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Behavioral and Physiological Differences in Migratory Strategies of a Long-distance Migrant, the Blackpoll Warbler, and a Facultative Short-distance Migrant, the Yellow-rumped Warbler

Rebecca L. Holberton
Principal Investigator; University of Maine, Orono

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Principal Investigator: Holberton, Rebecca L. **Award ID:** 0196091

Organization: University of Maine

Title:

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Project Participants

Senior Personnel

Name: Holberton, Rebecca

Worked for more than 160 Hours: Yes

Contribution to Project:

Post-doc

Name: Voltura, Karen

Worked for more than 160 Hours: Yes

Contribution to Project:

Dr. Voltura was a full-time post-doctoral assistant who helped collect hormone and behavioral data in the field (Churchill, MB, and Maine) and in the laboratory (Mississippi) during the first year of the project in Mississippi. She also learned to run the radioimmunoassay procedures to run the plasma steroid hormone samples as well as the colorimetric assays for running the plasma metabolite samples. Karen also assisted with a laboratory study on migratory feeding and fattening in the two warbler species held in captivity.

Graduate Student

Name: Wilson, Charles

Worked for more than 160 Hours: Yes

Contribution to Project:

Morgan was funded for two years as a full-time doctoral student graduate assistant at the University of Mississippi. He worked directly on this project in the field at Churchill, MB, and at Maine during the first two years when I was based at the Univ. of Mississippi. He also worked full-time on the laboratory studies done in captivity. He helped set up the field sites, collect blood samples for hormone and metabolite analyses, and played an integral role in running the feeding and fattening studies on captive birds in the laboratory. Morgan also assisted in running the radioimmunassays for plasma steroid analyses. His contribution has warranted co-authorship on several presentations at national meetings and several manuscripts to come from this and several related projects. Morgan has been a tenure-track faculty member in Virginia since 2003.

Name: Perkins, Deborah

Worked for more than 160 Hours: Yes

Contribution to Project:

Deborah (as a Master's student at the University of Maine) worked full-time on the project as a graduate assistant during the first full year after the project was moved to the University of Maine. Deborah assisted in field work at Churchill, MB, and in Maine. She also assisted with the feeding and fattening studies on warblers held in captivity. Her contribution has warranted co-authorship on several presentations at national meetings and at least one manuscript to come from the project. She will defend her thesis, an offshoot of this project, in August, 2004.

Name: Long, Jennifer

Worked for more than 160 Hours: Yes

Contribution to Project:

Jennifer (as a doctoral student at the University of Maine) worked full-time on the project as a graduate assistant during the first full year after the project was moved to the University of Maine. Jennifer assisted in field work at Churchill, MB, and in Maine. She also assisted in the laboratory studies on migratory feeding and fattening and with the radioimmunoassays for plasma hormone studies. Jennifer also set up and revised the assays we use for the plasma metabolite studies. Her contribution has warranted

co-authorship on several presentations at national and international meetings and several manuscripts that have come from the project. Jen has also been first author on several published papers related to this project. She has developed a doctoral dissertation project directly related to some of the questions outlined in this study.

Name: Hunter, Meredith

Worked for more than 160 Hours: Yes

Contribution to Project:

Meredith first worked on the project for research credit while as an undergraduate at the University of Mississippi. She assisted with the field work at Churchill, MB in 1999. She later joined my lab as a doctoral student in Maine after I moved to Maine. Meredith was funded as a full-time graduate research assistant for a year in Maine. She worked at Churchill, MB, on the project for three summers and assisted in the fall field work in Maine. She completed a master's degree at the University of Mississippi. She also assisted with the studies on feeding and fattening in captive birds and helped run hormone assays until she left graduate school in Maine to pursue a career as a vet technician back home in Louisiana. Her contribution has warranted co-authorship on several presentations at national meetings and at least one manuscript to come from the project.

Name: Cash, William

Worked for more than 160 Hours: No

Contribution to Project:

Ben (as a doctoral student at the University of Mississippi) assisted for several years in the feeding and fattening studies on captive warblers during the first two years of the project in Mississippi. Ben also assisted in running radioimmunoassays. He was not paid off of the grant as he had his own funding. However, some of his doctoral work was integrated with this project's activities. His contribution has warranted co-authorship on several presentations at national meetings and at least one manuscript to come from the project. Ben has also been first author on several published papers related to this project. He has not been funded directly on this project. Ben has been a tenure-track faculty member since 2000.

Name: Sims, Christopher

Worked for more than 160 Hours: No

Contribution to Project:

Chris (as a doctoral student at the University of Mississippi) assisted the project during the first two years it was based in Mississippi. Chris helped maintain birds in captivity and helped with data collection on the feeding and fattening studies with captive birds. He also assisted in running the steroid hormone assays. His contribution has warranted co-authorship on several presentations at national meetings and at least one manuscript to come from the project. Chris has also been first author on several published papers related to this project. He has not been funded directly on this project. Chris has been a tenure-track faculty member since 2003.

Name: Johnston, Jason

Worked for more than 160 Hours: No

Contribution to Project:

Jason (as a doctoral student at the Univ. of Maine) has been instrumental in helping with the Maine field studies for this project. He has helped capture birds for captive studies on feeding and fattening and has collected a lot of the blood samples from free-living birds during migration. He has not been funded directly on this project. Jason is currently working on his doctoral dissertation focussing on a topic related to this project.

Name: Horton, Brent

Worked for more than 160 Hours: No

Contribution to Project:

Brent (as a doctoral student at the Univ. of Maine) has helped collect field samples from free-living warblers in Maine and has also helped with some of the captive studies on feeding and fattening. He has not been funded directly on this project. Brent has developed a doctoral dissertation project indirectly related to many of the questions outlined in this project.

Undergraduate Student

Name: Lee, Anthony

Worked for more than 160 Hours: No

Contribution to Project:

As an undergraduate (at the University of Mississippi) working for independent study credit, Tony helped with field work in Churchill, MB, and with some of the laboratory studies in Mississippi. He did several undergraduate research projects indirectly

related to some of the questions outlined on this project. After one year as a Master's student in my laboratory at Mississippi, he was accepted to dental school.

Name: Desjardins, Christopher

Worked for more than 160 Hours: No

Contribution to Project:

As an undergraduate at the University of Maine working on an independent research project, Chris helped with several feeding and fattening studies on migratory birds in captivity. He assisted in sample collection and bird care. Chris graduated from the University of Maine and is now applying to several graduate programs in behavioral ecology/endocrinology.

Name: Dietz, Joseph

Worked for more than 160 Hours: No

Contribution to Project:

As an undergraduate student at the University of Maine, Joe assisted in field work at Churchill, MB, in 2002. He helped set up mist nets and capture birds for hormone studies while also setting up his own independent study project on Arctic wolf den ecology, in collaboration with Michelle LeClair (see below). Joe (and Michelle) also gave a seminar about the warbler project to the ElderHostel group visiting the Churchill Northern Studies Centre, and another seminar on their fox ecology to the University of Maine community.

Name: LeClair, Michelle

Worked for more than 160 Hours: No

Contribution to Project:

As an undergraduate student at the University of Maine, Michelle assisted in field work at Churchill, MB, in 2002. She helped set up mist nets and capture birds for hormone studies while also setting up her own independent study project on Arctic wolf den ecology, in collaboration with Joe Dietz (see above). Joe and Michelle also gave a seminar about the warbler project to the ElderHostel group at the Churchill Northern Studies Centreand another seminar about their fox ecology project to the University of Maine community.

Technician, Programmer

Other Participant

Name: Winslow, Eleanor

Worked for more than 160 Hours: No

Contribution to Project:

Mrs. Winslow, a 75 year-old birding enthusiast, had heard of the NSF-funded warbler project and expressed a desire to work as a volunteer field assistant at Churchill. She is an active member of several birding organizations and travels the world on many bird tours. She has also volunteered at the Manomet Bird Observatory in Massachusetts for many years. I was able to support her room and board on a 'matching funds' grant through the Churchill Northern Studies Centre while she helped collect data on free-living warblers migrating through the Churchill area for the NSF-funded project.

Research Experience for Undergraduates

Organizational Partners

Churchill Northern Studies Centre

The Churchill Northern Studies Centre, through the Canadian Northern Research Fund, provided matching support for room and board, vehicle rental, and laboratory space, through a competitive award application process each year. They also provided support for fuel and a cash award for research supplies through the NRF program. The CNSC-NRF awards totaled CD$22,846.00 (~ US$17,000.00) and their support was critical to the success of the project.

University of Maine

The University of Maine Office for Excellence in Teaching awarded me $485.00 for support materials (bug suits, books, etc.) needed to take UMaine undergraduates Joe Dietz and Michelle LeClair to Churchill to work on the project in 2001. The UMaine Department of Biological Sciences also provided $3, 350.00 to support travel and research costs for these students to work on the project.

Eagle Hill-Humboldt Field Research Inst

Eagle Hill-Humboldt Field Research Institute in Steuben, Maine, in Washington County, has allowed me and my crew to use the site, situated on a peninsula along the Maine coast, to catch Blackpolls and Yellow-rumped warblers during fall migration. The Institute is situated in an area used by migratory birds during autumn migration. The Institute provided housing and bench space needed to process blood samples for storage. They also provided a secure indoor area in which to house birds until they were transferred to the University of Maine for studies in captivity.

Other Collaborators or Contacts

During the project period, I developed many collaborations with researchers outside my home institutions. Most of these are ongoing and thus far have resulted in several presentations at national and international meetings, published manuscripts, and a book chapter. Some of these activities have also provided opportunities for undergraduate and graduate students to gain experience in field and laboratory techniques.

