inhibition of HIV-Reverse Transcriptase by 4′-ethynyl-2-fluoro-deoxyadenosine”</td>
<td>Stefan Sarafanatos</td>
</tr>
<tr>
<td>Renae Mayes</td>
<td>Middle School Education</td>
<td>“Multicultural Competencies among School Counselor Trainees: Cultural Intelligence &amp; Attitudes”</td>
<td>Michael Mobley</td>
</tr>
<tr>
<td>Kelly Mottaz</td>
<td>Fisheries &amp; Wildlife</td>
<td>“Enhancing Pond Production of Large Food-Size Bluegill by Controlling Social Costs”</td>
<td>Robert Hayward</td>
</tr>
<tr>
<td>Diana Ortiz</td>
<td>Biological Sciences</td>
<td>“Genetic Variation Associated with Adaptive Traits in the African Forest (Loxodonta cyclotis) and Savanna Elephants (L. africana)”</td>
<td>Lori Eggert</td>
</tr>
<tr>
<td>Tamela Smith</td>
<td>Anthropology</td>
<td>“The Impact of Prior and Concurrent Exposure to Other Infectious Diseases on Variability in the 1918-19 Flu Epidemic on the Island of Newfoundland”</td>
<td>Lisa Sattenspiel</td>
</tr>
<tr>
<td>Brittany Smotherson</td>
<td>Middle School Education</td>
<td>“Closing the Gap: A Teacher’s Pedagogy and Lower SES Student Success”</td>
<td>Karen Cockrell</td>
</tr>
<tr>
<td>Jenniffer Stetler</td>
<td>Animal Sciences &amp; Biochemistry</td>
<td>“Role of Cyclooxygenase-1 during the Immunological Response in Lyme Arthritis”</td>
<td>Charles Brown</td>
</tr>
<tr>
<td>Calera Wilder</td>
<td>Biological Engineering</td>
<td>“Developing an Adhesion Barrier for Hernia Repair”</td>
<td>Sheila Grant</td>
</tr>
</tbody>
</table>
2007-2008 McNair Scholars

Back row: Jeremy Bloss (Student Services Advisor), Darlene Dixon (Program Assistant), NaTashua Davis (Director)
Fifth row: Kelly Mottaz, Jimmie Jones, Brittany Smotherson,
Fourth row: Renae Mayes, Sean Crockett
Third row: Lindsey Lanfersieck, Valeska Araujo, Kamara Jones, Michelle Clark, Danielle Graef
Second row: Catera Wilder, David Aguayo, Olga Mafotsing Fopoussi, Jenniffer Stetler
First row: Diana Ortiz, Tracey Latimore, Tamela Smith, Brittani Brown, Miriam Galenas
(Not pictured): Alyssa Hollins, Shannon Arnold