
ROBERT L. UNCKLESS

Assistant Professor

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EDUCATION

2011	Ph.D.	Biology, University of Rochester (John Jaenike and H. Allen Orr advisors)
2008	M.S.	Biology, University of Rochester (John Jaenike and H. Allen Orr advisors)
2005	M.S.	Biology, State University of New York, College at Brockport (Joe Makarewicz advisor)
1999	M.S.	Science Education, Cornell University (Carol Conroy advisor)
1997	B.S.	Education, Cornell University

SCIENTIFIC POSITIONS

8/2016-present	Assistant Professor, Department of Molecular Biosciences, University of Kansas, Lawrence, KS
8/2011-7/2016	Postdoctoral Research Associate (Brian Lazzaro and Andy Clark), Cornell University, Ithaca, NY
3/2011-7/2011	Postdoctoral Research Associate (John Jaenike and H. Allen Orr), University of Rochester, Rochester, NY

CURRENT GRANT SUPPORT

NIH – R01 AI139154	05/01/18-04/30/23
Role: PI	\$1,855,000
The causes of balancing selection on immunity genes: from populations to molecular interactions <i>The goal of this project is to use antimicrobial peptides to study the molecular causes of balancing selection in populations. We use a combination of in vitro tests with peptides and in vivo work with CRISPR/Cas9-edited flies.</i>	
NIH – R00 GM114714	09/15/2016-09/14/2020 (NCE)
Role: PI	\$731,624
Antimicrobial peptides as models for the evolution of gene duplication <i>The goal of this project is to use antimicrobial peptides to examine evolution after gene duplication using genomics and genome editing with replication across gene families.</i>	

PUBLICATIONS

Submitted manuscripts and preprints:

Hill, T, HL Rosales-Stephens and **RL Unckless**. 2020. Rapid divergence of the copulation proteins in the *Drosophila dunni* group is associated with hybrid post-mating-prezygotic incompatibilities. *bioRxiv*. doi: 10.1101/2020.05.20.106724. (in review at *G3*)

Unckless, RL, PA Lansdon and BD Ackley. 2020. A comparative analysis of *Caenorhabditis* and *Drosophila* transcriptional changes in response to pathogen infection. *bioRxiv*. Doi: 10.1101/2020.03.04.977595.

Research publications since KU faculty appointment:

Hill, T, and **RL Unckless**. 2020. Adaptation, ancestral variation and gene flow in a ‘Sky Island’ *Drosophila* species. *Molecular Ecology*. (Online early: doi:10.1111/mec.15701)

Hill, T, and **RL Unckless**. 2020. Recurrent evolution of high virulence in isolated populations of a DNA virus. *eLife*: e58931.

Price, TAR, N Windbichler, **RL Unckless** ... (19 total authors). 2020. Resistance to natural and synthetic gene drive systems. *Journal of Evolutionary Biology*: 33:1345-1360.

Nunez, MAB, IM Sabbarini, LE Eide, **RL Unckless** and SE Zanders. 2020. Atypical meiosis can be adaptive in outcrossed *S. pombe* due to *wtf* meiotic drivers. *eLife*: 9:e57936.