These include

A. Dr. Frank R. Moore at the University of Southern Mississippi, and Dr. Roland Sandberg and his graduate student, Mare Lohmus, at the University of Lund in Sweden. These collaborations involved several related projects in which we investigated relationships between energetic condition, migratory state/orientation, and corticosterone secretion. These studies added greatly to our understanding of how the two focal warbler species in the NSF-funded project fit into the 'big picture' of migration strategies and environmental constraints on them. Publications thus far from these collaborations with Drs. Moore and Sandberg include:

1. Holberton, R.L., Marra, P.P. and Moore, F.R. 1999. Endocrine aspects of physiological condition, weather and habitat quality in landbird migrants during the non-breeding period. In Proceedings of the 22nd International Ornithological Congress, (N. J. Adams and R. H. Slotow, Eds), pp. 847-866. Johannesburg, South Africa: BirdLife South Africa.

2. L§hmus, M., Sandberg, R., Holberton, R. L. and Moore, Frank R. 2003. Corticosterone levels in relation to migratory readiness in Red-eyed vireos (Vireo olivaceus). Behavioral Ecology and Sociobiology 54:233-239.

B. Dr. Peter P. Marra, at the Smithsonian Environmental Research Center, and I have been collaborating on the ecological physiology of migrants on the wintering grounds for several years. We are collaborating on several projects investigating winter habitat effects on overwintering success in several areas in Central America, Mexico and the Caribbean. We have published several manuscripts thus far including publication #1 above and #3 below:

#3: Marra, P. P. and Holberton, R.L. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. Oecologia: 116:284-292.

Dr. Marra and I are preparing the results of our studies on relationships between winter habitat quality and overwinter survivorship in migratory birds in Belize and Mexico. These results have been presented at a recent international meeting (August, 2004 - American Ornithologists' Union meeting in Quebec City) and are being prepared for publication. We are preparing a proposal to the National Science Foundation to look further at winter ecology and physiology of migratory birds with respect to spring departure schedules and breeding success.

C. Dr. David Mizrahi, now with New Jersey Audubon, Cape May Bird Observatory, and Dr. Sidney Gauthreaux, Jr., Clemson University, and I collaborated on a study investigating patterns of corticosterone secretion during spring migration in sandpipers. This study, in conjunction with our work on warblers, contributed to our understanding of the ecophysiological aspects of how migratory birds with different migration strategies meet their energy demands. This collaboration study resulted in the following publication:

#4:Mizrahi, D., Holberton, R.L. and Gauthreaux, S.A., Jr.. 2001. Plasma corticosterone and adrenocortical stress response in Semi-palmated Sandpipers, Calidris pusilla, at a major stopover site during spring migration. The Auk 118:79-91.

D. Dr. Kenneth P. Able, State University of New York at Albany (my former doctoral advisor) continues to collaborate with me on migration-related projects. We collaborated on a study looking at patterns of corticosterone secretion associated with differential migration patterns, resulting in the publication:

#5:Holberton, R.L. and Able, K.P. 2000. Latitudinal differences in the corticosterone stress response in winter: endocrine constraints on wintering capabilities and implications for differential migration in the Dark-eyed Junco. Proc. Royal Soc. 267:1889-1896.

E. I was asked to contribute to a symposium and a chapter to the Birds of Two Worlds Volume organized by Marra and Greenberg at the Smithsonian Environmental Research Center. I collaborated with Dr. Alfred M. Dufty, Jr., at Boise State University, on writing the chapter for the book that has resulted from the symposium (publication #6).

#6:Holberton, R.L. and Dufty, Jr., A.M. 2004. Hormone Patterns and Variation in Life History Strategies of Migratory and Non-migratory Birds in Birds of Two Worlds: The Ecology and Evolution of Migratory Birds (Marra, P. and Goldberg, R., Eds.), Johns Hopkins Press.

F. Through the activities of this NSF-funded project, I continue to collaborate with Dr. Joseph M. Wunderle, and his student, Edgar Vasquez, at the International Institute of Tropical Forestry, U.S. Forest Service in Puerto Rico on a project looking at the ecophysiology of winter habitat (shade versus sun coffee) on overwintering success in Black-throated Blue warblers. This graduate thesis project is ongoing. Hormone samples from the 2003-4 winter season have been analyzed in my laboratory and more samples are currently being analyzed for plasma corticosterone concentration. By extending our findings from the Blackpoll/Yellow-rumped warbler project to other migratory birds, we continue to develop a more thorough understanding of how migratory birds regulate energy reserves with respect to different ecological factors.

G. Recently (August, 2004), the US Fish and Wildlife office at Petit Manaan Wildlife Refuge in Maine, approached me about a study to look at indicators of breeding success and chick survival in seabirds (primarily Arctic, Common, and Roseate terns) breeding in the Gulf of Maine. We are developing a project to look at several indicators of reproduction and growth in Maine's breeding populations of these species (some of which are listed as 'of concern' or 'threatened' in Maine). The project is scheduled to begin in May, 2005.

H. I have had numerous contacts with many scientists outside my institution and outside the United States (these include Germany, Sweden, Argentina, the United Kingdom - Scotland, France, and Canada) who have expressed interest in various hormone-related collaborations, as a direct result of the activities of this project.

I. I have also collaborated with Dr. John Cockrem at Massey University in New Zealand on hormone studies related to several endangered species programs including the Kakapo Recovery Program.

J. I have been contacted to provide expertise about hormone analyses, hormone manipulation methods, and experimental design to numerous colleagues at many institutions including University of Missouri, University of Washington, University of Iowa, Cornell University, and the CEBC - CNRS in France. Several of these contacts have developed into collaborations on the endocrine basis of bird migration and breeding success.

K. I serve on the Steering Committee for the NSF-RCN (#0342242) Research Coordination Network: Integrating Ecology and Endocrinology in Avian Reproduction, with John C. Wingfield as PI.

L. As a result of our findings, I have recently developed a collaboration with Maine's Inland Fisheries and Wildlife department on a study of black bear hibernation ecology and physiology, which has become a doctoral dissertation project by one of my new doctoral students.

Activities and Findings

Research and Education Activities:

The primary focus of these studies has been to investigate the functional role of corticosterone in the development of migratory condition (i.e. hyperphagia, lipogenesis, and migratory restlessness) and to investigate the underlying endocrine mechanisms of migratory condition in two species that differ dramatically in their strategies for reaching their wintering grounds. The main approach has been to measure and to manipulate the peripheral signal molecule, corticosterone, and look at the resulting patterns of feeding behavior, body mass and fat reserves, migratory activity, and metabolites of energy use (fat deposition and protein use). In the comparative component, the Blackpoll warbler (Dendroica striata) was selected as the model for a long-distance migrant to be compared with its closely related and co-occurring congener, the Yellow-rumped warbler (D. coronata). Both species were sampled for plasma hormone and metabolite levels at two field sites representing two different stages in autumn migration. Free-living birds were sampled at Churchill, Manitoba, where both

species breed and pass through the area early on migration on their way further south and east. At that stage of migration, both species have similar energetic needs as they travel overland and are able to rest and replenish energy reserves along the way. However, at the second field site in coastal New England, both species co-occur in the same habitats but are preparing for the continuation of their journeys to their respective wintering grounds. In the northeastern United States, Blackpolls can double their body mass in fat reserves to prepare for a trans-oceanic, non-stop journey of 3-5 days over the North Atlantic to reach their wintering grounds in South America. In contrast, Yellow-rumped warblers will continue overland until they reach their wintering grounds in the southern United States. While some may cross the Gulf of Mexico to winter in Mexico, the journey can be reached in less than 20 hours. The objective of this part of the study was to compare seasonal changes in baseline corticosterone and the adrenocortical response, and plasma metabolite levels within and between the two species during the initial/early stage of migration where the species have similar migration strategies (Churchill), and during the latter stage where the two species diverge in their migration strategies and energy needs (coastal Maine).
The entire project was divided into four major questions. These were:

Questions #1 and #2: In earlier laboratory and field studies, we had found that baseline corticosterone often rises during the migratory period. However, while this change in corticosterone has been positively correlated with a change in fat deposition, the actual role that corticosterone plays in these events has been unknown. To investigate the functional role of corticosterone during migration, we asked,

Question #1: Can birds develop migratory hyperphagia and fattening when the rise in baseline corticosterone is prevented? Question #2: If corticosterone is necessary, are its effects on migratory condition dose-dependent? This aspect is important to consider when trying to understand how these characteristics may be regulated. In an earlier study (Holberton 1999), I proposed that, as with mammals, responses to various levels of corticosterone have different physiological effects on energy reserves (fat anabolism at low-intermediate levels, protein catabolism at high levels) in migratory birds. If migrants express dose-dependent effects of corticosterone and if these effects change as a function of migratory state, they may be regulated through changes in the two main glucoocorticosteroid receptor types found in mammals and birds. One of the main objectives in the present study was to set the stage for future research on cellular level mechanisms of energy regulation in migratory birds.
The glucocorticosteroid agonist, Dexamethasone, had been found in earlier studies to effectively inhibit endogenous corticosterone via negative feedback on the hypothalamic-hypophyseal-adrenal axis in birds while not eliciting glucocorticosteroid effects on peripheral tissue. Dexamethasone (DXM) has since become an important tool in our studies manipulating endogenous corticosterone levels. In this project, we used different doses of DXM to manipulate endogenous corticosterone to ask if corticosterone is necessary for the development of migratory condition and, if so, does it work in a dose-dependent manner. We had initially planned the
first experiment (1 treatment group with one dose of DXM that completely inhibited endogenous corticosterone to compare with a saline-injected control group) to be done in captive Yellow-rumped warblers but the birds that had been captured in Maine and transported to Mississippi in 1999 began to exhibit the symptoms of salmonella contamination, which
was later confirmed by Dr. Ward Stone, the wildlife pathologist for New York State. Maine had experienced a salmonella outbreak in the wild songbird populations the previous 1-2 years and it is believed that our birds came in with the bacterium acquired in the field. We were directed to euthanize all of the birds immediately as they were not responding to the prescribed antibiotic treatments and would contaminate wild populations in Mississippi if released. After

decontaminating the bird facilities in Mississippi, we set up the experiment using a comparable short-distance migrant, the Dark-eyed Junco (Junco hyemalis).
A second study, again with Juncos, incorporated 2 additional treatment groups in which DXM was delivered in intermediate doses, with the goal being to have a 'no corticosterone' group, a 'low corticosterone' group, an 'intermediate corticosterone' group, and a control, 'endogenous corticosterone' group. In both studies, the birds were maintained in individual cages with free access to food. Daily food intake, body mass, and fat score were measured regularly as the birds experienced the transition from short (winter) day photoperiod to long-day (spring) photoperiod. Blood samples for baseline corticosterone and (in the second experiment only) plasma triglycerides were taken at key times during the study. This study was repeated using Yellow-rumped warblers after the project was moved to Maine.
In the original proposal, similar injections of DXM or saline had been proposed at each of the two field sites in birds captured on passage and held for 2-3 days in captivity. The objective of this part of the study was to provide some supplemental information about the effect of inhibiting corticosterone on short-term changes in body mass and fat in birds on migration. However, this was abandoned because of the problems that the Polar bears, which congregate at our site in Churchill during that time of year, caused with our holding facilities. In spite of our failure to perform these short-term studies, I feel that they would have been redundant and would add little if anything to the overall study.

