Statement of Research Achievements, Goals, and Outreach

A) MY RESEARCH PROGRAM

I am an integrative behavioral ecologist and evolutionary biologist. In my research, I address questions about both how and why animals display exaggerated features. Nearly 150 years ago, Charles Darwin himself viewed these traits, such as the enlarged horns of deer and complex songs of birds, as some of the most awe-inspiring and demanding of special biological explanation. We too as humans display exaggerated features, including the large size and musculature, deep voice, and facial hair of men compared to women. The process of sexual selection has long been recognized to drive the elaboration of many of these characteristics, but until recently the intrinsic and extrinsic factors that govern the active development and expression of these features were rarely studied. In my novel interdisciplinary studies of animals, predominantly in birds, I aim to explain both what environmental and physiological factors (e.g. diet, hormones, health) affect these the production of these traits currently as well as the evolutionary and behavioral processes that have favored their existence over time.

As a model for studying the control and function of sexually selected traits, I focus on vibrant colors in birds, like the orange of an oriole or the blue of a bluebird, that may serve as signals for acquiring mates. Theory states that these exaggerated traits are costly to produce (e.g. energy) or maintain (e.g. predator detection); thus only individuals who are of the highest quality can afford to develop these features, remain alive in so doing, and thus acquire mates for passing on genes to future generations. Among the many lines of work in this field of "honest advertisement" in animals is the interest in why so many different traits – from songs to dances to colors to smells to sizes – have evolved. An emergent hypothesis is that each type of trait may serve different communicative functions (e.g. opposite-sex attraction versus same-sex competition). This has been a central question guiding much of my research over the last decade – to try to understand what factors affect the expression of different traits, what information is contained in them, and ultimately how and why they are used as signals today. I have used field- and lab-based approaches, capitalizing on studies in nutrition, immunology, parasitology, endocrinology, physiology, biochemistry, and behavior, to identify the information that is communicated by sexual signals and hence the benefits that individuals gain by using such signals in mating or competitive contexts. Because of the diversity of rich colors that passerines (i.e. songbirds) display, I have used avian species like finches and sparrows as models for investigating the costs and benefits of sexual signal development and use.

In my M.S. thesis and Ph.D. dissertation work, I investigated the two primary means of pigment-based coloration in birds—carotenoid pigmentation (reds, oranges, and yellows) and melanin pigmentation (blacks, browns, and grays)—and demonstrated, in a variety of songbird species (e.g. zebra finches and house sparrows), considerable differences in both the requirements for producing the two forms of coloration and in their signaling roles. Carotenoid colors tend to be sensitive to nutritional and health factors in adult birds and are used in mate attraction, whereas melanin colors are less sensitive to diet and disease and instead come under stronger hormonal control (e.g. testosterone) and are used more often as indicators of aggression ("status signals"). In my post-doctoral work, I undertook a series of investigations into the physiological trade-offs that animals face when allocating pigments to different endpoints (e.g. coloration, health, offspring), primarily in domesticated avian species (e.g. chicken, quail).

These two information bases on avian pigments and colors (which I published in over 40 peer-reviewed papers prior to arriving at ASU in Fall 2004) have set the stage for my recent, current, and near-future lines of research, which will occur at each of the four "levels of evolutionary analysis" (mechanistic, developmental, functional, and historical). Using start-up funds from SoLS and the Graduate College at ASU, I have set up a laboratory dedicated to analyzing and manipulating animal colors and pigments, the mechanisms that control their expression, and the physiological and behavioral roles they play, in both wild local study animals as well as captive laboratory subjects. My students, post-docs, and I, along with other collaborators (> 65 researchers from 13 countries), have published > 40 journal articles and two edited books on these topics since I arrived at ASU. We are currently expanding upon this body of work in seven main directions, which I outline below:

1) Comparative approach to understanding pigment-based coloration and trade-offs

The idea that color signals incur distinct costs/trade-offs has been tested in a number of avian species by myself and others, but in far too few avian lineages and never within a comparative framework (e.g. accounting for species differences in diet, health, coloration, etc.). The idea behind how carotenoid colors serve as "honest signals" is based on the notion that the colorful pigments must be acquired from the diet and also play a role in health modulation, hence generating a trade-off and leaving only the best animals, with the highest nutrient supplies and lowest health challenges, to become most colorful. I am currently beginning a large-scale, multi-species, phylogenetically controlled experiment in which I test the robustness of this prediction in four different avian lineages. My students, post-doc (Dr. William Medina-Jerez, now an assistant professor at the University of Wyoming), and I have conducted two studies (one published in Ethology; another in review at Behav. Ecol.) that served as pilot data for this project. A grant proposal in the amount of $345K was funded by the National Science Foundation (Functional and Regulatory Systems panel; IOS-0746364) in Dec. 2007 to conduct this 3-year project. I hired a post-doctoral researcher in August 2008 (Melissah Rowe) and, in conjunction with myself and my Ph.D. student (Mike Butler), we will begin this work in September 2008.

