Ketterson / Nolan Research Group Collection

This document is part of a collection that serves two purposes. First it is a public archive for data and documents resulting from evolutionary, ecological, and behavioral research conducted by the Ketterson-Nolan research group. The focus of the research is an abundant North American songbird, the dark-eyed junco, *Junco hyemalis*, and the primary sources of support have been the National Science Foundation and Indiana University. The research was conducted in collaboration with numerous colleagues and students, and the objective of this site is to preserve not only the published products of the research, but also to document the organization and people that led to the published findings. Second it is a repository for the works of Val Nolan Jr., who studied songbirds in addition to the junco: in particular the prairie warbler, *Dendroica discolor*. This site was originally compiled and organized by Eric Snajdr, Nicole Gerlach, and Ellen Ketterson.

Context Statement
This document was generated as part of a long-term biological research project on a songbird, the dark-eyed junco, conducted by the Ketterson/Nolan research group at Indiana University. For more information, please see IUScholarWorks (https://scholarworks.iu.edu/dspace/handle/2022/7911).

PROJECT SUMMARY

I propose to synthesize research I have conducted over the past 40 years on a single species of songbird, the dark-eyed junco. The junco is a classic system for studies of avian speciation and reproductive timing. Its morphology varies greatly in space, which has puzzled evolutionary systematists for more than 100 years. It is also the first bird to reveal the role of day length in the timing of reproduction.

Early in my research, I focused on migration and demography during the non-breeding season (1970-1985), and then on mating systems (1983-1986). I next focused (1987-2003) on the evolution of trade-offs in life histories by means of experimental phenotypic manipulations in the field, using hormones to simultaneously modify the expression of numerous traits related to viability, fecundity, and sexual selection. Results of these studies led to novel insights regarding hormonal pleiotropy and the nature of adaptation and constraint. The most recent years (2003-2010) have been the most exciting. By studying individual variation in hormonal phenotypes, we have learned how various forms of selection act on hormone-mediated characters, giving rise to varying degrees of phenotypic integration and independence. By extending our approach across populations, we are breaking new ground in understanding the role of hormones in rapid, divergent phenotypic evolution.

The core contribution will be a multi-authored volume that will focus on population divergence in the junco in light of hormonal pleiotropy and correlational selection. It will include perspectives from other evolutionary biologists who study the junco, and it will consider population divergence in the junco in relation to ecological speciation and sexual selection. A key question will be the degree to which the junco's variety is driven by divergent selection on migratory and reproductive timing. Geographic variation in optimal timing of reproduction can select against hybrids between populations that breed allopatrically, despite having sympatric distributions during winter (heteropatry). Sexual selection on plumage or song variants can also lead to divergence. The volume will explore these alternatives, as well as the possibility that timing and reproductive traits share common mediation by hormones. The book will use the junco to bridge ecological physiology and microevolution, and I offer that only a person who has traveled my research path would be likely to combine the ideas in the way that it will.

My other goal is to create an archive of the research path itself by preserving both data and what librarians call metadata. Additional products of the synthesis will include a) a relational database that will be enhanced by further investment and made available to the community in a timely way, b) a web-based scholarly archive, and c) a series of media products designed for scientists and the public, including a documentary.

Intellectual Merit: NSF has supported research by Ketterson, colleagues, and students since 1985. The questions have evolved as one discovery engendered the need to seek another, but a constant has been the foundational evolutionary framework and the songbird species under study. The goal of this synthesis is to articulate the common themes that drove and united the investigations, and to articulate emergent themes and a future research agenda for other ecological and evolutionary biologists, so as to maximize the utility of findings to date. **Broader impacts:** A second and critical goal is to archive and share data and to produce a media product that will convey key findings to diverse audiences. The resulting synthesis will be of strong interest to students, educators and fellow scientists who study microevolutionary processes and evolutionary ecology. It will also appeal to public consumers of scientific research, young and old.

PROJECT DESCRIPTION

For nearly 40 years, I have conducted research on a songbird, the dark-eyed junco, and NSF has supported that research almost continuously since 1978. The study species has been invariant, but the topics have varied. Chronologically, I have studied avian migration, mating systems, phenotypic engineering with hormones, adaptation and constraint, rapid evolution, and population divergence. The research has benefitted greatly from the contributions of a series of extremely talented students and colleagues**. I believe that the research is at a stage where the evolution and population biology community will benefit most if the findings are presented in a cohesive set of traditional and media-based products to be described here.**