In a third study, in which we wanted to use a different method to get at Question #2, we attempted to expose birds to different levels of corticosterone by first treating them with high levels of DXM to inhibit endogenous corticosterone and then administering different levels of exogenous corticosterone to the three treatment groups (low, medium, and high corticosterone exposure) and a saline-injected control group. This pilot study was done, after moving the project to the University of Maine, using on Dark-eyed juncos and Yellow-rumped warblers, but was abandoned after preliminary trials indicated physiologically aberrant and huge variation in plasma corticosterone levels produced by our injections. While this study seemed redundant in its objectives, I felt it was worth pursuing if it provided us with a more reliable way of producing different and physiologically relevant ranges of corticosterone in the plasma. However, it did not.

Question #3: Earlier studies in our laboratory and elsewhere have reported that the acute adrenocortical response to capture and handling is often reduced during migration, presumably to reduce exposure of the individual to the potentially dangerous/catabolic levels of corticosterone during migration when protein reserves should be conserved. However, many birds are observed to have extremely high levels of corticosterone during migration, suggesting that the reduction of the corticosterone response can be overcome to allow birds facing extremely challenging conditions with little or no fat reserves left, to access skeletal muscle protein. In order for birds to utilize higher levels of corticosterone under extreme conditions, adrenocortical tissue may retain the ability/capacity to produce corticosterone as needed. In this part of the study, we planned to ask if the adrenocortical tissue retained the same sensitivity to adrenocorticotropin hormone (ACTH) during migration as it does during the non-migratory period. To do so, birds were to be first treated with DXM to inhibit the endogenous production of ACTH leading to corticosterone secretion that would compound our observations, and then challenged with an injection of exogenous ACTH to measure the subsequent response via endogenous corticosterone secretion. As mentioned, unfortunately, the birds planned for this work had to be destroyed due to their exposure to salmonella. Further, recent work by me and other researchers on several sparrow and warbler species (including Dark-eyed juncos and Dendroica warblers) have now shown that the variation in expression of the adrenocortical response is controlled at the level of the pituitary, although it is still unknown if migrants utilizing different levels of corticosterone maintain different levels of adrenocortical sensitivity and future work should pursue this

question further.

Question #4: What are the behavioral and physiological differences between Blackpoll and Yellow-rumped warblers that may contribute to differences in migratory fattening?

We asked -
- 4A) Do Blackpolls have greater food intake than Yellow-rumped warblers?
- 4B) Do Blackpolls have greater rates of fat deposition?
- 4C) Do Blackpolls maintain higher corticosterone levels and/or lipid metabolite levels that could influence or reflect greater food intake and lipogenesis?
- 4D) Do Blackpolls differ in their diet in such a way as to facilitate greater fat deposition?

Some of these questions were addressed in the laboratory under controlled conditions while some were addressed in free-living birds.

We set up a monitoring site at Churchill (July-August, 1999, 2000, 2001, and 2003) and in Maine (1999, 2000, 2001, 2002) where we measured fat reserves, body mass, and plasma corticosterone and metabolite levels in both species (100-200 individuals of both species) captured by mist nets.
We had expected to use Poulin and Lefebvre (1995) method of collecting diet samples by making the birds regurgitate in response to a tartaric emetic. However, in initial trials in the laboratory where we could monitor the birds' response to the treatments, we observed 100% mortality (n = 7), even when we cut the suggested dose by 1/2 and then 1/2 again. Since this time, other researchers have reported similar results and I now feel that we made the right decision to not go on with the use of the emetic. However, we did collect fecal samples, preserved in 30% EtOH, from birds captured at both sites. Such samples provide information about major arthropod food items ingested by the birds.

We captured both species at Steuben, Maine in September- October, 1999, and transported them to Mississippi. We maintained them in the laboratory and monitored changes in body mass, fat reserves, food intake, migratory activity (Zugunruhe), and plasma corticosterone and triglyceride levels (corrected for free glycerol) at key times during the pre-migratory/migratory period.

The field and laboratory activities associated with this project have been disseminated ina variety of ways to an equally diverse audience. In addition to peer -reviewed publications and presentations at professional meetings, the project has been featured in several public interest media. These include two articles published by the University of Maine and the California Academy of Sciences (also featured on the internet) 'Survival of the Fittest - and the Least Stressed' by Margaret Nagle, UMaine Today, pp 11-14, Sept./Oct., 2002, http://www.umaine.edu/research/UMTSurvival.htm; and 'Fit and Fat' by Kathleen M. Wong, California Wild - California Academy of Sciences, pp 4-5, Fall, 2003, http://www.calacademy.org/calwild/2003fall/stories/horizons.html.

Major presentations at professional meetings and by invitation at institutions:

Invited Plenary Presentations

(2004) Geneva Sayre Lecture Annual Lecture Series for Women in Science. Russell Sage College, Troy, New York

Invited Symposia Presentations

(2003) 'Exploring the Nature of Diversity in Migration Strategies - North and

South', Symposium on Austral bird migration, Neotropical Ornithological Congress, Puyehue National Park, Chile

(2002) 'The Role of Corticosterone in Migratory Feeding, Fattening and Orientation' , Symposium 'Physiological Ecology of Migration: How to Feed, Fast, and Fly en route', North American OrnithologistsÆ Conference, New Orleans, LA, (J. Long and R. Sandberg, co-authors)

(2002) 'When, Where and How to Go: Endocrinology of a Transitional Lifestyle', Birds of Two Worlds symposium hosted by the Smithsonian Institution, Smithsonian Environmental Research Center, Washington, D.C.

(2000) 'Corticosterone and Changes in Energy Demand in Migratory Birds', Winter Animal Behavior Conference, Jackson Hole, WY

(1998) 'Endocrine Aspects of Habitat Quality and Energy Demand in Landbird Migrants', Symposium on Stopover Ecology of Landbird Migrants, XXII International Ornithological Congress. Durban, South Africa, (P.P. Marra, co-author)

Related Papers Given at Professional Meetings

(2004) 'Potential Consequences of Failing to Show an Adrenocortical Response to Stress'. American OrnithologistsÆ Union, Quebec City, Quebec. (presented by C. M. Wilson, R. L. Holberton, co-author)

(2004) 'Across- and Within-Season Adjustments in Hematocrit, Corticosterone Secretion, and Energy Reserves in North American Migratory Songbirds'. American OrnithologistsÆ Union, Quebec City, Quebec. (B. Horton, J. Johnston, J. Long, D. Perkins, S. Wilder, and W. Wright, co-authors)

(2002) 'Patterns of Corticosterone Secretion Vary with Energetic Condition in Hermit Thrushes During Autumn Migration' North American OrnithologistsÆ Conference, New Orleans, LA. (J. Long, co-author)

(2002) 'Sex Differences in the Adrenocortical Stress Response of Incubating Ruddy Turnstones'. Colonial Waterbird Society Meeting (presented by D. Perkins, co-authored by R. Holberton, J. Long)

(2001) 'The Blackpoll Warbler: Little Bird - Big Journey'. American OrnithologistsÆ Union, Seattle, WA (C. M. Wilson, M.J. Hunter, co-authors)

(2001) ' The Endocrine Basis for Trade-offs Between Immediate Survival and Reproductive Success in Arctic- and Termperate-Breeding Yellow Warblers', American OrnithologistsÆ Union, Seattle, WA (C. M. Wilson, co-author)

(2001) 'The Endocrine Basis of Different Migratory Strategies Of Long- and Short-distance Neotropical Migrants'. SICB, Chicago, IL (C. M Wilson, M. J. Hunter, and A. W. Lee, co-authors)

(2001) 'The Role of Corticosterone as a Stress Avoidance Hormone, and the Effects of its Inhibition During the Development of Migratory Condition'. SICB, Chicago, IL (C. M Wilson, W. B. Cash, and C. G. Sims, co-authors)

(1999) 'Latitudinal Differences in an Endocrine Response to Stress in Wintering Dark-eyed Juncos'. American Ornithologists' Union, Cornell U., Ithaca, NY (K. P. Able, co-author)

(1999) 'Corticosterone and the Development of Migratory Condition: Is Corticosterone Necessary?'. American Ornithologists' Union, Cornell U., Ithaca, NY (W. B. Cash, C. G. Sims, and C. M. Wilson, co-authors)

Websites featuring work supported on this project (both are still under construction):
1. http://www.ume.maine.edu/cortico/

2. Established by Alex Jahn, Douglas Levey, Kim Smith - Symposium on Austral Bird Migration, Neotropical Ornithological Congress, Puyehue National Park, Chile (under construction) - I constructed a web page that describes the type of work I do, the type of questions under investigation and how they may apply to Austral migration systems, the the type of collaborations one can develop with this type of research focus.

Database
We have developed an extensive database comprising data on several measures of energetic condition, plasma hormone and metabolite levels for over 3,000 songbirds sampled in North America under different stages of the annual cycle. This database was established to serve as a 'library' to be shared with other researchers.