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- Chapman, JR, MA Dowell, R Chan and **RL Unckless**. 2020. The genetic basis of natural variation in *Drosophila melanogaster* immune defence against *Enterococcus faecalis*. *Genes*: 11:234.
- Unckless, RL** and HA Orr. 2020. The population genetics of evolutionary rescue in diploids: X chromosomal vs. autosomal rescue. *The American Naturalist*: 195: 561-568.
- Hill, T and **RL Unckless**. 2019. A deep learning approach for detecting copy number variation in next generation sequencing. *G3: Genes, Genomes, Genetics* 9: 3575-3582.
- Hanson, MA, B Lemaitre, and **RL Unckless**. 2019. Dynamic evolution of antimicrobial peptides underscores trade-offs between immunity and ecological fitness. *Frontiers in immunology* 10: 2620.
- Chapman, JR, T Hill and **RL Unckless**. 2019. Balancing selection drives the maintenance of genetic variation in *Drosophila* antimicrobial peptides. *Genome Biology and Evolution*. 11: 2691-2701.
- Benomar, S, KC Evans, **RL Unckless** and JR Chandler. 2019. Efflux pumps in *Chromobacterium* species increase antibiotic resistance and promote survival in a co-culture competition model. *Applied and environmental microbiology* 85: e00908.
- Lea, JK and **RL Unckless**. 2019. An assessment of the immune costs associated with meiotic drive chromosomes in *Drosophila*. *Proceedings of the Royal Society B*. 286: 20191534.
- Perlmutter, JI, **RL Unckless**, SR Bordenstein, DP LePage, J Metcalf, T Hill, J Martinez, FM Jiggins, SR Bordenstein. 2018. The phage gene *wmk* is a candidate for male killing by a bacterial endosymbiont. *PLoS Pathogens* 15: e1007936.
- Zanders, SE, and **RL Unckless**. 2019. How meiotic drivers selfishly drive infertility. *Current Biology* 29: R512-R520.
- Duxbury EM, Day JP, Maria Vespasiani D, Thüringer Y, Tolosana I, Smith SC, Tagliaferri L, Kamacioglu A, Lindsley I, Love L, **Unckless RL**, Jiggins FM, Longdon B. 2019. Host-pathogen coevolution increases genetic variation in susceptibility to infection. *Elife* 8: e46440.
- Hill T, Koseva BS, **Unckless RL**. 2019. The genome of *Drosophila innubila* reveals lineage-specific patterns of selection in immune genes. *Mol Biol Evol*. 36: 1405-1417.
- Pieper, KE, **RL Unckless** and KA Dyer. 2018. A fast-evolving X-linked duplication of *importin-alpha2* is overexpressed in *sex-ratio* drive in *Drosophila neotestacea*. *Molecular Ecology* 27: 5165-5179. doi: 10.1111/mec.14928.
- Smith, BR and **RL Unckless**. 2018. Draft genome of *Lysinibacillus fusiformis* Strain Juneja, a laboratory-derived pathogen of *Drosophila melanogaster*. *Genome Announcements* 6(5), e01571-17. doi:10.1128/genomeA.01571-17.
- Hill, T and **RL Unckless**. 2018. The dynamic evolution of the *Drosophila innubila* Nudivirus. *Infection, Genetics and Evolution* 57: 151-157. doi:10.1016/j.meegid.2017.11.013.
- Ahmed-Braimah, YH, **RL Unckless** and AG Clark. 2017. Evolutionary dynamics of male reproductive genes in the *Drosophila virilis* subgroup *G3: Genes, Genomes, Genetics*. 7: 3145-3155. doi: 10.1534/g3.117.1136.
- Hill, T and **RL Unckless**. 2017. Baculovirus molecular evolution via gene turnover and recurrent positive selection of key genes. *Journal of Virology* 91: e01319-17. doi: 10.1128/JVI.01319-17.
- Unckless, RL**, AG Clark and PW Messer. 2017. Evolution of resistance against CRISPR/Cas9 gene drive. *Genetics* 205:827-841. doi: 10.1534/genetics.116.197285. (Highlighted article, Journal Cover, covered in Nature, Quanta and Nova magazines)
- Akhund-Zade, J, AO Bergland, SO Crowe and **RL Unckless**. 2017. The genetic basis of natural variation in *Drosophila* (Diptera: Drosophilidae) virgin egg retention. *Journal of Insect Science* 17: 1-9. doi: 10.1093/jisesa/iew094.
- Lindholm, AK, ... **RL Unckless, et al.** (22 authors). 2016. The ecology and evolutionary dynamics of meiotic drive. *Trends in Ecology and Evolution* 31:315-326. doi:10.1016/j.tree.2016.02.001.

Research publications from prior to arrival at KU:

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- Unckless, RL** and BP Lazzaro. 2016. The potential for adaptive maintenance of diversity in insect antimicrobial peptides. *Philosophical Transactions of the Royal Society B* 371:20150291. doi: 10.1098/rstb.2015.0291.
- Unckless, RL**, VM Howick and BP Lazzaro. 2016. Convergent balancing selection on an antimicrobial peptide in *Drosophila*. *Current Biology* 26:257-262. Doi: 10.1016/j.cub.2015.11.063. (F1000 recommended)
- Unckless, RL** and AG Clark. 2015. Driven to extinction: on the probability of evolutionary rescue from sex-ratio meiotic drive. bioRxiv doi: <http://dx.doi.org/10.1101/018820>.
- Unckless, RL**, PW Messer T Connallon and AG Clark. 2015. Modeling the Manipulation of Natural Populations by the Mutagenic Chain Reaction. *Genetics* 201:425-431. doi: 10.1534/genetics.115.177592. (Highlighted article) (F1000 recommended)
- Unckless, RL**, SM Rottschaefer and BP Lazzaro. 2015. The Complex Contributions of Genetics and Nutrition to Immunity in *Drosophila melanogaster*. *PLoS Genet* 11: e1005030. doi:10.1371/journal.pgen.1005030.
- Unckless, RL**, SM Rottschaefer and BP Lazzaro. 2015. A genome-wide association study for nutritional indices in *Drosophila*. *Genes, Genomes and Genetics* 5:417-425. doi: 10.1534/g3.114.016477.
- Unckless, RL**, AM Larracuenta and AG Clark. 2015. Sex-ratio meiotic drive and Y-linked resistance in *Drosophila affinis*. *Genetics* 199:831-840. doi:10.1534/genetics.114.173948.
- Orr, HA and **RL Unckless**. 2014. The population genetics of evolutionary rescue. *PLoS Genetics* 10(8): e104551.
- Unckless, RL** and AG Clark. 2014. Sex-ratio meiotic drive and interspecific competition. *Journal of Evolutionary Biology* 27(8): 1513-1521.
- Unckless, RL** and J Jaenike. 2012. Maintenance of a male-killing *Wolbachia* in *Drosophila innubila* by male-killing dependent and male-killing independent mechanisms. *Evolution* 66(3):678-689.
- Unckless, RL**. 2011. The potential role of the X chromosome in the emergence of male-killing from mutualistic endosymbionts. *Journal of Theoretical Biology* 291: 99-104.
- Unckless, RL**. 2011. A DNA virus of *Drosophila*. *PLoS ONE* 6: e26564.
- Jaenike J, **RL Unckless**, SN Cockburn, LM Boelio, and SJ Perlman. 2010. Adaptive evolution via symbiosis: recent spread of a defensive symbiont in *Drosophila*. *Science* 329: 212-215. (F1000 recommended)
- Unckless, RL** and HA Orr. 2009. The population genetics of adaptation: multiple substitutions on a smooth fitness landscape. *Genetics* 183: 1079-1086.
- Jaenike J, JK Stahlhut, LM Boelio and **RL Unckless**. 2009. Association between *Wolbachia* and *Spiroplasma* within *Drosophila neotestacea*: an emerging symbiotic mutualism. *Molecular Ecology* 19: 414-425.
- Unckless, RL** and JK Herren. 2009. Population genetics of sexually antagonistic mitochondrial mutants under inbreeding. *Journal of Theoretical Biology* 260: 132-136.
- Unckless, RL**, LM Boelio, JK Herren and J Jaenike. 2009. *Wolbachia* as populations within individual insects: causes and consequences of density variation in natural populations. *Proceedings of the Royal Society B* 276: 2805-2811.
- Unckless, RL**, LM Boelio, C Cornish and KA Dyer. 2008. Isolation and characterization of 30 polymorphic microsatellite loci from the mycophagous fly *Drosophila innubila*. *Molecular Ecology Research* 8: 939-942.
- Unckless, RL** and HA Orr. 2009. Dobzhansky-Muller incompatibilities and adaptation to a shared environment. *Heredity* 102: 214-217.
- Orr, HA and **RL Unckless**. 2008. Population extinction and the genetics of adaptation. *American Naturalist* 172: 160-169.

Unckless, RL and J Makarewicz. 2007. The impact of nutrient loading from Canada Geese (*Branta canadensis*) on water quality, a mesocosm approach. *Hydrobiologia* 586: 391-401.

PRESENTATIONS

Invited seminars (extramural): **denotes national meetings; ***denotes international meetings

Unckless, RL. 2020. The causes of balancing selection on immunity genes: from populations to molecular interactions. Departmental seminar at Kansas State University, Manhattan, KS.

Unckless, RL. 2020. Recurrent evolution of a virulent viral haplotype in a *Drosophila*/DNA virus system. Talk at the 2020 Kansas INBRE Symposium, Wichita, KS.

Unckless, RL. 2019. The genetic basis of immune divergence between species. Talk at the 2019 UNVEIL Symposium, Lincoln, NE.

Unckless, RL. 2019. The causes of balancing selection on immunity genes: from populations to molecular interactions. Departmental seminar at the University of Montana, Missoula, Montana, February 2019.

Unckless, RL. 2019. The causes of balancing selection on immunity genes: from populations to molecular interactions. Departmental seminar at the University of Toronto, Toronto, Ontario, Canada, January 2019.

Unckless, RL. 2018. The causes of balancing selection on immunity genes: from populations to molecular interactions. Departmental seminar at the University of Nebraska, Lincoln, Nebraska, September 2018.

Unckless, RL. 2018. Mechanistic convergence in genetic conflict across species. Speaker. Midwest Population Genetics Meetings, St. Paul, Minnesota.

Unckless, RL. 2018. The landscape of resistance to natural and synthetic drive systems. Arolla Gene Drive Resistance Workshop, Arolla, Switzerland. Plenary speaker. ***

Unckless, RL. 2017. Adaptation of Nucleopolyhedroviruses in *Drosophila* and other arthropods. Entomological Society of America's North Central Branch Meeting. Invited Speaker. Indianapolis, IN.

Unckless, RL. 2017. Balancing Selection and Convergence in Insect AMPs and/or the Role of Gene Duplication in AMP Evolution. Gordon Research Conference. Invited Speaker. Pasadena, CA. ***

Unckless, RL. 2016. Convergence and balancing selection in insect antimicrobial peptides. Department of Biochemistry and Molecular Biophysics, Manhattan, Kansas.

Unckless, RL. 2016. Convergent evolution of insect antimicrobial peptides. Invited Speaker. AMP2016 international symposium on antimicrobial peptides, Montpellier, France. ***

Invited seminars (KU):

Unckless, RL. 2016. The maintenance of genetic variation through conflict. Ecology and Evolutionary Biology Departmental Seminar, University of Kansas, Lawrence, Kansas.

Unckless, RL. 2016. Adaptive maintenance of genetic diversity in insect immunity genes. Invited Speaker. Department of Molecular Biosciences Graduate Student Symposium, University of Kansas, Lawrence, Kansas.

Oral presentations by lab member: **denotes national meeting; ***denotes international meeting

Hill, T and **RL Unckless.** 2019. Host-virus co-evolution in *Drosophila innubila*. Midwest Population Genetics Meeting, Minneapolis, MN. *won best talk by a postdoc

Chapman, JR and **RL Unckless.** 2019. Machine learning AMPs up: Discovery and validation of new antimicrobial peptides in *Drosophila melanogaster*. Midwest Population Genetics Meeting, Minneapolis, MN.

Hill, T and **RL Unckless**. 2019. Host-virus co-evolution in *Drosophila innubila* highlights non-RNAi pathways as key to antiviral response. Platform talk at the 2019 *Drosophila* Research Conference, Dallas, Texas. **

Darby, AM, SR Mullinax and **RL Unckless**. 2019. Tradeoffs between immune defense and resistance to environmental stress at a single amino acid polymorphism. Platform talk at the 2019 *Drosophila* Research Conference, Dallas, Texas. **

Hill, T and **RL Unckless**. Antiviral genes are not rapidly evolving in *Drosophila innubila*. SMBE Satellite Meeting: Evolution of the Cell in Deer Valley, Utah, May 2018. **

Chapman, JR and **RL Unckless**. 2017. Balancing selection is pervasive in *Drosophila* antimicrobial peptides. Ecological Immunology Workshop, Blossin, Germany. ***

Hill, T and **RL Unckless**. 2017. Adaptation of Baculoviruses and Nudiviruses in *Drosophila* and other arthropods. Society for Molecular Biology and Evolution Meeting, Austin, TX. **

Poster presentations by lab members: **denotes national meeting;

Neighbors, MA and **RL Unckless**. 2020. The genetic basis of divergence in immune defense between species. Kansas IDEA Network of Biomedical Excellence Symposium, Wichita, KS. (undergraduate)

Neighbors, MA and **RL Unckless**. 2019. The genetic basis of divergence in immune defense between species. *Drosophila* Genetics Research Conference, Dallas, TX. (undergraduate) **

Pagella, EA, JR Chapman and **RL Unckless**. 2019. A survey of the microorganisms colonizing three *Drosophila* species in the wild. *Drosophila* Genetics Research Conference, Dallas, TX. (undergraduate) **

Chapman, JR and **RL Unckless**. 2019. Balancing selection in *Drosophila* AMPs may be maintained via functional diversity amongst alleles. *Drosophila* Genetics Research Conference, Dallas, TX. **

Lea, JK and **RL Unckless**. 2019. Immune costs associated with meiotic drive. *Drosophila* Genetics Research Conference, Dallas, TX. **

Mullinax, SR and **RL Unckless**. 2019. Determining the causes and consequences of genetic variation in Dipteracin, a *Drosophila* antimicrobial peptide. *Drosophila* Genetics Research Conference, Dallas, TX. **

Hill, T and **RL Unckless**. The genome of the mushroom-feeding fly, *Drosophila innubila*, adapting to parasites and toxin exposure. Population Evolutionary and Quantitative Genetics in Madison, Wisconsin, May 2018. **

Chapman, JR, T Hill and **RL Unckless**. Balancing selection is pervasive in *Drosophila* antimicrobial peptides. Population Evolutionary and Quantitative Genetics in Madison, Wisconsin, May 2018. **

Hill, T and **RL Unckless**. Adaptation of Baculovirus via recurrent positive selection and gene flow. *Drosophila* genetics research conference, San Diego, California, March 2017. **

HONORS AND DISTINCTIONS

2020 Genetics Society of America Editors' Choice Spotlight Article in Genes|Genomes|Genetics in 2020

2018 Genetics Society of America Editors' Choice Award for an outstanding Population & Evolutionary Genetics article published in GENETICS in 2017

PROFESSIONAL SERVICE

- Invited editor for *mBio*.
- Organized "Graduate Admissions Workshop" designed to provide undergraduate students from historically underrepresented groups with information and assistance with the graduate admissions process (October 2020).

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- Organized regional meeting, “Great Plains Genetic Conflict Meeting” (~30 attendees from four states), Lawrence, KS (2020).
 - Co-chaired and organized workshop, “Intro to the *Drosophila* microbiome: how can I control the microbiome in my research?” at the *Drosophila* Research Conference, Dallas, TX (2019).
 - Genetics Society of America (GSA) working group for benefits of GSA membership (2018).
 - Emceed GSA *Drosophila* Genetics Research Conference Science Slam (2018).

Manuscript reviews: (since arrival at KU)

American Naturalist (2), *BMC Genomics* (2), *Ecology Letters* (1), *Evolution* (3), *Evolutionary Applications* (1), *Frontiers in Ecology and Evolutionary Biology* (2), *Frontiers in Immunology* (1), *Genetics* (3), *Heredity* (1), *Insect Biochemistry and Molecular Biology* (2), *Journal of Evolutionary Biology* (1), *Journal of Responsible Innovation* (1), *Molecular Biology and Evolution* (2), *PLoS Biology* (3), *PLoS Genetics* (2), *PLoS Pathogen* (2), *PLoS ONE* (1), *Proceedings of the National Academy of Sciences* (2), *Proceedings of the Royal Society B* (4), *Research Square* (3), *Royal Society: Open Science* (1), *Scientific Reports* (1), *Virus Evolution* (1). 42 total.

Grant reviews: (since arrival at KU)

- *Ad hoc* grant reviewer for Field Institute (2018)
- Reviewed University of Kansas New Faculty General Research Fund grants (2020)

University service:

- Immunology Faculty Search Committee – Spring 2020.
Note that this search was cancelled due to Covid-19
- Organized a Bioinformatics Data Skills group informal class (20 participants) – Spring 2019.
Worked through Bioinformatics Data Skills by Vince Buffalo and worked on individual projects
- Wrote department statement on Diversity, Equity and Inclusion – Fall 2018/Spring 2019.
- KU Postdoctoral Association seminar on the transition from postdoc to academia. November 2018.
Gave a talk over lunch about job searches, negotiating, getting started
- Department Graduate Student Recruiting Committee (appointed). Chair. Molecular Biosciences. Fall 2018-present.
Worked to improve recruitment of graduate students (especially from underrepresented groups): developed welcome packet, worked on website redesign, organized Graduate Admissions Workshop (see above), led an effort to directly contact promising students and had several of those students apply and enroll at KU.
- Department Social Committee (appointed). Member. Molecular Biosciences. Fall 2017-present.
Organize faculty and student social events (trivia night, happy hour, etc.)
- KU Undergraduate Honors Thesis Evaluation Committee. Spring 2018.
- Hosted speakers for departmental seminars (12 total). 2016-2019.
- Free State Fly Group. Organizer. Molecular Biosciences and EEB. August 2016 – Present.

Outreach:

February 2020	Hosted Girl Scout troop in lab
May 2014	Organized guest scientist panel for 1 st grade class Dr. Walter Cooper Academy, Rochester, NY
February 2013	Guest scientist for 1 st grade class World of Inquiry School, Rochester, NY
March 2010	Panelist for biology majors career dinner St. John Fisher College, Rochester, NY

TEACHING AND MENTORING:

Note: R00 award stipulated a 75% research effort during the duration of the award (9/15/2016-9/14/2020).

Undergraduate teaching:

Fall 2020: BIOL350 – Principles of Genetics
(256 students, 4 credits, 50% effort)

BIOL599 – Senior Seminar in Molecular, Cell and Developmental Biology
(19 students, 1 credit, 100% effort)

Fall 2019: BIOL350 – Principles of Genetics
(203 students, 4 credits, 50% effort, instructor evaluation = 4.53/5)

Fall 2018: BIOL350 – Principles of Genetics
(191 students, 4 credits, 50% effort, instructor evaluation = 4.25/5)

Fall 2017: BIOL350 – Principles of Genetics
(190 students, 4 credits, 50% effort, instructor evaluation = 4.01/5)

Graduate teaching:

Spring 2020: BIOL905 – Advanced Molecular Genetics
(19 students, 1 credit, 100% effort)

Spring 2019: BIOL905 – Advanced Molecular Genetics
(19 students, 1 credit, 100% effort)

Mentoring:

Postdocs: Dr. Tom Hill (August 2016-present)
Max Kade fellow (2017-2018), K-INBRE postdoctoral fellow (2018-2019, 2020-2021)

Dr. Joanne Chapman (January 2017-February 2020)
K-INBRE postdoctoral fellow (2018-2019)

Dr. Jessamyn Perlmutter (March 2020-present)

Dr. WenJaun Ma (August 2020-present)

PhD students: Sarah R. Mullinax (March 2017-present)
University of Kansas Self Graduate Fellow (2017-present)
University of Kansas University Graduate Fellow (2016-2017)

Kent Mulkey (August 2019-present)

Undergraduates: *indicates authorship on published work

Alyssa Lynn Rosales-Stephens, Emerging Scholar (August 2018-present)*

Emma Beason (September 2018-present)

Kavya Nataraj (September 2018-May 2019)

Emma Pagella (September 2018-present)

K-INBRE Undergraduate Research Scholarship (Awarded Spring 2020)

Poster presentation at Drosophila Research Conference, Dallas, TX (April 2019)

Mariaelena Nabors, McNair Scholar (May 2018-present)

K-INBRE Star Trainee (Awarded Spring 2019)

MacNair Scholar (2018-2020)

Poster presentation at Drosophila Research Conference, Dallas, TX (April 2019)

Poster presentation at K-INBRE meeting, Wichita, KS, Honorable Mention (January 2020)

Poster presentation at the Allied Genetics Conference, Washington, DC (April 2020)

Poster presentation at SACNAS, Honolulu, HI (November 2019)

Uma Desai (Fall 2017-present)

Samantha Walker (Fall 2019-Spring 2020)

Carly Straight (Fall 2019)

Meena Sreedhara (Spring 2019-Fall 2019)

Liam Magathan (Spring 2019)

Patrick Chan (Spring 2020)

Claire Hathcoat (Spring 2020)

Brett Norris (Spring 2020)

Sidney Budinas (Spring 2020)

Mary Reed-Wesson, Carleton College (Summer/Fall 2019)

Dawson Clark (September 2018-present)

Nicole Oblon (Summer 2017)

Katie Pileggi, student hourly employee (Fall 2017-present)

Maureen Dowell (January 2017-July 2018), graduated. *

Rosanna Chan (January 2017-May 2018), graduated. *

Judith Ikerionwu (Fall 2016-May 2018), graduated.

Outstanding presentation award at KU Undergraduate Research Symposium

Randie Rudder (Fall 2016-Fall 2017), graduated.