The key conceptual insights that have emerged from the research and that will be addressed in the synthesis are these: 1) Hormones are environmentally mediated, act systemically, and interact with target tissues to give rise to attributes we refer to as traits; 2) this coordinated trait expression mediated by a single hormone is referred to as hormonal pleiotropy; 3) if selection favors, or acts against, one or more traits, other hormone-mediated traits will be dragged along, at least in the short run; 4) if co-expressed traits have multiplicative effects on fitness, then selection is correlational and the result can be tight phenotypic integration; 5) dependence of traits on hormones is dynamic; selection also can act on tissue sensitivity to a hormone and sensitivity to a hormone comes and goes, i.e., phenotypic independence; 6) on the short run, tight phenotypic integration can act as a constraint on adaptive evolution; 7) phenotypic integration can also enable rapid adaptation in response to environmental change because it causes traits to co-occur in individuals when recombination might otherwise be required and take longer; 7) hormone-enabled rapid evolution can also lead to population divergence; and 8) the nature of the traits that hormones influence 'makes sense' in terms of trade-offs in life histories, e.g. coordinating trait values that balance viability and sexual selection or pace of life. These interactions are under constant revision in response to the ever-changing environment. The synthesis will apply these conceptual insights, using the junco as the example. [Citations in section II; please see Kitano et al. 2010, Current Biology, as measure of how these ideas have spread.]

The nature of the support requested for the synthesis reflects the way I work. All my life in science I have been part of teams, in the field, in the lab, and writing collaboratively first with Val Nolan now deceased and with other colleagues, post-docs and students. Increasingly over time, I have become less the legs and more the agenda-setter and the coordinator. I believe it is a role I play well, and **what I propose is to work closely with current and former colleagues and students to produce a series of products that will document what we have learned and how we have learned it.** I will 1) write a multi-authored volume that will summarize past research, but far more importantly, have emergent properties to guide future research, 2) oversee the completion and sharing of a powerful, long-term (18-year) relational data base, 3) create a repository for data, metadata, and publications associated with the 'junco project' in Scholarworks, and 4) create broader impacts with electronic media to convey the excitement of the work to a range of audiences. I am the only one who can guide and make the final decisions, but to accomplish these ends I request the support of a team with diverse talents, some of which I lack. These team members have also been a critical source of the ideas, so a joint product is appropriate for that reason as well.

The avian genus *Junco,* also known as the snowbird, is a classic research

subject in two disciplines: **avian speciation** (Wright 1918, Miller 1941, Mayr 1942, Mila et al. 2007), **and avian seasonality** (Rowan, 1925). Co-consideration of these areas in a scholarly book will permit synthesis of two significant literatures that bear on the question of how populations respond to rapid environmental change and on the processes that generate biodiversity in nature. [Citations by author-date except for those listed under core articles, which are referred to in bold italic numbers].

The genus *Junco* currently consists of three recognized species, the volcano junco, the yellow-eyed junco and the dark-eyed junco, the third of which is the northernmost, most broadly distributed, and most diverse (Figure 1). The dark-eyed junco consists of five groups (classified as species until 1973) and 15 sub-groups (sub-species until 1973) that were originally identified by plumage, eye color and body size and that possess largely allopatric breeding distributions (Miller 1941, ***1***, Mila et al. 2007).

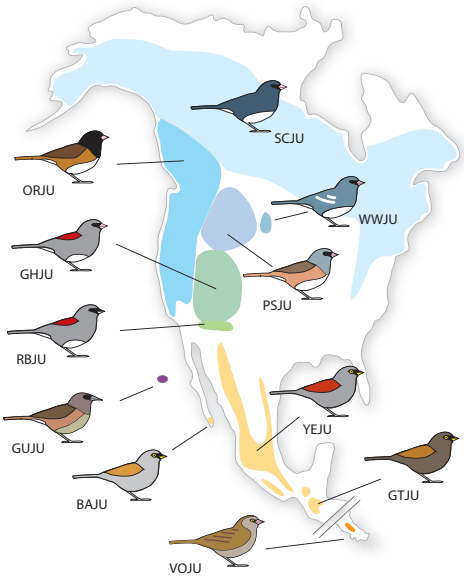

Figure 1 from Mila et al. 2007. Diversity in the avian genus junco. VOJU = volcano junco, YEJU = yellow-eyed junco in Guatemala (GTJU) Mexico YEJU) and Baja (BAJU). Dark-eyed juncos are Guadalupe junco (GUUU), red-backed junco, (RBJU), gray headed junco (GHJU), Oregon junco (ORJU), pink-sided junco (PSJU), white-winged junco (WWJU) and slate-colored junco (SCJU). I have studied juncos in Ontario, Indiana, Virginia (SCJU), South Dakota (WWJU) and southern California (ORJU).