Education activities (please also see sections on 'Outreach': 'Contributions', and 'Experience and Training'
This project has provided many outreach activities to the general public, including local K-12 school children, and public interest talks to various groups including Maine Audubon, Penobscot Valley Chapter of Maine Audubon, and ElderHostel.

Findings:

A brief outline of some of the major findings from this project (this information is also provided in the 'contributions' section). (Please note that there are still components of this project still undergoing analyses and collating.):

1. First, baseline corticosterone and the acute adrenocortical response change with the development of migratory condition. Free-living birds initiating migration or on passage during the early stage of migration at Churchill carry little fat reserves and have relatively low levels of baseline corticosterone accompanied by an adrenocortical response to capture and handling stress. As birds put on greater amounts of fat to meet increased energy demand later in migration, baseline corticosterone levels rose in concert, but were accompanied by a reduced adrenocortical response. These results support the tenets of the Migration Modulation Hypothesis proposed to explain how corticosterone secretion can be regulated to meet the energetic demands of migration (Holberton et al. 1996). The changes in corticosterone secretion co-occurring with changes in migratory fat deposition and food intake were also found in laboratory studies under controlled conditions (Holberton 1999; Dufty and Holberton, in press; Holberton et al. ms in preparation). These results are congruent with those now reported in other bird taxa, suggesting that the role corticosterone plays in regulating the energy reserves of migrants is well conserved. Further, these patterns provide correlational support for MeierÆs model.

2. Second, the expression of baseline corticosterone and the adrenocortical response is flexible and can be adjusted to meet the changing energetic needs of migrants throughout the migratory period (Long and Holberton, 2004, Holberton et al. ms in preparation). In earlier inquiries into patterns of corticosterone related to migration, it was unknown if the adjustments in corticosterone secretion were turned on at its onset and remained in place throughout the migration period or if it corticosterone and the adrenocortical response could be modulated as energy demand changed. In

light of results from other studies, it is believed that this modulation is regulated at the level of the pituitary but how this seasonal change in glucocorticosteroid regulation is achieved is presently unknown. This area of inquiry will hopefully stimulate more research into the neuroendocrinology of migratory as well as non-migratory birds and other taxa.

3. Third, an increase in baseline corticosterone is necessary for migratory fat deposition but not for increased food intake. By demonstrating that the inability to increase baseline corticosterone in preparation for migration prevents migratory fat deposition, we gained better insight into the functional role this hormone plays, not only with respect to migration but also with lipogenesis. Although the results point to corticosterone as a major player in the development of migratory condition, confirming to some parts of MeierÆs model, these results showed for the first time that the hormone does not, by itself, directly regulate all of the major characteristics of migratory condition (e.g. feeding, fattening, and locomotor activity). Further, relationships between corticosterone and food intake appear to change between the non-migratory and migratory stage. In contrast to previous studies in which increased food intake has been linked with acute increases in corticosterone during the non-migratory period or in non-migratory species, corticosterone-inhibited birds showed the same increase in food intake as controls did as they came into migratory condition (Holberton et al. ms submitted, ms in preparation). These findings provide interesting hypotheses to test about how seasonal shifts in food intake and fat deposition is regulated. And, earlier studies have illustrated links between corticosterone, various hypothalamic neuropeptides such as Neuropeptide Y (NPY), leptin, insulin, and other feeding signals. The results from this study illustrate the rich potential that migratory birds have for testing hypotheses about seasonal shifts in interactions among various feeding signals such as Neuropeptide Y (NPY), leptin, insulin, and many others (Holberton and Dufty, 2004). Work is already underway in my laboratory, and I am preparing more proposals, to look into how these feeding and fattening signals are linked in migratory birds.

Not only was migratory fat deposition inhibited when an increase in baseline corticosterone was blocked, but so, too, were levels of nocturnal migratory activity, Zugunruhe. Although, previous studies on a variety of vertebrate taxa (including work on freshwater turtles by one of my doctoral students who also contributed to this project; Cash and Holberton, 1999) have established a direct link between elevated corticosterone and increased non-migratory locomotor activity, further study would be required to determine if the reduced activity observed in my study was a direct result of low corticosterone levels or an indirect result of some signal not produced because of insufficient fat reserves. Exciting work lies ahead teasing apart corticosteroneÆs role as proximate stimulator of Zugunruhe, and other measures of motivation such as orientation, which has already been shown through work supported by this project to be positively correlated with elevated corticosterone levels during migration (Lohmus et al. 2003). Clearly, there is much work to do and this study has provided a foundation for new inquiry into the neuroendocrine basis of migratory behavior and physiology. Such studies can bring together disciplines at multiple levels, spanning the molecular and cellular to the organismal levels of inquiry.

4. While basic physiological control mechanisms may be conserved across species with different migration strategies, the rate or intensity of their activity may provide the underlying difference in how different energetic demands are met. The intensity of migratory fat deposition can change within a species as its migration strategy changes. However, the interaction between exogenous cues (i.e. photoperiod, food availability, etc.) and endogenous control mechanisms influencing this change warrants further research. The two species, Blackpoll and Yellow-rumped warblers, were sampled at two key times during autumn migration: first, at Churchill, where

both species breed and prepare for the same challenges of the initial stages of overland migration and, again, later in the migration period at a time when they diverge dramatically in their autumn migration strategies. The endocrine profiles and metabolite levels at Churchill were, as expected, identical implying that the two species utilize corticosterone in the same way. However, later in the season, as energy needs diverge, Blackpolls, who can gain as much as two times their lean body mass as they prepare for a 3-5 day non-stop flight, had higher baseline corticosterone levels compared to Yellow-rumped warblers. Similar patterns were observed in the laboratory under controlled conditions. Higher corticosterone levels appear to stimulate greater production of plasma triglycerides and may facilitate the rate at which they are stored. It was clear from the captive studies that the difference in fat deposition is not mediated through differences in the amount of food eaten as Blackpolls ate exactly the same amount and kind of food that the Yellow-rumped warblers did as they came into migratory condition. Also, Blackpolls provided food ad libitum in captivity during the initial stage of autumn migration in August at Churchill showed little or no mass or fat gain over a 7-day period. In contrast, when Blackpolls were placed in cages and provided the same food, also ad libitum, in September and early October in Maine, showed dramatic gains in body mass and fat deposition in the same amount of time.

Comparatively greater fat deposition may not be attained by substantially increasing food intake due to either food limitation in the environment and/or by fixed physical (via bill, gut, wing morphology) and physiological (via limits to absorption, digestion, and assimilation) constraints. Therefore, differences in the degree of lipogenesis may be accomplished by differentially regulating rates of triglyceride absorption and/or de novo synthesis. And, increased fat deposition could be facilitated by increased efficiency in plasma triglyceride transport and fatty acid deposition into adipose tissue. Corticosterone has been implicated in other avian and non-avian systems to facilitate the up regulation of the enzymes that support fatty acid synthesis (Fatty Acid Synthase, FAS) and storage (Adipose Lipoprotein Lipase, ALPL). My results pave the way for migration studies that compare seasonal changes and species differences in these two key lipogenic enzymes and to determine the functional significance of corticosterone in lipogenic enzyme activity. Clearly, the ômachineryö involved with across and within-season differences in fat deposition is time-and context/site-dependent and this study has offered exciting results pointing to new areas of research into the endogenous versus exogenous nature of the cues stimulating physiological changes in fat metabolism.

In summary, this study was the first to look more closely at the functional role played by corticosterone in the development of migratory condition. Further, it was the first to use two species of Neotropical migrant warblers in an ecological and ecophysiological migration paradigm. The findings, much still under analyses, begin to reveal some of the endocrine aspects of migratory behavior and physiology, particularly in a group of birds for which little has been known. As importantly, the study has stimulated new research ideas, many of which are already underway in my laboratory.

Training and Development:

Much of the information in this section is also provided in the ôOutreach Activitiesö section as professional development skills are often linked with the promotion of participation in and learning about science by the general public.

People in a various stages of development in their career and personal growth contributed greatly to this project. Both the field and laboratory component required many hands to get the job done and those that worked on the project, at any level, learned a great deal about the topic, the process of doing science including experimental design and data analyses, and project organization and completion. Because I feel that scientists also have a responsibility to consider ethics and

accountability (including regulations and permits for working with animals), these issues are discussed regularly in my laboratory. Collectively, the activities associated with this project provided a great opportunity for learning communication skills (essential for doing science and teaching) and learning about the process of doing science in a laboratory and field based environment.

The professional training and development aspects associated with this project included learning a lot about birds, bird ecology, behavior and physiology, general ecological principles (via working at the two distinct field sites), a variety of techniques for capturing and handling birds and maintaining them in captivity, taking and handling blood and other samples, performing laboratory techniques such as radioimmunoassay for steroid hormone analysis as well as enzyme-based colorimetric assays for plasma metabolites, and collecting food intake and other data related to feeding and fattening. I meet regularly with all people working on my projects, often soliciting them for input throughout the studies and having them assist me in data preparation and I think these meetings helped undergraduate and graduate students helped students think through problems more readily.

Development of skills by undergraduates

Mississippi:
1. Meredith Hunter: her experience doing a year-long undergraduate research project with me investigating hormonal control of migratory feeding and fattening in captive birds, and her experience as a research assistant on this project, gave her enough confidence to apply to and complete the requirements for a masters degree (on the endocrine control of pre-basic molt). She became an important coordinator on my project, overseeing most of the studies in captivity and running many of the hormone assays. The skills she got while working on my project (capturing, handling, and sampling birds in the field, maintaining them in the laboratory, and manipulating hormone levels) were central to the masterÆs project she developed and later got accepted for publication (but see below). Meredith eventually spent 3 summers at Churchill working on this NSF-funded, and other, similar projects.

2. Anthony (Tony) Lee: Tony did not get accepted on his first attempt to enroll in dental school but after working as an undergraduate, and later as a masterÆs student, he was able to improve his writing and communication skills to get accepted into the dental program.

Maine:

1.Joseph Dietz: Joe is now a middle school/high school science teacher in Maine.
2. Michelle LeClair: Michelle is now in a pre-health professional program.

