

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>).

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Nature of the research

I. NSF PROJECT SUMMARY (Ketterson and Nolan)

"Hormones and life histories: Exploring the Mechanistic and Functional Bases of Fecundity Trade-offs in a Male Bird"

Our primary objectives are to explore *in nature* the mechanistic bases for trade-offs in life-histories, as well as the evolutionary significance of phenotypic variation. We treat free-living male dark-eyed juncos (*Junco hyemalis*) with slow-release implants of testosterone (T) that maintain naturally occurring spring maximum levels of T for the entire breeding season. Controls receive empty implants. We then observe behavior, take physiological measurements, and monitor reproductive success and survival rates. We ask whether fitness of our experimental phenotype (T-males) is greater than, less than, or equal to that of controls (C-males).

We call this technique 'phenotypic engineering' and suggest that the engineering of hormonal phenotypes is a very useful way to determine when and how natural selection acts at the level of the organism. This is because hormones and their target tissues form an integrated whole. As the hormone increases or decreases, often in response to environmental stimulation, various targets are affected and traits appear and disappear as suites. Hence experimental treatment with hormones may increase fitness along some measures through its action on one or more traits, while simultaneously decreasing fitness by affecting other measures and other traits. It is only by considering the net effects of treatment on an array of hormone-dependent traits *and* a variety of fitness measures that we can hope to understand what maintains existing distributions of hormonal phenotypes.

Another important feature of phenotypic engineering with hormones is that the phenotypes created, while they may be rare or even absent in nature, are *possible*. That is, they arise in response to our application of a hormone, but they could occur naturally simply by alterations in secretion or receptors. Thus, it is of real interest to know why such phenotypes are not more common, and their rarity provides possible support for three different views of the maintenance of phenotypic variation. 1) If the fitness of an experimental phenotype is greater than that of controls, this suggests that existing phenotypes must be maintained by constraints; otherwise the experimental phenotype should replace the norm. 2) If the control phenotype is more fit than the experimental one, this suggests that optimizing selection maintains the norm. 3) Finally, if there is little difference in the fitness of different phenotypes, this suggests neutrality and soft selection.

In the research carried out at Mountain Lake we have continued our exploration of the phenotypic consequences for male juncos of treatment with testosterone, placing special emphasis on the trade-off between mating effort and parental effort. During the summer of 1994 we examined treatment-related differences in the extent of mate-guarding, response to nest predators, and indices of immune function (parasites and leukocytes). We also documented indirect effects that treatment of the male have on begging behavior of the young and explored temporal variation in fertility (sperm reserves) by counting and measuring sperm. With respect to fitness, we completed the data collection phase of our effort to document the effect of T on within- and extra-pair matings and to compare the frequency of extra-pair matings on our experimental study area with the frequency at control sites where no males are treated.

Once analyzed, these data will help to reveal how testosterone affects the weight males attach to stimuli that ordinarily elicit parental effort as opposed to mating effort, and the potential adaptive importance of flexible (natural) as opposed to fixed (experimental) hormone profiles. Because the trade-offs between mating effort and parental effort underlie the reproductive patterns of many animals, the work is significant because it contributes to our basic understanding of the organismal and environmental factors that affect reproductive decision making.

Professional presentations of work done at MLBS

Departmental seminars by Ketterson

1985: Yale University

1986: University of Virginia, Mountain Lake Biological Station

1987: Indiana State University; Bowling Green State University; Illinois State University

1988: Ohio State University; North Carolina State University; University of North Dakota

1989: University of Michigan; University of Illinois; Purdue University

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1991: University of Virginia, Mountain Lake Biological Station

1992: Virginia Polytechnic and State University; University of Missouri; Ohio State University; University of Kentucky

1993: Michigan State University; University of California, Irvine; Dartmouth College

1994: University of Arizona

Contributed papers presented at scientific meetings (list incomplete)(presented by Ketterson unless noted)

"Biparental Care in the Dark-eyed Junco: do males benefit?" presented June, 1985 (by Wolf) to the annual meeting of the Animal Behavior Society (ABS), Raleigh, North Carolina (with L. Wolf and V. Nolan).

"Biparental care in the monogamous Dark-eyed Junco: an experimental study" presented October 1985 (by Wolf) to the AOU, Tempe, Arizona (with L. Wolf and V. Nolan).

"Male parental care in the Dark-eyed Junco: An experimental study" presented June 1985 (by Wolf), XXth International Congress (IOC), Ottawa, Canada (with L. Wolf and V. Nolan) (poster).

"Does female choice enforce male parental care in the Dark-eyed Junco?" presented August 1987 to the International Ethological Conference, Madison, Wisconsin (with L. Wolf and V. Nolan) (competitive acceptance).

"Maternal behavior and the fate of broods after experimental removal of male dark-eyed juncos" presented (by Wolf) to the AOU, 1988.

"Testosterone and Corticosterone in breeding dark-eyed juncos" presented August 1989 (by Wolf) to the AOU, Pittsburgh, PA, 1989 (with L. Wolf, V. Nolan, A. Dufty, G. Ball, and C. Ziegenfus).

"Effects of Testosterone-implants on Male Parental Behavior and Female Tendency to Disperse after Nest Failure" presented to the AOU, Pittsburgh, PA, 1989 (with L. Wolf, V. Nolan, and C. Ziegenfus).

"Should selection favor male dark-eyed juncos with higher levels of testosterone?" to the 3rd International Conference of Behavioral Ecology, Uppsala, Sweden, 1990 (with V. Nolan and L. Wolf).

"Testosterone and male parental behavior," Winter Animal Behavior Conference, Park City, Utah, 1990.

"Testosterone and Avian Life Histories," Winter Animal Behavior Conference, Jackson Hole, Wyoming, 1991

"Effects of experimentally elevated testosterone on patterns of biparental care in the dark-eyed junco," presented (by Chandler) to the AOU, Montreal, Canada, 1991 (with C.R. Chandler, V. Nolan, and C. Ziegenfus).

"Testosterone and home range size in the dark-eyed junco," presented to 4th international Conference of Behavioral Ecology, Princeton, New Jersey, 1992 (with C.R. Chandler, V. Nolan, and C. Ziegenfus)

"Extra-pair paternity in the dark-eyed junco" presented (by Raouf) to the Animal Behavior Society, Seattle, Washington 1994 (with S.Raouf, P. Parker, T. Peare, V. Nolan).

Invited talks

"Winter Social Organization in Dark-eyed Juncos," presented at symposium entitled "Winter Social Organization," XX International Ornithological Congress, New Zealand, 1990 (with V. Nolan).

"Hormones and Life Histories: An Integrative Approach," presented at symposium entitled "Behavioral Mechanisms in Evolutionary Ecology," American Society of Naturalists, Hilo, Hawaii, 1991.

"Phenotypic Engineering: Using Hormones to Explore the Mechanistic and Functional Bases of Life-History Trade-offs," plenary address presented to the XXI International Ornithological Congress, Vienna, Austria, 1994

"Engineering phenotypes: An Experimental Approach to the Study of Phenotypic Variation," to be presented at Symposium on Experimental Ecology, American Society of Zoologists, St. Louis, Missouri, 1995

Publications and manuscripts based on work done at MLBS (i.e., some, usually most, of the data were collected at MLBS)

Wolf, L. 1987. Host-parasite interactions of brown-headed cowbirds and dark-eyed juncos in Virginia. *Wilson Bull.* 99:338-350

Nolan, Val Jr., E.D. Ketterson, and L. Wolf. 1986. Long-distance homing by non-migratory Dark-eyed Juncos. *Condor* 88:539-542

Wolf, L., E.D. Ketterson, and V. Nolan Jr. 1988. Paternal influence on growth and survival of dark-eyed junco young. *Animal Behaviour* 36:1601-1618

Sniegowski, P., E.D. Ketterson, and V. Nolan Jr. 1988. Can experience alter the avian annual cycle? Results of migration experiments in indigo buntings. *Ethology* 79:333-341

Ketterson, E.D. and V. Nolan Jr. 1990. Site attachment and site fidelity in migratory birds: experimental evidence from the field and analogies from neurobiology. *In*: Bird Migration, E. Gwinner (ed.). Springer Verlag, p. 117-129

Wolf, L., E.D. Ketterson, and V. Nolan Jr. 1990. Behavioral response of female dark-eyed juncos to the experimental removal of their mates: implications for the evolution of male parental care. *Animal Behaviour* 39:125-134

Ketterson, E.D., V. Nolan, Jr., L. Wolf, and A. Goldsmith. 1990. Effect of sex, stage of reproduction, season, and mate removal on prolactin in dark-eyed juncos (*Junco hyemalis*). *Condor* 92:922-930

Wolf, L., Ketterson, E.D., and V. Nolan, Jr. 1991. Female condition and delayed benefits to males that provide parental care: a removal study. *Auk* 108:371-380