In the classic view, the groups of juncos diverged in allopatry, perhaps during glacial advances, or even earlier (Kllicka et al. 1997), but recent research has shown that genetic divergence in North America may have occurred in as few as the past 10,000 years (Mila et al. 2007). Further, our own research is demonstrating rapid phenotypic divergence in southern California on the scale of decades (Yeh 2004, Price and Yeh 2008, **61**). Just 30 years ago, a population of juncos colonized the campus of the U of California San Diego, and when compared to a nearby population in the ancestral range at Mount Laguna, it has already diverged in plumage, body size, aggression, parental behavior, and immune function, and the variation observed persists in a common garden (Yeh 2004, ***61***). Thus, whether the dark-eyed junco is one species or more, its rate of divergence has been extremely rapid, and its degree of phenotypic and genetic differentiation requires explanation that the proposed book will address through synthesis.

One explanation the book will explore is the importance of migratory and reproductive timing in population divergence. Traditionally, avian species were defined by morphological measures that manifested in preserved specimens (Figure 1, Mila et al. 2007), and modern systematists measure genetic divergence with an array of tools that

have supplanted morphology. However, some of the critical traits leading to population divergence may not be gleaned from skins or sequences (at least not yet); and these relate to timing of population movements and reproduction (Winker 2010). In the case of the polytypic junco, some populations are sedentary, but many are migratory, exhibiting all degrees of movement from altitudinal to latitudinal, obligate to facultative, and partial to differential. The timing of migration varies geographically, and breeding dates also differ widely from north to south and along altitudinal gradients. **Importantly, however, many junco groups overlap in their winter distributions, and southern populations initiate reproduction while northern populations are still present, which has a significant implication**. Despite the opportunity to interbreed, timing mechanisms have apparently led to and maintain divergence. If we are to understand population divergence in this polytypic species, and other migratory species, then we need to understand not only differences in morphology and sequences, but also differences in physiology. Also missing from skins and sequences is behavior, and the role that sexual selection plays in initiating and hastening divergence. The synthesis proposed here will focus on the interaction of natural and sexual selection acting on physiology and behavior and the role of hormonal pleiotropy in allowing coordinated, rapid divergence.

Returning to the diverging junco populations in southern California, in just 30 years they have come to differ in their migratory behavior (sedentary in San Diego), in the timing of initiation and termination of reproduction (earlier and later in San Diego), and in the numbers of broods produced (more in San Diego). **Critically, the population-level phenotypic divergences in morphology, behavior, immune function and timing are all correlated with population divergence in the hormone testosterone (*61*).** The observations that 1) a single hormone coordinates the expression of numerous traits (hormonal pleiotropy) (***39***) potentially favoring phenotypic integration via correlational selection (***57, 58, 59***), and 2) that divergence in the hormone predicts population divergence (**61**) has enormous underappreciated implications for the nature of rapid adaptation to changing environments. The decades of research my group has conducted on numerous aspects of junco biology including the timing of migration, courtship behavior and mate choice, plumage variation, hormone-mediated trade-offs in life histories, and phenotypic integration, will allow a synthesis that can inform the junco's rapid divergence(s) and also be applied much more broadly.

New insights expected to emerge from the synthesis: In addition to a cohesive overview of findings to date, this synthesis will extend the utility of prior findings by providing an explication that will 1) emphasize the generality of findings on the junco, 2) focus on hormones as both a proxy for genetic pleiotropy, but also as an emergent property of pleiotropy adding a layer of understanding to the causes and consequences of selection on multiple traits; 3) stress how hormone-mediated phenotypic plasticity followed by genetic assimilation can give rise to evolutionary phenotypic divergence among populations that may – or may not – ultimately lead to speciation, and finally 4) explore the whole new landscape created by environmentally and hormonally driven variation in gene expression and phenotypic outcomes that relates to population divergence and will challenge and excite evolutionary biologists in the coming decade.

Relation of synthesis to Evolutionary Processes (EP) and Population and Community Ecology (PCE): This synthesis will help to inform topics included within the mission statements of both programs: (EP) "… investigations (that) attempt to explain causes and consequences of genetically-based change in the properties of

groups of organisms (at the population level or higher) over the course of generations, and particularly with respect to…selective pressures imposed by abiotic or biotic environments and the evolutionary responses to these pressures… phenotypic plasticity; life-history evolution, (PCE) "…conceptual or theoretical understanding of population ecology… [Projects that] promote synthesis across spatial and temporal scales …behavioral ecology…wide range of habitats and taxa across multiple spatial and temporal scales.