Michelle and Joe signed up for my Arctic Biology course as preparation for their opportunity to work as field assistants on the warbler project at Churchill, Manitoba. I applied for and received university and departmental support for their airfare and some field equipment for them. The Churchill Northern Studies Centre awarded significant support for their room and board during the study. While both students worked on my NSF-funded warbler project in the field, they became interested in Arctic mammal ecology. They soon developed, entirely on their own, a study on Arctic fox den ecology at Churchill. They wrote up their findings up for an independent study research paper and, upon their return to campus, presented their research, as well as their experiences on the warbler project, to the university community at large. This seminar was entirely voluntary and they received no academic credit for it. The seminar was well attended by students, faculty, and administrators and the students were later interviewed about their experience for the campus newspaper. While at Churchill, Joe and Michelle were asked by the director of

the Churchill Northern Studies Centre (where we were staying) to give a talk to a group of Elderhostel visitors at the Centre. This they did, with only about an hour to prepare. They gave an accurate overview of the warbler project, including its goals and significance, and expressed so much enthusiasm that the Elderhostel group continued to ask questions long after their talk was over. Their willingness to give a seminar ôon the spotö was deeply appreciated by the CentreÆs director as it helps promote the kind of activities that the Centre supports. Both of the students have said, in person and in letter sent to me, that the opportunity to work on this kind of project at a place like Churchill not only strengthened their abilities to organize their ideas and present them to a general audience with confidence, but to experience some of the cultural diversity and rich history of the area. (The Churchill part of the warbler project also provided me an opportunity to take the students to several historical sites in the region and to attend several natural history-related activities going on there.)

Graduate students:

Many similar opportunities for developing other research projects and giving oral presentations to general and professional audiences have also occurred for the graduate students who worked on this project.

1. Meredith Hunter, Meredith came to Maine after completing her undergraduate and MasterÆs degree with me at Mississippi, but she was unable to continue in the doctoral program here in Maine after her mother, in Louisiana, fell critically ill. However, Meredith has been able to use her laboratory skills and is now a research technician at Tulane University in New Orleans.

Mississippi:

2. W. B. Cash: now Assistant Professor at Maryville College in Tennessee
3. C. M. Wilson: now Assistant Professor at Hollins University in Virginia
4. C. G. Sims: now Assistant Professor at Arkansas State

All of my doctoral students at Mississippi completed their degrees (C. M. Wilson, W. B. Cash, and C. G. Sims), while either being funded directly on this project (C. M. Wilson as research assistant) or helping out when needed. All of their dissertations included some aspect of hormonal regulation of energy demand, based on the key components of the Blackpoll-Yellow-rumped warbler project. They have all obtained the tenure-track positions they wished. Dr. WilsonÆs dissertation on the modulation of the adrenocortical response as a function of variation in reproductive effort in Arctic versus temperate breeding warblers was significantly supported by this project. The first manuscript from this work is now published in the major ornithological journal (The Auk) and at least two more manuscripts are in review or in preparation. WilsonÆs airfare and other major expenses could be covered by this grant because his work on breeding birds at Churchill could be done before I and the other field crew arrived later in the season for the work on pre- and early-migration parameters in Blackpolls and Yellow-rumped warblers. All of the techniques used by Dr. Wilson in his field and laboratory studies were learned while he was a research assistant on the migration project. He was funded year-round for at least two years, allowing him to devote full time to project during the fall and winter field and laboratory components and to concentrate on his breeding biology work during the summer. Wilson and Cash received student research awards at professional meetings and many grants as students (including helping to secure a $125,000.00 cooperative agreement with USDA). I believe that the project provided all of the students opportunities to learn field and laboratory techniques, practice the process of science, and communicate their work to a wide variety of audiences. All of the students also gave many talks to elementary and middle school classes and local bird groups in Mississippi. Dr. Cash,

after helping with the hormone treatments and blood sampling aspects with the warbler work, developed his dissertation on corticosterone and the role it plays in the behavioral and physiological aspects of energy regulation in reptiles. His studies resulted in several publications (and more evidently are in press or in preparation) and have been cited extensively in the herpetological field. Dr. Sims has at least one publication from his dissertation and has at least one more in preparation.

In Maine, I have four doctoral students and two mastersÆ students in my laboratory and, after transferring the project in 2000 from Mississippi to Maine, most of them have contributed to the field and laboratory work associated with this project. They, too, have developed dissertations or thesis related to some aspect of hormonal aspects of energy demand in birds using concepts stemming from this project. The students have also co-authored several presentations made at international and national meetings and, in some cases, been first-author and presenter of the work. Brent Horton (Ph.D. student), Jennifer Long (Ph.D. student), and Deborah Perkins (M.S. student) have all been or are NSF GK-12 fellows. Brent, through his development of bird-related activities in his 5-grade classroom at Hamden ReedÆs Brook school (as part of his K-12 fellowship program), has received many accolades from the teachers. A 5-th grade student was so enthusiastic about hearing about birds, bird migration, and hormones that he made a videotape showing how birds are captured, banded, and sampled for a variety of health parameters. This videotape has evidently been shown at various NSF activities in Washington, D.C. and has even been seen by several members of Congress. Before coming to my graduate program and helping with many aspects of this project, Brent had had no experience with handling birds or giving presentations to either a general public audience or a scientific one. He has now given several research talks at national meetings, including a symposium presentation and is one of the most sought-after students for giving general public presentations for our universityÆs outreach activities. Through his experience on this and other projects, Brent has also learned how to organize a field crew for his own extensive research program which is now a popular program for our undergraduates looking for research experience. Similarly, Deborah Perkins has been extremely successful in developing her teaching skills in the middle school system. She is locally known for her ability to develop science-based educational activities; she has used her experience on this project, which she later used to develop her own masterÆs project on the endocrine basis of breeding constraints in Arctic shorebirds, to develop learning programs for middle school science teachers. She has also made several trips to NSF in D.C. to discuss further development of the K-12 programs and has presented her masterÆs work at several national and international meetings. Deb will defend her thesis this autumn and I know that DebÆs skills were strengthened considerably by her experience as a research assistant funded on this project, providing her with new laboratory and field experiences with birds. Similarly, Sarah Wilder (MasterÆs student) helped collect hormone samples in the field and helped with the experiments in captivity on this project. She was able to take those skills and apply them to her own thesis project looking at the hormonal basis of female aggression and its direct and indirect costs to survivorship and reproduction. Sarah learned to perform radioimmunoassay on samples taken for corticosterone and gonadal steroid concentration in her birds. She presented her first paper at an international meeting this year. Jennifer Long (Ph.D. student) has presented work from this project at several meetings and was first author on a recently published paper in The Auk on questions that came directly from the objectives of this project. Jen is co-authoring several other manuscripts on the projectÆs findings with me. Her dissertation topic (the cellular/molecular aspects of migratory feeding and fattening) is a direct result of the findings of this NSF-funded project. Her excitement about it while working as a research assistant during her first year in the program resulted in the development of her dissertation topic. Jen has independently developed contacts with several major researchers in the field who are now helping her with some of the cellular aspects of her work. Through her experience on this project she has

developed several lines of inquiry that will take our findings into the next level of cellular control which we know very little about in migratory birds.

Dr. Karen Voltura, the post-doctoral research associate hired during the first year of the project, took a teaching job at a small college after completing the first year on the project. She is now a consultant, contracted to work with Dover Air Force Base via a private contractor, on bird aircraft collisions, providing information about the ecology and behavior of migratory birds and running bird-deterrent programs using dogs.

Indirect contributions of the project to professional development:

I have had several graduate students or post-doctoral researchers come to my laboratory to learn some of the field or laboratory techniques used in this project. Dr. Jennifer Owen, a recent graduate of the University of Southern Mississippi, will spend some time here this autumn learning some methods for hormone manipulation and measurement.
The project, its objectives and results, stimulated the development of other investigations in other systems by many students in other institutions. Ms. Mare Lohmus, a graduate student at the University of Lund in Sweden, asked to collaborate with her on her dissertation work looking at the role of corticosterone in ômigratory readinessö and orientation and has since published her work in a major ornithological journal. Mr. Edgar Vazquez, at the University of Puerto Rico, has also asked for help with his ideas looking at corticosterone and energy regulation in migratory birds. His graduate work is ongoing but his ideas have come from many of the objectives and results from this project. The project also stimulated the development of other thesis questions at other universities. These included Sarah HamiltonÆs thesis on testing the Migration Modulation Hypothesis in raptors, and a similar study by a student at Boise State.

Outreach Activities:

Much of the information in this section is also provided in the ôTraining and Developmentö section as professional development skills are often linked with the promotion of the participating and learning about science by the general public.

I have always encouraged activities promoting public education and involvement in research. I, too, have presented seminars to the general public, such as Audubon, local ornithological clubs, and Elderhostel groups. I asked Mrs. Eleanor Winslow, an avid birder and long-time volunteer at Manomet Bird Observatory in Massachusetts, to work with us on the project at Churchill. Mrs. Winslow, who had had some experience with handling birds, learned how the process of scientific research is done, how to manage a data base, how to run a research field project, and, an important consideration when working at Churchill, how to work under potentially difficult field conditions (e.g. polar bear activity) in a remote area. Mrs. Winslow belongs to various bird clubs and has described her experiences and knowledge to many as she travels extensively with groups around the world.

Undergraduate and graduate students, from both institutions at which I was based during the project period, were given the opportunity to see an entirely different culture at Churchill which is an intersection of Native American, Inuit, and European cultures. Before each trip to Churchill to work on the project, I provided a mini-course on the geological, ecological, and cultural history of the region so that they would have a better appreciation for the area and its past and present.

Proposed on-line searchable database:
We have developed an extensive database comprising data on several measures of

energetic condition, plasma hormone and metabolite levels for over 3,000 songbirds sampled in North America under different stages of the annual cycle. The field data collected during this project, including many other species besides the focal ones, are included in this database. This database was established to serve as a 'library' that may be shared with other researchers if so needed. We hope to make this database accessable on-line.