Ketterson, E.D., V. Nolan, Jr., C. Ziegenfus, D.P. Cullen and M. Cawthorn. 1991. Attributes of yearling dark-eyed juncos that acquire breeding territories. *Proc. XX Inter. Ornith. Congress, Vol II*, 1229-1239

Ketterson, E.D., L. Wolf, C. Ziegenfus, A.M. Dufty, G. Ball and T. Johnsen. 1991. Testosterone and avian life histories: the effect of experimentally elevated testosterone on Corticosterone, body mass, and annual survivorship of male dark-eyed juncos. *Hormones and Behavior* 25:489-503

Nolan, V. Jr., E.D. Ketterson, C. Ziegenfus, D.P. Cullen and C.R. Chandler. 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on prebasic molt and survival in male dark-eyed juncos. *Condor* 93:364-370

Ketterson, E.D. and V. Nolan, Jr. 1992. Hormones and life histories: an integrative approach. *American Naturalist* 140:S33-S62

Ketterson, E.D., V. Nolan, Jr., L. Wolf and C. Ziegenfus. 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). *American Naturalist* 140:980-989

Chandler, C.R., E.D. Ketterson, V. Nolan Jr., and C. Ziegenfus. 1994. Effects of testosterone on spatial activity in free-ranging male dark-eyed juncos. *Animal Behaviour* 47:1445-1455.

- Ketterson, E.D. and V. Nolan, Jr. 1994. Hormones and life histories: an integrative approach. In: Behavioral Mechanisms in Evolutionary Ecology, L. Real, Ed., pp 327-353. University of Chicago Press, Chicago.
- Ketterson, E.D. 1994. Male parental behavior in birds. *Ann. Rev. Ecol. Syst.* 25:601-628.
- Chandler, C.R., Ketterson, E.D., Nolan, V. Jr. 1995. Roost site selection in dark-eyed juncos. *Condor* 97:279-282
- Ketterson, E.D., and V. Nolan Jr. in press. Phenotypic engineering: exploring the functional and mechanistic bases of life history trade-offs. *Proc. XXIst Intern. Ornith. Cong. (Vienna)*. *Ibis*
- Chandler, C.R., E.D. Ketterson and V. Nolan, Jr. MS. Experimentally elevated testosterone disrupts male-female cooperation in the biparental dark-eyed junco (*Junco hyemalis*). Submitted to *Behavioural Ecology*, in revision
- Parker, P.G., E.D. Ketterson, V. Nolan Jr., T. Peare, S. Raouf and C. Ziegenfus, and C.R. Chandler. MS. Genetic analysis of a monogamous bird indicates apparent sexual selection for males parental care. to be submitted to *Evolution*
- Christensen, L., Cawthorn, M., Ketterson, E.D., and V. Nolan Jr. MS. Effects of testosterone on corticosterone and corticosterone binding globulin in captive dark-eyed juncos (*Junco hyemalis*). to be submitted to *General and Comparative Endocrinology*
- Cawthorn, M., Ketterson, E.D., Christensen, L., and V. Nolan Jr. MS. Effects of testosterone on body mass, locomotor activity, song, and sperm counts in captive dark-eyed juncos (*Junco hyemalis*). To be submitted to *Hormones and Behavior*

Students who trained with Ketterson and Nolan at MLBS

Postdoctoral Students:

Wolf, Licia	1988-89
Chandler, C. Ray	1989-92
Cawthorn, Michelle	1989-92
Enstrom, David	1992-94

Ph.D. Students:

Wolf, Licia	1982-88
Raouf, Samrrah	1988-
Titus, Russ	1990-

M.A. Students:

Sniegowski, Paul	1984-88
Christensen, Lori	1993-94 (switched to School of education)
Kast, Tracey	1993-

Undergraduate students (only since 1989)

Cullen, Dan (REU, U. of Illinois)	1989, summer
Tavel, Mike (REU, Wesleyan Univ.)	1989, summer
Callahan, Larry (REU)	1990-91

Sanam Radej (REU)	1990-91
Christensen, Lori	1992,summer
Morris, Dana (REU, U. Missouri)	1993, summer
Hill, Jennifer (REU, Purdue University)	1993, summer
Gonzalez, Gigi (RTG, U. Texas)	1994, summer
Steele, Jennifer (HHMI)	1994, spring, summer
Soenksen, Michelle(REU, Calvin College)	1994, summer