I. Results of Prior NSF Support
Junco-related grants in chronological order

NSF DEB 78-11982, 1978-80, $59,567 (with V. Nolan Jr.); NSF DEB 81-10457, 1981-1983, $47,000 (with V. Nolan Jr.); NSF BNS 83-15348, 1984-1986, $59,567 (with V. Nolan Jr.); NSF BSR 87-18358, 1988-1991, $215,512 (with V. Nolan Jr.), 2 REU supplements; NSF BSR 91-11498, 1991-1994, $250,000 (with V. Nolan Jr.); NSF IBN 94-08061, 1994-1997, $275,000, (with V. Nolan Jr.), 1 ROA supplement; NSF IBN 97-01334, 1997-1999, DDIG to J. Lipar, $9,600

NSF IBN 97-28384, 1998-2003, Using Hormones to Explore Adaptation and Constraint in a Male Bird, $360,000, (with V. Nolan Jr.), 2 supplements

NSF IBN 02-16091, 2002-2006, Sex Differences and Resemblances: natural, sexual, and correlated selection, $441,792 (D and I), 3 REU supplements

NSF DEB 02-00692, 2005-07, DDIG to J. McGlothlin, ~$11,000 (D and I)

NSF BSC-05-19211, 2005-2008, Testosterone in female songbirds: natural, sexual, and correlated responses to selection, ~$325,000 (D and I), 3 REU supplements,

NSF DEB-0808051, 2008-2010, DDIG to N. Gerlach, $10,000 (D and I)

NSF DEB-0808284, 2008-2010, DDIG to J. Atwell, $11,000 (D and I)

NSF IOS-0820055, 2008-2011, Hormones and phenotypic integration: comparing sexes, individuals, and populations, $570,000 (D and I, plus 2 $6,000 supplements)

NSF IOS-0909834, 2009-2011, DDIG to C Bergeon, Coordination of testosterone-mediated phenotypes and underlying endocrine mechanisms across divergent populations of the dark-eyed junco (J. hyemalis), ~$15,000 (D and I)

NSF IOS-0910036, 2009-2011, DDIG to K Cain, Androgyny & Androgens in Females: Relating Hormones to the Evolution of Sexual Dimorphism, ~$15,000 (D and I)

NSF IOS-1011145, 2010-2012, DDIG to D. Reichard, The function and speciation potential of short- and long-range song in dark-eyed juncos, ~$15,000 (D and I)

Research conducted by Ketterson, Nolan, colleagues and students, and supported by NSF since 1978, has resulted in a series of merit-reviewed articles not yet integrated into a single synthetic product.[1] According to web of science, 12/27/2010, a search under Ketterson ED identified 136 items. The range of citation frequency was 0-186, with 27 articles cited more than 50 times, 10 articles cited more than 90 times, and 7 articles cited more than 100 times and an h of 36. Of the 10 most cited articles, four appeared in *American Naturalist* (1st 1992, 4th 1999, 7th 2001, 8th 1992), one in *Ecology* (2nd 1976), two in *Proceedings Royal Society* (3rd 2000, 10th 1997), one in *Hormones and Behavior* (5th 1991), one in *Ibis* (6th 1996) and one in *Physiological Zoology* (9th 1977). Three of the most-cited papers have been synthetic in nature, which bodes well for the synthesis proposed here.

[1] A Birds of North America account on the dark-eyed junco has appeared (Nolan et al. 2001, see core article ***1***) but it was written to a preordained format and was not a concept-driven product.

Results of prior support have accumulated in two phases. **Phase I** was related to sex- and age-related variation in distance migrated, and adaptations to migration including restlessness, winter fattening, timing mechanisms, and dominance. I have recently returned to this topic in light of the impact of climate change on migration. **Phase II** continues as a long-term research program addressing the role of hormones in the evolution of trade-offs in life histories, adaptation and constraint, phenotypic integration, and population divergence.

Phase I.— In a series of papers that appeared between 1976 and 1985, recently added to in 2008 and 2010 (see core articles below), we studied differential migration in the junco, a form of migration in which distance migrated differs by sex or age. We found that females migrate farther than males, and that the migratory system is maintained by demographic trade-offs that differ by sex and age. Males experience greater mortality during winter, females during transit. The balance of viability, fecundity and sexual selection thus differs by sex, with earlier return to the breeding range of greater importance to males than females (sexual selection), and the benefit of avoiding colder climate and social competition during winter more important to females than males (viability selection). Related papers used common garden approaches to 'migratory restlessness' in captive males and females, and metabolic adaptations to winter climate (fattening) in free-living males and females deriving from different wintering populations. Sex and population differences are partly 'programmed' (maintained in common garden) and partly responsive to local environment. Most recently, we have learned that the recent milder winters have led to sex ratios that are less male-biased in the northern portion of the winter range, suggesting changes in winter distribution, relaxation of sexual segregation or both. The huge resurgent interest in adaptations to changing environments, particularly climate, has kept the earliest of these articles timely despite their having been written decades ago. In terms of the synthesis proposed here they demonstrate my long-standing interest in timing mechanisms and the importance of time spent in non-breeding environments to adaptation and population divergence.