Education activities:
This project has provided many outreach activities to the general public, including local K-12 school children, and public interest talks to various groups including Maine Audubon, Penobscot Valley Chapter of Maine Audubon, and ElderHostel.

Journal Publications

J. A. Long
R. L. Holberton, "Corticosterone secretion, energetic condition, and a test of the Migration Modulation Hypothesis in the Hermit Thrush (Catharus guttata), a short distance migrant", The Auk, p. 1094, vol. 121, (2004). Published

C. M. Wilson
R. L. Holberton, "An alternative method for delivering adrenocorticotropin hormone in birds", Gen. Comp. Endocrinol, p. 1, vol. 122, (2001). Published

Mizrahi, D., Holberton, R.L. and Gauthreaux, S.A., Jr., "Plasma corticosterone and adrenocortical stress response in Semi-palmated Sandpipers, Calidris pusilla, at a major stopover site during spring migration.", The Auk, p. 79, vol. 118, (2001). Published

Holberton, R.L. and Able, K.P., "Latitudinal differences in the corticosterone stress response in winter: endocrine constraints on wintering capabilities and implications for differential migration in the Dark-eyed Junco.", Proc. Royal Soc., p. 1889, vol. 267, (2000). Published

Sims, C.G. and Holberton, R.L., "Development of the corticosterone stress response in young mockingbirds, Mimus polyglottos.", Gen. Comp. Endocrinol., p. 193, vol. 119, (2000). Published

L?hmus, M., Sandberg, R., Holberton, R. L. and Moore, Frank R., "Corticosterone levels in relation to migratory readiness in Red-eyed vireos (Vireo olivaceus).", Behavioral Ecology and Sociobiology, p. 233, vol. 54, (2003). Published

Holberton, RL, Wilson, C.M., Hunter, M.J., Cash, W.B. Sims, C.G., "Effect of endogenous corticosterone inhibition on the development of migratory
condition", Journal of Experimental Biology, p. , vol. , ( ). Submitted

Holberton, RL, Wilson, C.M., Hunter, M.J., Long, J.A., Perkins, D.E., "The role of corticosterone in migratory fattening: Is it dose-dependent?", Comparative Biochemistry and Physiology A, p. , vol. , ( ).

Holberton, RL, Wilson, C.M., Hunter, M.J., "Differential fat deposition, corticosterone secretion and metabolite levels in two Neotropical migrants with different migration strategies: a long-distance migrant, the
Blackpoll warbler, versus a short-distance migrant, the Yellow-rumped warbler", Journal of Avian Biology, p. , vol. , ( ).

C. M. Wilson
R. L. Holberton, "Personal risk versus immediate reproductive success: a basis for latitudinal differences in the adrenocortical response to stress in Yellow warblers, Dendroica petechia", The Auk, p. 1238, vol. 121, (2004). Published

Books or Other One-time Publications

Holberton, R.L. and Dufty, Jr., A.M., "Hormone Patterns and Variation in Life History Strategies of Migratory and Non-migratory Birds",

(2004). Book, Published
Editor(s): Marra, P. and R. Goldberg
Collection: Birds of Two Worlds: The Ecology and Evolution of Migratory Birds
Bibliography: Smithsonian Press

Joseph R. Jehl, Jr.
(I contributed information about breeding and migration patterns for several species including Blackpoll and Yellow-rumped warblers, at Churchill, as a direct result of this project), "Birdlife of the Churchill Region: Status, History, Biology", (2004). Book, Published
Bibliography: Trafford Publishing Co.

Web/Internet Site

URL(s):

1.http://www.zoo.ufl.edu/centers/migration/participants/rebecca%20holberton/rebecca%20holberton.htm
2.http://www.umaine.edu/research/UMTSurvival.htm
3.http://www.calacademy.org/calwild/2003fall/stories/horizons.html
4.http://www.ume.maine.edu/cortico/

Description:

There are currently 4 websites related to this award:
1. This website was developed by Dr. Douglas Levy and his student, Alex Jahn, at the University of Florida, as part of the symposium on Austral Migration at the Neotropical Ornithology Congress, in Chile, October, 2003. Dr. Levy, in collaboration with Dr. Kim Smith at the University of Arkansas, received NSF money to fund a symposium on Austral migration in an effort to expand and strengthen interactions between researchers in North and South America. The primary goal of the symposium was to serve as a format for the exchange of ideas and research information in order to promote better understanding of Austral migration systems, in particular, and of the ecology, physiology, and behavior of migratory birds, in general. During the oral presentation in the symposium, I provided an overview of the work funded by this award, i.e. the major findings of how Blackpoll and Yellow-rumped warblers differ in their behavior and physiology during autumn migration, and the endocrine aspects of how these differences are regulated. The symposium was a great success and I have maintained contact with several South American researchers since the meeting. The symposium website includes pages in which participants describe what they do, etc. I included additional information about the importance of collaboration in the development of new ideas and techniques, and provided some suggestions on how to develop such collaborations. The goal of my contribution to the website is to encourage young researchers to think beyond borders and to develop links that can be rewarding academically/professionally as well as personally. I now have much of this information available in my other websites.
2. This website was developed by the University of Maine and directly features the work funded by this award. The article and website were developed to reach a more general audience. I received several requests for interviews by several newspapers and magazines.
3. This website was developed by the California Academy of Sciences and features the migration studies funded directly by this award, again taking this information to the general public.
4. This website has been constructed by my graduate students and is a work in progress. It features many of the other projects related to the endocrinology and behavioral ecology of migratory birds. Some of these students have been funded by this award.

Other Specific Products

Product Type:

Data or databases

Product Description:

We have now compiled information on morphometrics (fat, mass, wing cord, bill length, tarsus, etc.), breeding or migratory state, plasma hormone concentrations (baseline corticosterone and acute adrenocortical response, androgens, and estrogen), plasma metabolite concentrations (triglyceride, glycerol), hematocrit, and, in many cases, environmental conditions, and several other parameters related to annual cycle stage, for almost 3000 songbirds. The data span a decade of studies on a multitude of free-living birds, with over 1200 Parulid warblers alone contributing to much of the database. The database has already allowed researchers to compare some of these parameters taken from birds under one set of conditions with those coming from other conditions. It has also been used recently by several graduate students at other institutions (e.g. Tulane, Southern Mississippi, University of British Columbia) to develop testable hypotheses in the design of their own dissertation work. Collaborators at the Smithsonian Environmental Research Center have contributed to the database (e.g. data collected on

birds wintering in Belize, Mexico, and Jamaica) and have also consulted the database in their own work. The ultimate goal is to make the database available on-line in a searchable way. I now have a technician who is responsible for maintaining and developing this database.

Sharing Information:

I receive many requests for help in developing graduate student research programs and I readily make any relevant data available to the students, and collaborators. It has also been used recently by several graduate students at other institutions (e.g. Tulane, Southern Mississippi, University of British Columbia) to develop testable hypotheses in the design of their own dissertation work. Collaborators at the Smithsonian Environmental Research Center have contributed to the database (e.g. data collected on birds wintering in Belize, Mexico, and Jamaica) and have also consulted the database in their own work. The ultimate goal is to make the database available on-line in a searchable way. I now have a technician who is responsible for maintaining and developing this database and we hope to have it on-line within the next year.

Contributions

Contributions within Discipline:

Contributions to this and other disciplines (I've combined the discussion of contributions within the discipline with contributions to related disciplines):
This project contributed significantly to our knowledge of the ecophysiology of birds and bird migration, as well as that of other animal taxa, in the disciplines of ecophysiology and behavioral endocrinology. They did so: 1. by its approach of integrating ecology, behavior, and physiology in a combination of field and laboratory studies, 2. by its findings, which increased our current knowledge of corticosterone and its role in supporting the energy demands of migration, 3. by fostering the development of new collaborations, 4. by stimulating new research, and 5. by providing opportunities for the professional development of undergraduate and graduate students and post-doctoral researchers.

1. Through its integration of ecology, behavior, and physiology, and by combining field and laboratory studies, this project offered great breadth in its approach to the questions of how migrants reach their destinations and how different migration strategies might be supported by different physiological mechanisms. - Patterns of hormone secretion and changes in body condition were first measured in the field at different stages of the migratory period that represented different levels of energy demand. These patterns lead to the development of hypotheses about the functional role of corticosterone and how it may influence migratory behavior and physiology. Laboratory studies were designed to look at seasonal changes in food intake, body condition, fat deposition, hormone secretion and metabolite production under controlled conditions. These were followed by experimental studies manipulating circulating corticosterone levels and looking at the resulting patterns in migratory feeding and fattening. One species was used in most of the laboratory studies as an initial exploration of these questions (a similar species was substituted when it became necessary). However, one of the objectives was to compare patterns in the variables of interest in the field and in the lab in two closely related and co-occurring species whose life histories differ only in their autumn migration strategies. The value of combining field and laboratory research is that it keeps the objectives of laboratory work rooted in what is observed in the natural world. The comparative approach allows greater insight into the evolutionary aspects of behavioral and ecological endocrinology while field studies consider behavioral and physiological events in light of the selection pressures that may have shaped them. Maintaining an ecological context to behavioral and physiological phenomena is also more appealing to a broader audience. For example, historically, physiology has been poorly represented at American OrnithologistsÆ Union (AOU) and other ornithological meetings compared to other disciplines. I feel that the work from this project has been well received at these meetings because we have framed much of the physiology in an ecological context. Also, this project was fairly novel in that it focused on New World warblers, a group that has been used less in physiological studies compared to New World sparrows and Old World taxa. Although concern for Neotropical migrant population decline has been in place over the past few decades, interest in the physiological

aspects underlying constraints on key events in the annual cycle, including migration, molt, overwinter survival, and reproductive success has developed much more recently. Through its integration of ecology, behavior, and physiology, and its combination of field and laboratory studies, this project has helped cultivate a greater interest by behavioral ecologists, resulting in new collaborations among them and ecophysiologists.