2) Color perception in colorful birds

"Beauty is in the eye of the beholder", and yet far too many studies of animal coloration have ignored the visual perceptual abilities of signal receivers that make mating or competitive decisions based on color variations. In particular, the idea that color vision itself varies among individuals within a species, such that some can better discriminate rivals, mates, or other colored substrates vital to signaling (e.g. pigment-containing foods) than others, demands attention. Carotenoid-based color systems provide an unusual opportunity for such an investigation, because the very pigments used to color feathers also are present in the eye, where they filter light and both tune retinal photoreceptors as well as protect them from photodamage. Color vision, as affected by carotenoid pigments in the eye, may thus be subject to the same nutritional and health constraints that color production is. A 3rd-year Ph.D. student in my lab (Matt Toomey) is studying the control and function of retinal carotenoids in the house finch (*Carpodacus mexicanus*)—a model songbird for studying sexual selection and found as an abundant, native Sonoran desert songbird in and around Phoenix. We have conducted several pilot studies, describing pigment variation in the eye as a function of season, sex, health, diet, and plumage color, and published one methodological paper on this work (in Invest. Ophthalmol. Vis. Sci.). This topic interfaces nicely with the aforementioned study of pigment trade-offs, has broad implications for human visual health (where dietary carotenoid intake aids in preventing macular degeneration), and is the central theme of the 5-year CAREER grant proposal that I resubmitted to NSF in July 2008.

3) Microgeographic variation in sexual selection

Sexual selection is recognized as a process that can promote population divergence and even speciation, but the intraspecific scales, strength, and mechanisms by which this occurs are poorly known. Theories predict that shifts in either traits or preferences can generate a new adaptive phenotypic peak in the diverged population/ species, and while empirical evidence in some species suggests that microgeographic variation in lighting environment can shift color signal efficacy, it is not clear how traits (e.g. production or perception of color) change as populations diverge. I am initiating a new line of work on the microgeography of sexual signaling in house finches from Arizona, who show dramatic spatial variation in coloration, largely as a function of very recent human intervention. In pilot work, we have found that city-dwelling Phoenix house finches are significantly less colorful than are finches inhabiting surrounding natural desert environs. We are interested both in the mechanism underlying this spatial color variation, whether a similar mechanism is at work for color perception, and the consequences that carotenoid variation in the plumage or eye have for sexual selection and potential population divergence. This topic is subsumed into the NSF CAREER grant proposal mentioned above, and also provides an excellent urban-rural outreach opportunity, where we can involve local schools, parks, zoos, and neighborhoods in data collection and comparison.

4) Ontogenetic control of color

Investigations into proximate control of color (and most sexual traits) have largely been restricted to the adult phase of life (so-called "activational" effects), and yet we know that conditions early in life ("organizational" effects) can contribute substantially to adult health and phenotype in animals. Since early in 2007, my 2nd-year Ph.D. student (Mike Butler) has been investigating this often-overlooked ontogenetic component, in a study of how nutrition and health during development shape health and sexual coloration in adult Mallards (*Anas platyrhynchos*). This species is ideal for such work because they have sexually-dichromatic/-selected carotenoid coloration (in the beak), are precocial (hence easily raised in the lab), and display a variety of color types (allowing us to simultaneously assess how different color displays are controlled at the organizational level *within* a species). We plan to submit a grant proposal to NSF's Developmental Systems panel in July 2009 to fund this work. A post-doctoral associate in my lab (Dr. Paul Nolan, now assistant professor at The Citadel) and I also previously conducted a related study, in collaboration with Dr. Pierre Deviche in SoLS at ASU, on the effects of early carotenoid exposure on the brain, a neurally governed behavior (song), and beak coloration in male zebra finches; we are currently in the process of writing this up for publication.

5) Understudied color types in birds

Avian colors are an excellent system for investigating diversity in sexual signal production and value because birds use such a variety of mechanisms for producing color. Beyond the two main forms of pigment-based color mentioned above, there exist numerous other classes of pigment that generate color in avian feathers and bare parts (e.g. beaks, legs), such as the psittacofulvin pigments in parrot plumage as well as the pterin pigments in penguin feathers and bird irises. Moreover, there exists an altogether different type of color, not dependent upon pigments but on the internal anatomical architecture of tissue ("structural color"). For these color types, we ask the questions: as colors produced by different mechanisms, do they incur different costs than melanin and carotenoid colors, confer different benefits, and signal different things? Preliminary work done in collaboration with a parrot fancier, a former post-doc in my lab (Dr. Trevor Rivers, now a post-doc at the Barrow Neurological Institute in Phoenix, AZ), and several penguin researchers in the United States, France, and New Zealand, has yielded fascinating data on color communication in these birds (see 3 published papers; also two in review). The parrot work has been funded in part by donations made by parrot fanciers through the ASU Foundation. I currently have a 3rd-year Ph.D. student (Melissa Meadows) studying the costs and benefits of structural gorget and crown coloration in Anna's hummingbirds (*Calypte anna*) as well.

6) Non-avian patterns of color control and function

Brilliant sex-specific colors are by no means restricted to birds, and with a series of collaborators I am expanding these tests of color control and function to taxa ranging from jumping spiders (with 3rd-year Ph.D. student in my lab, Lisa Taylor) and butterflies (with members of Dr. Ron Rutowski's lab in SoLS at ASU) to lizards (with colleagues from Auburn University and the University of Puget Sound) and fish (with colleagues from Amherst College and the College of William and Mary). This work has yielded three publications to date (in Behav. Ecol., Comp. Biochem. Physiol. B., and Physiol. Biochem. Zool.) and allows us to broadly test the "multiple message" and "pigment trade-off" hypotheses for different color types (e.g. carotenoid, melanin, pterin, structural) in non-avian species.

7) Carotenoid accumulation in animal tissues

My lab has become internationally known as one of the primary locations for analyzing carotenoid pigments and other antioxidants (e.g. vitamins A and E) in animal tissues (e.g. plasma, feathers, brain, liver, eggs, yolk, body fat). Since 2004, we have collaborated on 50 different projects in which we analyzed pigments and vitamins in animals ranging from coral and crayfish to fish, reptiles, and many species of birds (e.g. guillemots, starlings, frigatebirds, owls, penguins). This includes work with three international zoos and with researchers from 10 countries; it has resulted in 11 publications to date (and many more to come).

B) RESEARCH OUTREACH

My research and outreach efforts since 2004 have helped raise the local, national, and international profiles of both the School of Life Sciences and Arizona State University. Papers I published in 2005 in the journals *Science* and *Biology Letters* received extensive press coverage worldwide, including pieces that appeared on *National Public Radio* and in the *New York Times*. In June 2008, a paper I co-authored in Current Biology attracted over 400 online and news articles as well as media coverage from recognized sources like CNN and Good Morning America. I have been invited to give seminars to discuss my work at several prestigious American universities (e.g. University of Chicago, University of California-Riverside), international research institutes (Max Planck Institute in Germany, CNRS in France), and local public-interest group meetings (e.g. Maricopa Audubon Society, Fountain Hills Parrot Club, McDowell Sonoran Conservancy). Because of my scientific achievements and participation in professional societies, I received two "Outstanding Young Investigator" Awards in 2005 from the Animal Behavior Society and the American Ornithologists' Union. In collaboration with my Master's advisor, I co-edited two landmark volumes on Bird Coloration (Harvard Univ. Press, 2006), which summarize the large body of work that has been performed in this field over the past seventy years (when the last book on this topic was written). I have reviewed over 125 papers for more than 40 journals since Fall 2004 and serve as Associate Editor for four journals in my field, whose focus is integrative behavior and/or ecology. I also serve as biochemical consultant for several zoos (e.g. St. Louis Zoo, Lincoln Park Zoo) and companies (Avian Advisors LLC), performing vitamin/antioxidant analyses of zoo diets and informing zoo nutritionists and private industry (e.g. bird feed suppliers) on aspects of animal nutrition, growth, and reproduction.

Intramurally, I am serving on the dissertation committees of ten Ph.D. students from other labs in SoLS. I previously participated in ASU's internship exchange program with York University in Canada, which brought an undergraduate minority to work as a researcher in my lab (who also completed his honor's research project at that time). I have served on three faculty committees within SoLS to improve undergraduate curriculum, to hire two new faculty members in Neuroscience and Behavior, and to enhance the visibility of Animal Behavior research on campus (through the iGELS program and the in-production Behavioral Biology graduate program). Linked to this, in my first two years at ASU I coordinated an in-house seminar series to foster information sharing among animal behaviorists on campus; we are resurrecting this group in the fall semester of 2008. An important, near-future goal of mine is to more closely involve local residents, especially schoolchildren and their instructors throughout the Valley, in my research. Studies of plumage coloration in house finches from Phoenix and surrounding areas will be ideal for such outreach, as students can assist in capturing, photographing, and color-scoring their local birds, and upload their results to an online database that can be accessed by several schools throughout the Valley, which will serve as the dataset from which various comparative school projects and cooperative science fairs are conducted.

SUMMARY OF RESEARCH & SERVICE ACCOMPLISHMENTS AT ASU (SINCE FALL 2004)

- Published 45 journal articles (including in top journals from my field, such as *Science*, *Proc. R. Soc. Lond. B*, and *Behav. Ecol.*), 2 edited books, 7 book chapters, and 2 popular articles
- Received $344K grant from federal granting agency (NSF) to study bird pigments and coloration; two additional grant-proposal submissions are in review, amounting to $600K more in proposed funds
- Received two outstanding young investigator awards from professional societies
- Served as research mentor for 4 Ph.D students, 4 post-doctoral researchers, and 35 undergraduates
- Ph.D. students received two prestigious NSF pre-doctoral fellowships (and 1 Honorable Mention) along with numerous other research awards
- Serve as associate editor for four journals in my field (*Behav. Ecol. Sociobiol., Funct. Ecol. Auk*, and *Condor*)
- Received extensive local, national, and international press coverage for four published papers (in *Science*, two in *Biol. Lett.*, and *Current Biology*).
- Gave invited seminars at 20 academic institutions, 7 conference symposia, and 9 public forums