Phase II.— Progress has been made in 5 stages. *The **first stage*** involved manipulation of male phenotypes in the junco through experimental elevation of testosterone (T). The goals were 1) to identify phenotypic characters that were enhanced, suppressed, or left unchanged by elevation of testosterone and 2) to determine the net effect of any alterations on fitness. We referred to this approach as phenotypic engineering. While acknowledging that many of the hormone's effects were probably indirect, we concluded that testosterone plays a key role in trade-offs between mating effort and parental effort and between reproductive effort and self-maintenance.

During *the **second stage*** we conducted similar studies on females with the goal of comparing the sexes for their sensitivity to testosterone in order to predict how co-evolution of the sexes might proceed. These studies indicated that many aspects of the female phenotype are similarly sensitive to T as in males, and that experimentally elevated testosterone can be highly costly to females. *The **third stage*** related individual variation in male testosterone to phenotypic characters that were identified as hormone-sensitive in the first stage. Variation was measured by the levels of testosterone released in response to stimulation of the hypothalmo-pituitary-gonadal axis (HPG) when challenged with gonadotropin releasing hormone (GnRH). The goals were 1) to quantify natural variation in testosterone and testosterone-mediated characters and 2) to explore how selection might build integrated phenotypes through

direct and correlational selection. We were able to relate natural variation in T to male fitness measured by viability selection, and we are applying the approach to females.

*The **fourth stage*** added a new dimension to the research by comparing testosterone levels across populations of juncos at new study sites in California and South Dakota. Here the goal was and is to enhance understanding of the role played by testosterone and other hormones in population divergence. The results from California referred to above have been submitted to *Science* because the findings are so startling and extremely exciting. The article, "Testosterone mediates rapid adaptation to a novel climatic regime in a passerine bird," **(61)** is led by Jonathan Atwell and is a collaboration with Trevor Price of the U of Chicago. It reports the multiple rapid changes following the establishment of a population of juncos in a novel, human-altered and climatically mild environment that have taken place in less than 30 years.

The California study reveals how the challenges faced by populations entering new environments can be overcome. Successful colonization of a novel habitat is expected to be difficult because so many different phenotypic adjustments are required simultaneously. We found that this problem can be 'solved' when multiple correlated

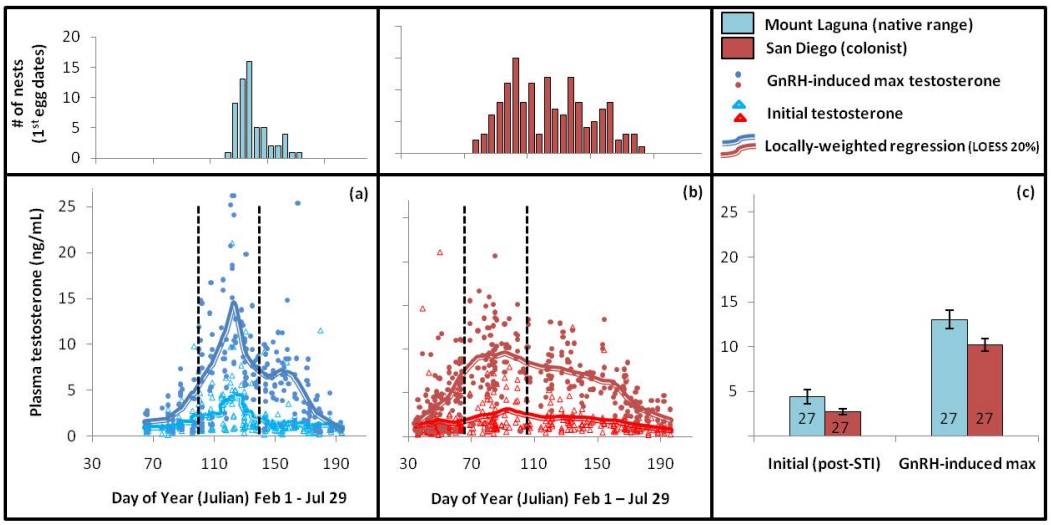

Figure 2. Seasonal and peak testosterone levels and breeding phenology in a native range and San Diego junco population. Initial and gonadotropin-releasing hormone (GnRH)-induced maximum plasma testosterone measured across the season at a) Mt. Laguna (native range; n= 88 males, 212 captures) and (b) San Diego (colonist; n= 95 males, 296 captures). The colonist population exhibits an extended but overall lower testosterone profile. (c) Histograms report hormone response to a 15-minute simulated territorial intrusion (STI) followed by a GnRH-challenge. Both initial (post-STI) and max (GnRH-induced) peak testosterone levels were lower in the colonist population. Top panels show breeding phenology (first laid egg dates for clutches of eggs) in each population. (**61**).

traits are organized by similar mechanisms, in this case, the hormone testosterone. The major findings (Figures 2 and 3) are: 1) that not one, but *multiple* traits changed rapidly, all in the directions predicted by a less seasonal environment and reduced peak testosterone levels, including a) increased investment in raising offspring, b) decreased investment into attracting mates, and c) increased immune defense in response to a higher pathogen load; and 2) that these changes are all along the same axis as the observed within-population trait correlations with testosterone seen in an ancestral population. If the traits were not organized in this way, the likelihood of successful colonization would have been reduced. This research is a compelling demonstration of

how range expansions and adaptation may be facilitated by previously evolved correlations among multiple traits mediated by a single physiological axis.

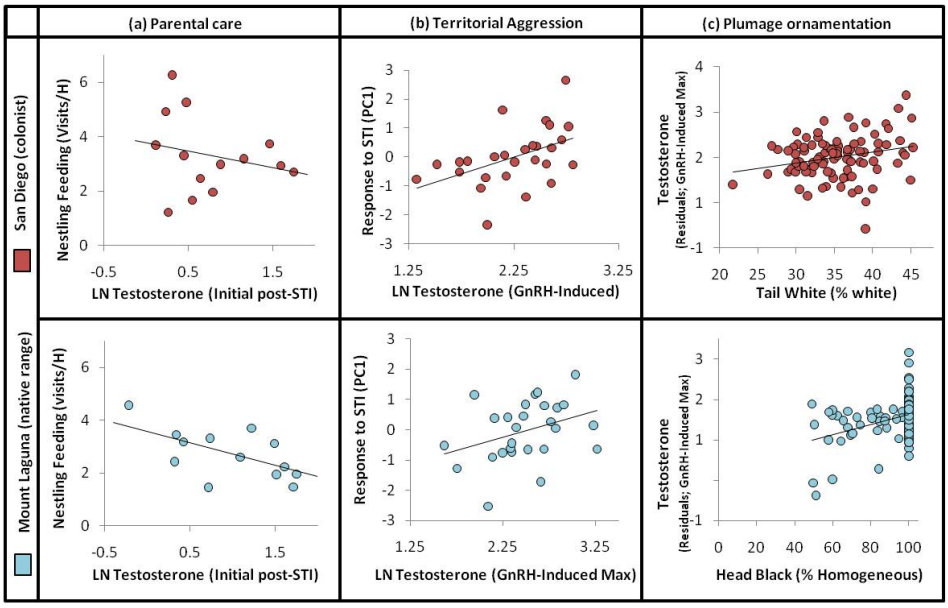

Figure 3. Covariation between testosterone and social behaviors and plumage ornamentation within both colonist and native range populations. Among males within both San Diego and Mt. Laguna populations, individual testosterone levels correlated negatively with (a) parental care and positively with (b) territorial aggression and (c) plumage ornamentation. (from ***61***).

The fifth phase of the research addresses phenotypic independence or variation in target tissue sensitivity to hormones and thus the capacity for hormone-mediated traits to evolve independently owing to the development of insensitivity to a hormone, when the ancestral condition was sensitivity. Current research is relating individual variation in behavior to circulating hormone levels to density of hormone receptors using quantitative PCR to quantify transcripts in neural tissue. Current research is also employing custom-made gene arrays from a junco transcriptome to measure the impact of experimental elevation of testosterone on gene expression. We are finding numerous differences in expression that relate to sex and/or testosterone in liver and brain. Inclusion of latest results in the synthesis will help guide future research directions for how to relate hormonal pleiotropy to the rate and direction of population divergence.