2. Through its findings about corticosteroneÆs role in the development of migratory condition and how migrants with different migration strategies meet their different energy demands, this project expanded our knowledge about the endocrinology of bird migration. - In the 1960-70Æs, Al Meier and his colleagues developed a model in which seasonal changes in the circadian expression of corticosterone and prolactin promoted migratory hyperphagia, fat deposition, and orientation. The model received mixed reviews over the years since its inception: it appears in textbooks but has been dismissed by many researchers, although none have investigated the model thoroughly. My study was not set up to test MeierÆs model directly but was designed with two major goals in mind that are related to MeierÆs work. The first goal was to develop a better understanding of the hormonal basis of bird migration behavior and physiology, by investigating the role that corticosterone plays in migratory feeding and fattening. The second major goal was to begin to reveal how different levels of energy demand, within and between species, are supported through the regulation of corticosterone secretion.

A brief outline of some of the major findings from this project:
a. First, baseline corticosterone and the acute adrenocortical response change with the development of migratory condition. Free-living birds initiating migration or on passage during the early stage of migration at Churchill carry little fat reserves and have relatively low levels of baseline corticosterone accompanied by an adrenocortical response to capture and handling stress. As birds put on greater amounts of fat to meet increased energy demand later in migration, baseline corticosterone levels rose in concert, but were accompanied by a reduced adrenocortical response. These results support the tenets of the Migration Modulation Hypothesis proposed to explain how corticosterone secretion can be regulated to meet the energetic demands of migration (Holberton et al. 1996). The changes in corticosterone secretion co-occurring with changes in migratory fat deposition and food intake were also found in laboratory studies under controlled conditions (Holberton 1999; Dufty and Holberton, in press; Holberton et al. ms in preparation). These results are congruent with those now reported in other bird taxa, suggesting that the role corticosterone plays in regulating the energy reserves of migrants is well conserved. Further, these patterns provide correlational support for MeierÆs model.
b. Second, the expression of baseline corticosterone and the adrenocortical response is flexible and can be adjusted to meet the changing energetic needs of migrants throughout the migratory period (Long and Holberton, 2004, Holberton et al. ms in preparation). In earlier inquiries into patterns of corticosterone related to migration, it was unknown if the adjustments in corticosterone secretion were turned on at its onset and remained in place throughout the migration period or if it corticosterone and the adrenocortical response could be modulated as energy demand changed. In light of results from other studies, it is believed that this modulation is regulated at the level of the pituitary but how this seasonal change in glucocorticosteroid regulation is achieved is presently unknown. This area of inquiry will hopefully stimulate more research into the neuroendocrinology of migratory as well as non-migratory birds and other taxa.
c. Third, an increase in baseline corticosterone is necessary for migratory fat deposition but not for increased food intake. By demonstrating that the inability to increase baseline corticosterone in preparation for migration prevents migratory fat deposition, we gained better insight into the functional role this hormone plays, not only with respect to migration but also with lipogenesis. Although the results point to

corticosterone as a major player in the development of migratory condition, confirming to some parts of MeierÆs model, these results showed for the first time that the hormone does not, by itself, directly regulate all of the major characteristics of migratory condition (e.g. feeding, fattening, and locomotor activity). Further, relationships between corticosterone and food intake appear to change between the non-migratory and migratory stage. In contrast to previous studies in which increased food intake has been linked with acute increases in corticosterone during the non-migratory period or in non-migratory species, corticosterone-inhibited birds showed the same increase in food intake as controls did as they came into migratory condition (Holberton et al. ms submitted, ms in preparation). These findings provide interesting hypotheses to test about how seasonal shifts in food intake and fat deposition is regulated. And, earlier studies have illustrated links between corticosterone, various hypothalamic neuropeptides such as Neuropeptide Y (NPY), leptin, insulin, and other feeding signals. The results from this study illustrate the rich potential that migratory birds have for testing hypotheses about seasonal shifts in interactions among various feeding signals such as Neuropeptide Y (NPY), leptin, insulin, and many others.

Not only was migratory fat deposition inhibited when an increase in baseline corticosterone was blocked, but so, too, were levels of nocturnal migratory activity, Zugunruhe. Although, previous studies on a variety of vertebrate taxa (including work on freshwater turtles by one of my doctoral students who also contributed to this project; Cash and Holberton, 1999) have established a direct link between elevated corticosterone and increased non-migratory locomotor activity, further study would be required to determine if the reduced activity observed in my study was a direct result of low corticosterone levels or an indirect result of some signal not produced because of insufficient fat reserves. Exciting work lies ahead teasing apart corticosteroneÆs role as proximate stimulator of Zugunruhe, and other measures of motivation such as orientation, which has already been shown through work supported by this project to be positively correlated with elevated corticosterone levels during migration (Lohmus et al. 2003). Clearly, there is much work to do and this study has provided a foundation for new inquiry into the neuroendocrine basis of migratory behavior and physiology. Such studies can bring together disciplines at multiple levels, spanning the molecular and cellular to the organismal levels of inquiry.

d. Lastly, this project contributed to our understanding of the endocrine physiology of different migration strategies. The two species, Blackpoll and Yellow-rumped warblers, were sampled at two key times during autumn migration: first, at Churchill, where both species breed and prepare for the same challenges of the initial stages of overland migration and, again, later in the migration period at a time when they diverge dramatically in their autumn migration strategies. The endocrine profiles and metabolite levels at Churchill were, as expected, identical implying that the two species utilize corticosterone in the same way. However, later in the season, as energy needs diverge, Blackpolls, who can gain as much as two times their lean body mass as they prepare for a 3-5 day non-stop flight, had higher baseline corticosterone levels compared to Yellow-rumped warblers. Similar patterns were observed in the laboratory under controlled conditions. Higher corticosterone levels appear to stimulate greater production of plasma triglycerides and may facilitate the rate at which they are stored. It was clear from the captive studies that the difference in fat deposition is not mediated through differences in the amount of food eaten as Blackpolls ate exactly the same amount and kind of food that the Yellow-rumped warblers did as they came into migratory condition. Also, Blackpolls provided food ad libitum in captivity during the initial stage of autumn migration in August at Churchill showed little or no mass or fat gain over a 7-day period. In contrast, when Blackpolls were placed in cages and provided the same food, also ad libitum, in September and early October in Maine, showed dramatic gains in body mass and fat deposition in the same amount of time.

Comparatively greater fat deposition may not be attained by substantially increasing

food intake due to either food limitation in the environment and/or by fixed physical (via bill, gut, wing morphology) and physiological (via limits to absorption, digestion, and assimilation) constraints. Therefore, differences in the degree of lipogenesis may be accomplished by differentially regulating rates of triglyceride absorption and/or de novo synthesis. And, increased fat deposition could be facilitated by increased efficiency in plasma triglyceride transport and fatty acid deposition into adipose tissue. Corticosterone has been implicated in other avian and non-avian systems to facilitate the up regulation of the enzymes that support fatty acid synthesis (Fatty Acid Synthase, FAS) and storage (Adipose Lipoprotein Lipase, ALPL). My results pave the way for migration studies that compare seasonal changes and species differences in these two key lipogenic enzymes and to determine the functional significance of corticosterone in lipogenic enzyme activity. Clearly, the ômachineryö involved with across and within-season differences in fat deposition is time-and context/site-dependent and this study has offered exciting results pointing to new areas of research into the endogenous versus exogenous nature of the cues stimulating physiological changes in fat metabolism.
In summary, this study was the first to look more closely at the functional role played by corticosterone in the development of migratory condition. Further, it was the first to use two species of Neotropical migrant warblers in an ecological and ecophysiological migration paradigm. The findings, much still under analyses, begin to reveal some of the endocrine aspects of migratory behavior and physiology, particularly in a group of birds for which little has been known. As importantly, the study has stimulated new research ideas, many of which are already underway in my laboratory.

3. Next, the project made significant contributions to this and related disciplines through the growth of new collaborations. - The integrative nature of the project has been attractive to other researchers, many of whom have had well-established study systems that focused on the ecology and behavior of Neotropical migrants. Although much of the data collected in this study are still being analyzed, I have been presenting portions of the study to the scientific and general public since 2000. When this project began, very little research had been done on the ecological physiology of Neotropical migrants. Through this project, I have helped open the doors for hormonal studies on this group of birds whose ecology is well known but whose physiology is poorly understood. This project provided opportunities to illustrate the exciting nature of studies that integrate ecology, behavior, and physiology in a ônewö group of birds. This is, until recently, most of our knowledge of the ecophysiology of bird migration had come from only a few New World species of sparrows, and from Old World species. I have promoted the idea that physiological phenomena represent the interface between an animalÆs environment and its genetic capability to respond to that environment. Several investigators who have had long-term ecologically rich studies with Neotropical migrants have now begun incorporating behavioral endocrinology questions into their study systems. For example, Dr. Thomas Sherry at Tulane, who has had a long-term study on ecological factors influencing population regulation in wintering American redstarts and Ovenbirds in Jamaica, now has graduate students measuring corticosterone and metabolites of fattening in these species, in collaboration with me. Dr. Peter Marra, now at the Smithsonian Environmental Research Center, and I have had a long-term collaboration looking at similar habitat-related aspects of corticosterone secretion and energy regulation in several species of Neotropical migrants wintering in the Caribbean, Belize, and Mexico. Dr. Joseph WunderleÆs student in Puerto Rico is now incorporating corticosterone sampling in their winter ecology studies, again, in collaboration with me. A graduate student at another institution is also collaborating with me on corticosterone and body condition in reptiles. The common theme with these examples is that all of these research programs were once entirely ecologically based. Encouraged by these examples, my own graduate students, have developed their own collaborations with researchers in Canada, France, and Scotland, and have

even begun to extend their work to non-avian systems such as hibernating bears. And, in another collaborative study supported by me through this project, a graduate student in Sweden published findings demonstrating that there may be threshold levels of corticosterone that act as signals for migrants to choose the appropriate direction only if energy reserves would support it (Lohmus et al. 2003). This may have been the first experimental study looking at links between corticosterone and orientation in a Neotropical migrant since MeierÆs model was first proposed almost 40 years ago.
Several new research activities with federal agencies are also underway as a direct result of this projectÆs activities. Studies in cooperation with the United States Forest Service, and with the United States Fish and Wildlife Service, have been initiated to look at the endocrine aspects of energy regulation in several species of concern. I believe that IÆve been able to use the current project to encourage agencies, whose mandates are much more applied, to incorporate a stronger basic research component and to consider ecophysiological approaches in their study systems.