Core articles. The core articles are listed in their own section in References Cited under 11 topic headings, and are largely in chronological order. The topics are

1. The Dark-eyed Junco (***1***)
2. Differential Migration (***2-4***)
3. Adaptations to migration, restlessness, winter fattening, dominance, migratory timing (***5-19***)
4. Phenotypic engineering, phenotypic responses to hormonal manipulation in males and in females (***20-38***)
5. Phenotypic Engineering, relating phenotypic manipulations to fitness (***39-44***)
6. Adaptation, exaptation, and constraint (***45-46***)
7. Correlational selection, plumage variation (***47-50***)
8. Individual variation in hormones, phenotype and fitness (***51-56***)
9. Phenotypic integration (***57-58***)

10. Population divergence (***59-61***)
11. Miscellaneous: mating systems, maternal effects, extended phenotype, ecological processes, conservation (***62-66***)

Contributions to human resources.— Briefly Ketterson has advised or co-advised 17 post-doctoral students and 17 Ph.D. students, and is currently advising or co-advising 6 Ph.D. students.

II. Time management

The products described in section III will involve a team of people including PI Ketterson, two post-doctoral researchers to be supported by this award, Jonathan Atwell, and Nicole Gerlach, a librarian Eric Snajdr who will act as a consultant, collaborating evolutionary biologists to include Joel McGlothlin, Borja Mila, and Trevor Price, current post-doc Kim Rosvall, and current students, Kristal Cain, Dustin Reichard, Christine Bergeon Burns, Mark Peterson. With all these people I have a history of intellectual collaboration. Ketterson's teaching schedule for the coming year is light, and the OPUS project is a top priority. During fall 2011 my teaching assignment includes a graduate seminar in professional ethics for the bio-behavioral sciences and coordination of a graduate lab course that calls for a 1-week module on field methods. I am free of teaching in the spring semester, and I also have a free semester in 2011-2012. What I do not have is the data and media skills to complete all the products described here, which is why I ask to support two post-doctoral researchers, each for one year.

The 4 products (book, data base, archive, and media project/documentary) are described in the next section. Work on the book will begin in year 1 and be completed in year 2. Atwell and I will hold an organization meeting as soon as we have funding. Work on the other products is already underway and can be completed by the end of year 1. During the summer of 2011, Ketterson and team will visit field sites to fill in holes in the footage for a documentary, and during fall 2011, Atwell and Ketterson will work with web professionals to develop web-based supporting media. During this same period, we will screen draft versions of the documentary film products with focus groups, scientists on the one hand and public audiences on the other, and after refining content and scope, we will finish the first broadcast format documentary film pieces.

III. Plans for a well defined, widely accessible and disseminated set of products

The objective of this OPUS synthesis is to provide multiple integrated products to convey to breadth and depth of the 'junco project.' The core product will be (1) a book that will synthesize conceptual and empirical advances resulting from the extended research on the study species by Ketterson, colleagues, and students. Related products with broader impacts will consist of (2) a permanent archival web site for preservation, curation, and sharing of data and metadata; (3) continued expansion of an existing electronic data base that will lead to ongoing publication of research papers based on already collected data; and (4) a broader impacts media project that will consist of living maps, animated concepts, and multiple documentary film modules designed to appeal to a range of scholarly and public audiences.

Core product.— The core product of the synthesis will be a co-edited or authored volume (book) that will summarize research completed to date but more importantly will lay out implications of that research for understanding population divergence in the junco and other migratory species. The rationale was described in the introductory

paragraphs, and the results of prior support were designed to convey how the research path I have followed has led to a 'world view' reflected in the chapter outline for the book. The authors are collaborators and past and current post-docs and students whose research contributions hang tightly together in the framework presented here. This OPUS proposal provides a timely opportunity for a unique and exciting synthesis. Ben Roberts of Roberts Publishing Company has expressed strong interest in being the publisher (**Please see letter from Roberts in Supplementary Documents.**)

Contributors: Jonathan Atwell (Co-Editor), Christine Bergeon Burns, Kristal Cain, Nicole Gerlach, Ellen Ketterson (Co-Editor), Joel McGlothlin, Borja Mila, Mark Peterson, Dawn O'Neal, Trevor Price, Dustin Reichard, Kim Rosvall, Danielle Whittaker **(Please see Letters from Price, Mila, and McGlothlin in Supplementary Documents.)**

Proposed chapter topics for book

- Ecological Speciation – an overview - Price
- The junco - a classic subject of speciation studies in birds and of the role of day length in timing reproduction and migration – Ketterson and Atwell
- Migration in the junco – Atwell, O'Neal and Ketterson
- Understanding population divergence, a hormonal perspective
    - Co-expression of correlated traits, hormonal pleiotropy – Ketterson and McGlothlin
    - Correlational selection builds integrated phenotypes – McGlothlin and Atwell
    - Life histories and hormones, comparative insights - Ketterson
    - Life histories and hormones, manipulative studies – Ketterson and Cain
    - Life histories and hormones revealed through long-term study – Gerlach and Ketterson
    - Population divergence and hormones, comparing populations – Atwell, Whittaker, and Price
- A genetical view of population divergence in the avian genus junco – Mila
- A physiological view of population divergence in the avian genus junco – Ketterson, Rosvall, Bergeon-Burns
- A behavioral view of population divergence in the avian genus junco – Ketterson, Reichard, Rosvall
- A transcriptomic view of reproductive timing and population divergence in the avian genus junco – Ketterson, Peterson, Rosvall, Whittaker
- A research agenda for the future to include population genetics, physiology, behavior, and genomics – All contributors

Additional products.— The second product of the synthesis will be an electronic database that we will expand and refine as part of the synthesis and that will allow ongoing publication of research papers based on already collected data, first by our group and then by others through data sharing (**please see Data Management Plan).** The database currently consists of seven interrelated tables, and the proposal is to add existing data from other field sites (California and South Dakota). There are currently 14,508 individually marked dark-eyed juncos represented in an one of the tables and detailed information on every nesting attempt located by researchers (n = 3,395) in another. The table on blood samples (7, 090) contains information on every sample taken, including genotype by microsatellite analysis if available. The data base is the work of Nicole Gerlach for whom I am requesting support. Data as extensive as these from a naturally nesting, as opposed to box-nesting species, are extremely unusual.

The third product of the synthesis will be a permanent web site for preservation of data and metadata to be mounted on Scholar Works at Indiana University (http://scholarworks.iu.edu/) and internationally accessible. The site will contain archival data ready to share. Here the term 'data' is broadly defined to include not only traditional data, but also metadata such as proposals, annual objectives in the field, protocols, photos, video and sound files, and information on the current location of biological samples (DNA, blood, etc.). Thus the data and metadata will document the development and maintenance of a long-term field study as well as the results of the study, and will include information about people as well as publications and data still to be analyzed. The site is not a 'lab web site,' which we already have, nor is it intended to be glitzy. Rather the intention is to create a site that is permanent because it will be maintained over time by the Indiana University library in formats that keep up with changing technology and widely accessible. The key collaborator for this objective is Eric Snajdr who is a professional science librarian at Indiana University-Indianapolis (UPUI) and who worked on the junco project for 15 years. (**Please see letter of support from Snajdr** in Supplementary Documents). A prototype on which much remains to be done can be found at the first of these two links and an e-publication describing the goals of the scholar works site and the development of the collaboration with Snajdr entitled, "Data curation in avian ecology: a case study from both the scientist's and librarian's view," can be found at the second.
https://scholarworks.iu.edu/dspace/handle/2022/7911
http://docs.lib.purdue.edu/cgi/viewcontent.cgi?article=1001&context=iatul2010

The fourth product of the synthesis is a significant **broader impact** in the form of a media project designed to share the other products of this synthesis with both professional and public audiences. This product will enhance the infrastructure for research by facilitating collaborative networks and partnerships among researchers. This product should also serve as a model for efforts of others to communicate research and to archive and share data products and supporting materials. The goal is to create web-based audiovisual media that will serve as educational resources for professional, student and public audiences worldwide. In short, we will produce documentary-style film modules to highlight the results of research on the junco that will convey fundamental topics in ecological and evolutionary biology as well as in animal behavior, animal physiology, and songbird biology. We will also film methods for archival and teaching purposes. This product will include a "junco web portal" (www.juncopoject.org) that will host supporting audiovisual materials and archival data and research content alongside the film modules. When combined with the Scholarworks product, the web portal will allow access to audio recordings, photos, video clips, maps, primary and secondary publications, and data archives. During 2010, Ketterson, Atwell, a videographer, other team members (Bergeon Burns, Snajdr) and Borja Mila, made an expedition to film yellow-eyed and Guadalupe juncos in Guatemala, s. Mexico, and Guadalupe Island. We also obtained footage from the traditional field site in Virginia and the more recent sites in California and South Dakota, and interviews with conservation biologists from Mexico, activists for the teaching of evolution (Eugenie Scott), and key participants in the junco research (Ketterson, McGlothlin, Snajdr). We will have the advice of experts (**e.g., support letter from Roger Hangarter**). This project is far more developed than space allows here, but it requires my attention and that of a member of the team, Atwell, to be completed. I believe the impact will be enormous. For a preview see (www.juncopoject.org).