4. This project contributes to this and other disciplines through its stimulation of new research. - The long-term goal of the project was to lay a foundation for further study of the hormonal regulation of cellular level processes (e.g. via regulation of enzyme activity related to fat synthesis and storage, and by the regulation of hormone receptors), and species differences in these processes. These next steps have already begun. One of my doctoral students has initiated a dissertation study on the functional role of corticosterone in regulating hepatic Fatty Acid Synthase and in adipose Lipoprotein Lipase activity in short and long-distance migrants. She and I are developing a model for relationships between various feeding peptides, pancreatic hormones, glucocorticosteroids and their receptors, and lipogenic enzymatic activity. We are also incorporating the use of a small flight tunnel to test hypotheses about season-dependent changes in these phenomena and will continue to integrate ecology, behavior, and physiology in our approach.

Since the mid-1990Æs, the number of studies on corticosterone and migration has grown. Some of these have used species, such as shorebirds and birds of prey, that are relatively new to the arena of migration behavioral endocrinology. A growing interest in understanding the physiological underpinnings of a greater diversity of migration strategies may have been influenced to some extent by my study. The corticosterone work from this study has been used by other researchers to design studies on immune activity related to migration (through corticosteroneÆs relationship to immunosuppression) and at least three masterÆs theses or doctoral dissertation projects and at least two proposals to the National Science Foundation prepared by principal investigators at other institutions were developed directly from the work IÆve published or discussed in presentations. I have been asked by several colleagues to supply information and photographs of the field sites and of the dramatic changes in body fat exhibited by Blackpoll warblers for use in their undergraduate or graduate ornithology classes. The work has been referred to extensively in other manuscripts and review chapters by other authors and I regularly get phone calls from local newspapers about the ecology and physiology of migrants for the general public interest after presenting the work to local and regional Audubon, Bird Club, and Elderhostel groups.

Much of the fieldwork on this project occurred at Churchill, where the taiga, boreal forest, and coastal plain biomes meet. The area is unique and offers great opportunities for research and teaching. While the boreal ecosystem itself was not a major focus of this project, data collected during this study provided important information about Neotropical bird breeding and migration patterns (for several species in addition to Blackpoll and Yellow-rumped warblers) in this relatively less studied biome (see Joseph JehlÆs Birdlife of the Churchill Region: Status, History, Biology, 2004, Trafford Publishing Co.). Our study site at Churchill provided an

opportunity to record breeding and passage dates of birds there, and to demonstrate, in oral presentations, the uniqueness of this biologically and culturally rich region. The need for greater knowledge about how birds, humans, and other animals use the boreal and sub-Arctic regions becomes more critical as we face the threat of global climate change.

5. This project contributed to this and other related disciplines through the opportunities it provided for professional development of post-doctoral researchers and undergraduate and graduate students. - This last may be the most important contribution that this project can make to this and other disciplines. The project involved a variety of skills and these young scientists gained experience into what goes into executing a large-scale project such as this. Field and laboratory studies require a lot of preparation and planning. To manipulate hormones, several methods were tested and the best were selected before the actual work began. Undergraduate and graduate students, post-doctoral research assistants, and others, were given an opportunity to learn a wide variety of skills. These included experimental design, data analyses, bird capture, humane blood collection and processing, analysis of hormone and metabolite samples via radioimmunoassay and colorimetric assays, maintaining birds in captivity, measuring individual food intake, Zugunruhe, body mass and fat change, preparing equipment for remote field sites, understanding the federal, state, and provincial permits involved with this kind of work, and coordinating and sharing the work with others. Prior to working on this project, the post-doctoral researcher had not had any experience in the field of migration, but is now employed by the United States Air Force helping them coordinate their activities to prevent potentially catastrophic bird-plane collisions. Three former doctoral students have continued their research activities in ecophysiology and two of them now undertake the logistics of taking their undergraduate students to the Churchill Northern Studies Centre for Arctic biology classes. One former masterÆs student completed her behavioral endocrinology project on shorebirds in the high Arctic under grueling, remote conditions after she had gotten field experience on this project. As only one of many examples of her self-motivated outreach activities, she recruited an Inuit high school student from Nunavut to help with behavioral data collection, resulting in an exciting exchange of culture and knowledge. This activity helped develop her well-established reputation as a public school educator and science program coordinator. One undergraduate who had never traveled beyond her small hometown in Louisiana, traveled to Churchill, and later came to Maine as a doctoral student after finishing a MasterÆs with me at my former institution in Mississippi. She worked on this project as laboratory and field research assistant while also fulfilling her role as a single mother. She is now a laboratory coordinator for a nationally recognized endocrine disruption laboratory at Tulane University and has co-authored several presentations with researchers there. Two other undergraduates who worked on this project have gone on to the public health or high school education fields. Two current doctoral students that worked on this project have developed international research collaborations of their own. Both of these students have presented their work, using techniques acquired on this project, at national and international symposia. The integration of ecology, behavior, and physiology and the combination of field- and laboratory-based studies have continued to be a common approach throughout all of the studentsÆ projects. And, the travel to Churchill provided all who worked there on this project (including an elderly private individual who volunteered as a field assistant) a unique opportunity to experience the rich biogeographical, political, and cultural history of the Hudson Bay region.

Contributions to Other Disciplines:

I have included the discussion of how this project contributed to 'other disciplines' in the discussion of contributions within the discipline.

Contributions to Human Resource Development:

1. Opportunities for research and teaching in science and engineering: Please see sections on 'Training' and 'Outreach' Activities for much of this information.
As stated elsewhere, the project provided opportunities, directly or indirectly, for 1 post-doctoral researcher, at least 10 full-time graduate students, as many as half a dozen undergraduate students, and one person from the public sector to participate in all aspects of experimental design, data collection and analyses, and information dissemination of science. Through the nature of the combination of field and laboratory studies, and the inclusion of several different assays and methods for manipulating hormones, students got an opportunity to get experience with a variety of techniques and to problem solve when needed. All individuals that worked directly or indirectly on the project had, at some time, to give an oral presentation about the work, often to non-science audiences (pre-college school groups, Audubon and other non-profit organizations, etc.). Three graduate students who have worked on this project have been very active as NSF GK-12 Fellows and have created many learning activities for elementary, middle and high school students. They have received recognition in the local media for their work and these three students have become very popular amongst the school teachers they have worked with. These graduates students have also used the methods and results of this study as examples for local teachers during our annual week of Science Camp on campus.
At Mississippi: All three doctoral students who have completed their degrees since the project began are in tenure-track academic positions. One master's student switched out of the program to enter dental school. One master's student completed her degree and went on to pursue a doctoral degree.
At Maine: The one graduate student who has completed her degree since the project was transferred to Maine, has continued with her goals of teaching high school biology, developing science programs for high schools, and working with indigenous groups. One undergraduate who worked on the project is currently teaching science courses in a high school in Maine.
2. improving the performance, skills, or attitudes of members of underrepresented groups that will improve their access to or retention in research and teaching careers- When I began this project at the University of Mississippi, five graduate and undergraduate students worked on it. These included one female. The post-doctoral researcher who worked on the project in Mississippi was female. When the project continued at the University of Maine, four out of the five graduate students working on the project were female, and one of two undergraduates on the project there were female. In summary, all but one of my female graduate student advisees (5 out of 6 females) were given opportunities to develop a multitude of skills. Unfortunately, only on of my graduate students, regardless of sex, is from an underrepresented group (Hispanic). Although I tried to recruit from a strong African-American pool in Mississippi (by directing my advertisement for a post-doctoral research assistant to several historically black colleges), I received no responses. The project indirectly supported at least five students at other institutions (by helping them with sample analyses); four of thes graduate students are female. The remaining student, a male, is Hispanic, from Puerto Rico. I participated in a symposium organized by Douglas Levy, Kimberly Smith, and Alex Jahn, at the Neotropical Ornithological Congress in Chile, as part of their goal to encourage similar research projects and to develop collaborations with students in Latin America.

3. developing and disseminating new educational materials or providing scholarships - I have not developed any new educational materials or provided scholarships through this project. I have, however, funded out of my own personal funds, round trip airfare to Churchill for one female undergraduate student, and one female graduate student. I have also funded several undergraduate research projects out of my own personal funds as needed.

4. providing exposure to science and technology for pre-college teachers, young

people, and other non-scientist members of the public.
Much of the information in this section is also provided in the ôOutreach Activitiesö and 'Training Activities' sections as I view professional development skills as being linked with the promotion of science and the encouragement of participation in the process of science by the general public.

Contributions to Resources for Research and Education:

I have not established any science-related society or organization. I have developed a large ecophysiology database (described elsewhere in this report) that will be put on-line in a searchable database.

Contributions Beyond Science and Engineering:

As mentioned in the section on 'Contributions within and beyond the discipline', much of the field work on this project was done at Churchill, a sub-Arctic region representing the intersection of four major biomes (tundra, taiga, boreal forest, and coastal plain) that are threatened by global climate change. Most studies on Neotropical migrants occur in the Tropics or the temperate regions and I have emphasized the need for more research on sub-Arctic and Arctic breeding birds in many of my presentations to the scientific and non-scientific audiences. I also use migrants as models for environmental monitoring, through discussion of endocrine disruption in my classroom or public lectures.
Understanding how animals regulate their energy demand during each stage of the annual cycle, and recognizing the connectivity between events during each stage of the annual cycle is the underlying theme in all of my professional activities. The activities of this project encouraged collaborations with several state and federal agencies (e.g. US Fish and Wildlife and US Forest Service), examples of taking this 'basic research' project to an 'applied research' arena.

Categories for which nothing is reported: