AN ANNUAL CYCLE APPROACH TO STUDYING BULLOCK'S ORIOLES: EXAMINING INFRASPECIFIC VARIATION IN MOULT-MIGRATION AND THE INFLUENCE OF PRIMARY PRODUCTIVITY ON BREEDING ABUNDANCE

By

Andrew Pillar
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Thesis examining committee:
Matt Reudink (Ph.D.), Assistant Professor and Thesis Supervisor
Biological Sciences, Thompson Rivers University

Nancy Flood (Ph.D.), Senior Lecturer and Co-Supervisor
Biological Sciences, Thompson Rivers University

Peter Marra (Ph.D.), Center Head, Migratory Bird Center
Smithsonian Conservation Biology Institute

Darryl Carlyle-Moses (Ph.D.), Associate Professor
Geography and Environmental Studies, Thompson Rivers University

David Green (Ph.D.), Associate Professor and External Examiner
Biology, Simon Fraser University

ABSTRACT

I investigated moult and migration in Bullock's orioles (*Icterus bullockii*) using a combination of geolocators and stable hydrogen isotope analysis. Our results clearly demonstrate that Bullock's orioles use a stopover site in the Mexican monsoon region to moult en route to their overwintering grounds. This migration strategy appears to be consistent across all age and sex classes of Bullock's orioles from our population at the Northern extent of their range in Kamloops, BC. We also assessed how breeding abundance throughout the oriole's breeding range varies with changes in primary productivity on their breeding, moulting, and overwintering grounds. Our data revealed that primary productivity on the breeding grounds, and potentially in some overwintering areas, affects subsequent season breeding abundance in several Bird Conservation Regions. This study has implications for other moult-migrant songbirds in Western North America and illustrates the importance of studying birds throughout their annual cycle.

Keywords: Bullock's orioles, moult-migration, NDVI, breeding abundance, stable isotope analysis, geolocator, Mexican monsoon region.

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DEDICATION

I dedicate this thesis to my family. Without your support and encouragement, I could have never have made it this far. Words cannot express how grateful I am for all of you.

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CHAPTER 1: INTRODUCTION

Each year, billions of birds embark on immense annual migrations from their breeding grounds to their over-wintering areas and back again. Understanding these migrations and how environmental factors influence populations and individuals throughout the annual cycle is key to understanding the ecology of these species. Here, I use a combination of well-tested tracking techniques to examine the migration and moult behaviour of a western North American songbird, the Bullock's oriole (*Icterus bullockii*). In addition, I investigate how breeding populations of this species are influenced by environmental factors throughout the annual cycle over a 25 year period.

Tracking bird movements and migration

There several methods by which birds can be tracked throughout their annual cycles, and each method has its own advantages and limitations. Birds can be captured and fitted with numbered aluminum, as well as coloured plastic, leg bands for identification purposes. Banding and then recapturing birds allows us to track them to different locations over the course of their lives. Banding and recapture is an inexpensive technique that can provide exact information on the locations of birds are at the start and end of their migration journey (Robinson et al. 2009). Banding stations set up along major bird migration pathways can also provide additional information on locations before, during, and after the trip. Another advantage is that bands are minimally invasive, generally being attached around bird's legs. However, banding is limited in some ways. For example, individual birds in a study population must be captured multiple times to give even a rough estimation of migratory connectivity. In addition, the small number of major banding stations, limits the quantity of data that can be obtained for a species. This problem can be further compounded in birds that are difficult to recapture, have low return rates, or winter in tropical areas, where fewer studies are being conducted (Hobson and Norris 2008).

Global Positioning System (GPS) trackers have been successfully deployed on larger migratory animals, including seabirds. GPS data loggers can determine an individual's location relative to signals from multiple GPS satellites in orbit around the planet. GPS trackers are also capable of being highly accurate (to within 5 meters) in a sufficiently open environment. Thus, the use of these GPS receivers can give incredibly detailed information on the migration of birds robust enough to carry the devices (Robinson et al. 2009). While GPS receivers have been rapidly miniaturized over the last decade, they are still not small enough to be a viable option for many songbirds. GPS loggers are also limited in that they must be retrieved in order to download the data and therefore require recapture of the bird. However, when combined with satellite transmitters, GPS can overcome this limitation for large animals. Satellite transmitters track an individual's location using telemetry with orbiting satellites which can transmit data to ground based satellite receivers (Hobson and Norris 2008, Robinson et al. 2009). Satellite tracking can also determine a fairly precise route of migration. However, trackers are both expensive and prohibitively heavy, and even more so when combined with GPS, thus limiting their use primarily to studies of larger animals.

Finally, radio transmitters provide a short-range method of tracking animal movements using Very High Frequency radio. The main drawbacks to radio transmitters is the limited range over which they can communicate with receivers, short battery life, and the potential to alter animal behaviour (Hobson and Norris 2008, Robinson et al. 2009). To track the migration of small songbirds throughout an entire annual cycle, we require different techniques that make use of smaller and lighter technology and analysis of markers of environmental variation that are actually part of the birds' own bodies.

Stable isotope analysis determines the ratios of naturally occurring isotopes of an element in bird tissues. As an animal's tissues grow, they incorporate stable isotopes in ratios that are reflective of the natural environment, since the isotopes incorporated via the food and water sources they consume (Wassenar 2008). These isotope ratios can thus provide important clues about the conditions in which the tissue was grown. In recent years, stable isotope analysis has become a popular technique for studying bird diet, migratory connectivity, and habitat quality. Nitrogen, carbon, and hydrogen are the most common elements used in stable isotope analysis. Stable nitrogen isotope signatures can provide information about an animal's diet at the time its tissues were grown, allowing us to estimate trophic level and assess nutritional stress (Hobson et al. 1993). Stable carbon isotope signatures can be used to estimate the proportion of C_3 and C_4 plants in the diet and thus the wetness of the region in which the tissue was grown (Bowen and West 2008). Stable carbon isotopes can thus be used to help differentiate birds from different breeding or winter habitats using tissues grown in these locations (Wassenar and Hobson 2000). The ratios of stable hydrogen isotopes vary across the globe by latitude, elevation and large-scale climate pattern. Stable hydrogen isotope analysis can therefore give us a rough approximation of the area in which tissues were grown. This is particularly useful for migratory birds as the analysis can be used to link breeding and wintering populations (Wassenar and Hobson 2000, Kelly et al. 2002, Rubenstein et al. 2002, Hobson 2004) and understand natal dispersal in a species (Studds et al. 2012). A major drawback of stable hydrogen analysis when working with Neotropical birds is the limited accuracy of isoscape maps, due to the relatively small number of samples resulting in a limited resolution. This is especially true of many areas where migratory birds overwinter in Mexico and Central America. This study will make use of stable hydrogen analysis, but combine it with geolocator data; used together, these techniques allow us to determine the general area in which moult occurred, or in which the bird has been residing recently, by analyzing feather and claw samples, respectively.

Light-level geolocators are an emerging technology that makes use of an internal clock, a memory, a battery, and a light sensor recording light-levels at set intervals throughout a day. By detecting the timing of sunrise and sunset, these devices can be used to derive a rough estimate of where birds carrying them were at midnight and noon each day. Geolocators have the potential to complement stable isotope analysis, and can help us avoid drawing what might be incorrect conclusions based isotope analysis alone (Hallworth et al. 2013). Geolocators have two main limitations.. First, they do not transmit data and therefore must be retrieved in order to access the data they have recorded. Second, during the time of the the vernal and autumnal equinoxes, the length of the day becomes similar across all locations on earth leading to unreliable estimates of latitude. However, geolocators are currently the only tracking devices compact and lightweight enough to be mounted on small songbirds (Bridge et al. 2011). Recently, studies using geolocators have become extremely popular and have helped reveal a wide variety of previously unknown aspects of bird migration and ecology. For example, geolocators studies have found faster than expected migration (Stuchbury et al. 2009), longer than expected migration (Hecksher et al. 2011), multiple wintering sites for the same species (Hecksher et al. 2011) or breeding population (Ryder et al. 2011), intraspecific differences in migration and stopover sites (Delmore et al. 2012), and the moult-migration strategies of painted buntings (*Passerina ciris*) (Contina et al. 2013). Recently, geolocators have also been used in conjunction with measures of primary productivity to investigate how this environmental factor influences migration (Renfrew et al. 2013).

Primary productivity can be measured using The Normalized Difference Vegetation Index (NDVI). NDVI is derived from remotely sensed satellite images and is calculated by dividing the difference of the near-infrared band and the red band by the sum of the near infrared and red band (NIR-Red)/(NIR+Red) (Jensen 2007, Pettorelli et al. 2011). This measurement is closely linked to leaf area index, canopy cover and other measures of plant productivity (Myneni et al. 1995, Hicke et al. 2002, Wang et al. 2005, Pettorelli et al. 2011). For birds, increased plant productivity leads to increased food resources in the form of greater arthropod abundance (Lassau and Hochuli 2007) and fruit yield (Mann et al. 2010). The use of NDVI has proven to be successful and widely applicable in a number of different wildlife studies (Pettorelli et al. 2011). For example, Renfrew et al. (2013) found that declines in productivity led bobolinks (*Dolichonyx oryzivorus*) to depart their breeding grounds and stopover sites early. In addition, NDVI appears to be positively correlated with population trends in barn swallows and American redstarts (*Setophaga ruticilla*) (Saino et al. 2004, Wilson et al. 2011). Our study will make use of NDVI measurements of sites used at distinct phases throughout the annual cycle (breeding, moulting, and overwintering) to examine how primary productivity impacts Bullock's oriole breeding abundances.

Environmental impacts

In migratory animals, carry-over effects occur when a phenomenon influencing an individual or population in one phase of the annual cycle has an impact on a subsequent phase (Inger et al. 2010). In order to be able to gauge how geographically and temporally separated events carry over to influence future outcomes, one must examine multiple phases of a bird's annual cycle. In the previous section, I described stable isotope analysis and remote sensing techniques. Both have revealed interesting carry-over effects in migratory birds. For example, stable carbon isotope analysis has been used to demonstrate that winter habitat quality can influence breeding arrival times and reproductive success (Marra et al. 1998, Norris et. al. 2004, Reudink et al. 2009a), as well as body condition on the breeding grounds (Bearhop et al. 2004). Similarly Saino et al. (2004) found that adult barn swallows (*Hirundo rustica*) arrived on their breeding grounds earlier, had earlier breeding dates and increased clutch sizes when the birds wintered in areas with more favourable conditions (i.e, with high NDVI values). These carry-over effects highlight the need for a comprehensive annual cycle approach to understanding migratory bird ecology and evolution. Although most bird species moult on their breeding grounds before beginning fall migration, some stopover en rount, make use of a moult location in the fall. This adds another layer of complexity and the potential for additional carryover effects.

Bird survival and abundance can be closely linked to environmental factors such as climate patterns and plant productivity. These factors affect individuals and populations at all stages of their life cycles. Climate and primary productivity are closely linked to the availability of resources, and relative habitat quality for migratory birds. Precipitation, temperature, and wind can influence birds in a number of ways. For example, increasing temperatures negatively influence populations of yellow-billed cuckoos (*Coccyzus americanus*) (Anders and Post 2006). Large scale climate patterns such as those caused by the El Nino Southern Oscillation (ENSO) can dramatically influence rainfall patterns and, by extension, plant and animal communities across North America. ENSO has been found to lower survival rates in drier years (Sillett et al. 2000), and accounts for a large part of the variation in reproductive success in a number of birds (Nott et al. 2002). These studies, in addition to those previously described, which examined plant productivity through NDVI, demonstrate how variation in climate and environment have important consequences for migratory bird species.

Moult and migration are two of the most energetically demanding aspects of a bird’s annual cycle (Lindstrom et. al. 1993). Most migratory songbirds have two distinct stationary phases (breeding and overwintering) in their annual cycle. However, in western North America, a small number of songbirds including Bullock’s oriole, lazuli bunting (*Passerina amoena*), Lucy’s warbler (*Vermivora luciae*), black-headed grosbeak (*Pheucticus* *melanocephalus*), western kingbird (*Tyrannus verticalis*), warbling vireo (*Vireo gilvus*), ash throated flycatcher (*Myiarchus cinerascens*), and western tanager (*Piranga ludoviciana*)), employ a strategy that includes at least one stopover during fall migration, during which they moult (Leu and Thompson 2002, Rohwer et al. 2005, Pyle et al. 2009); species with this strategy are referred to as moult-migrants. It is believed that the Mexican monsoon region in which these birds moult provides abundant resources following annual summer rains. These resources become available just as the birds' breeding regions are becoming drier and less productive (Leu and Thompson 2002, Rohwer et al. 2005, Pyle et al. 2009). Thus, this monsoon region is potentially important to all Western moult-migrant songbirds. My thesis examines moult-migration of one of these species, the Bullock's oriole, and the influence of environment from each phase of the annual cycle on its breeding abundance.

Bullock's orioles

The Bullock's oriole (Figure 1.1) is a relatively small, migratory songbird with brilliant yellow to orange plumage in adulthood. Relatively few studies have been conducted on Bullock's orioles, and most are limited to the breeding grounds. Little is known about migratory connectivity of Bullock's oriole or its ecology and behaviour on the wintering grounds (Rising and Williams, 1999). Bullock's orioles make use of a stopover site in the Southwestern United States or Northwestern Mexico during fall migration to moult before moving on to their overwintering grounds (Leu and Thompson 2002, Rohwer et al. 2005, Pyle et al. 2009). By analyzing the differences between the stable hydrogen isotope signatures of feathers, which grown during moult, and claws, which are continuously growing, we can determine if these tissues were grown in different locations and investigate moult-migration in detail. In addition, Bullock's orioles are large enough to be fitted with geolocators, have very high breeding site fidelity (mean distance between nests of adult males: 111 m) (Rising and Williams 1999), and a high adult return rate (31-79%) (Butcher 1991), which increases the chance of retrieving geolocators fitted to individuals in one year upon their return to their breeding sites the following spring. Using Bullock's orioles for this study gives us an opportunity to investigate moult migration with tracking techniques that have so far been used on only a single species, an eastern moult migrant, the painted bunting

(*Passerina ciris)* (Contina et al. 2013). The goal of my thesis is to gain a more complete picture of moult-migration in Bullock's orioles and to understand how environmental factors influence Bullock's oriole populations during each phase of their annual cycle.

Literature cited

Anders, A. D., and E. Post. 2006. Distribution-wide effects of climate on population densities of a declining migratory landbird. Journal of Animal Ecology 75:221-227.

Bearhop, S., G. M. Hilton, S. C. Votier, and S. Waldron. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:S215–S218.

Boone, R. B., S. J. Thirgood, and J. G. C. Hopcraft. 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. Ecology 87:1987–1994.

Bowen G. J., and J. B. West. 2008. Isotope Landscapes for Terrestrial Migration Research. Pages 79-105 in K. A. Hobson, and L. I. Wassenaar, editors. Tracking animal migration with stable isotopes. Elsevier, London, UK.

Bowlin, M. S., I.-A. Bisson, J. Shamoun-Baranes, J. D. Reichard, N. Sapir, P. P. Marra, T. H. Kunz, D. S. Wilcove, A. Hedenström, and C. G. Guglielmo. 2010. Grand challenges in migration biology. Integrative and Comparative Biology 50:261–279.

Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. Hartl, R. Kays, J. F. Kelly, and W. D. Robinson. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. BioScience 61:689–698.

van den Brink, B., R. G. Bijlsma, and T. M. Van der Have. 2000. European Swallows *Hirundo rustica* in Botswana during three non-breeding seasons: the effects of rainfall on moult. Ostrich 71:198-204.

Butcher, G. S. 1991. Mate choice in female northern orioles with a consideration of the role of the black male coloration in female choice. The Condor 93:82-88.

Carroll, M.L., C.M. DiMiceli, R.A. Sohlberg, and J.R.G. Townshend. 2004. 250m MODIS Normalized Difference Vegetation Index, 250ndvi28920033435, Collection 4, University of Maryland, College Park, Maryland, Day 289, 2003.

Commission for Environmental Cooperation (Montréal, Q., and Secretariat. 1997. Ecological regions of North America: toward a common perspective. The Commission.

Comrie, A. C., and E. C. Glenn. 1998. Principal components-based regionalization of precipitation regimes across the southwest United States and northern Mexico, with an application to monsoon precipitation variability. Climate Research 10:201-215.

Contina, A., E. S. Bridge, N. E. Seavy, J. M. Duckles, and J. F. Kelly. 2013. Using geologgers to investigate bimodal isotope patterns in Painted Buntings (*Passerina ciris)*. The Auk 130:265–272.

Delmore, K. E., J. W. Fox, and D. E. Irwin. 2012. Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. Proceedings of the Royal Society of London Series B: Biological Sciences 279:4582-4589.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. M. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. The American Naturalist 158:17-35.

Hallworth, M. T., C. E. Studds, T. S. Sillett, and P. P. Marra. 2013. Do archival light-level geolocators and stable hydrogen isotopes provide comparable estimates of breeding-ground origin? The Auk 130:273-282.

Heckscher, C. M., S. M. Taylor, J. W. Fox, and V. Afanasyev. 2011. Veery (*Catharus fuscescen*s) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. The Auk 128:531–542.

de la Hera, I., J. A. Díaz, J. Pérez-Tris, and J. Luis Tellería. 2009. A comparative study of migratory behaviour and body mass as determinants of moult duration in passerines. Journal of Avian Biology 40:461–465.

Hicke, J. A., G. P. Asner, J. T. Randerson, C. Tucker, S. Los, R. Birdsey, J. C. Jenkins, and C. Field. 2002. Trends in North American net primary productivity derived from satellite observations, 1982–1998. Global Biogeochemical Cycles 16:2–1–2–14.

Hobson, K. A., R. T. Alisauskas, and R. G. Clark. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. The Condor 95:388-394.

Hobson, K. A., Y. Aubry, and L. I. Wassenaar. 2004. Migratory connectivity in Bicknell's Thrush: Locating missing populations with hydrogen isotopes. The Condor, 106:905-909.

Hobson K. A., and D. R. Norris 2008. Animal Migration. Pages 1-19 in K. A. Hobson, and L. I. Wassenaar, editors. Tracking animal migration with stable isotopes. Elsevier, London, UK.

Hobson K. A. 2008. Isotopic Methods to Track Animal Movements. Pages 45-78 in K. A. Hobson, and L. I. Wassenaar, editors. Tracking animal migration with stable isotopes. Elsevier, London, UK.

Hobson, K. A., S. L. Van Wilgenburg, K. Larson, and L. I. Wassenaar. 2009. A feather hydrogen isoscape for Mexico. Journal of Geochemical Exploration 102:167–174.

Hobson, K. A., S. L. Van Wilgenburg, L. I. Wassenaar, and K. Larson. 2012. Linking hydrogen (δ2H) isotopes in feathers and precipitation: sources of variance and consequences for assignment to isoscapes. PLoS One 7:e35137.

Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecological Monographs 56:201-220.

Holmes, R. T., T. W. Sherry, P. P. Marra, and K. E. Petit. 1992. Multiple brooding and productivity of a Neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. The Auk 109:321-333.

Hutto, R. L. 1998. On the importance of stopover sites to migrating birds. The Auk 115:823-825.

Illera, J. C., and M. Díaz. 2006. Reproduction in an endemic bird of a semiarid island: a food-mediated process. Journal of Avian Biology 37:447-456.

Inger, R., X. A. Harrison, G. D. Ruxton, J. Newton, K. Colhoun, G. A. Gudmundsson, G. McElwaine, M. Pickford, D. Hodgson, and S. Bearhop. 2010. Carry-over effects reveal reproductive costs in a long-distance migrant. Journal of Animal Ecology 79:974–982.

Jensen J. R. (2007) Remote sensing of the environment: an earth resource perspective, 2nd edition. Prentice Hall, Upper Saddle River, NJ, USA

Kelly, J. F., V. Atudorei, Z. D. Sharp, and D. M. Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia 130:216–221.

Ktitorov, P., F. Bairlein, and M. Dubinin. 2008. The importance of landscape context for songbirds on migration: body mass gain is related to habitat cover. Landscape Ecology 23:169–179.

Langin, K. M., M. W. Reudink, P. P. Marra, D. R. Norris, T. K. Kyser, and L. M. Ratcliffe. 2007. Hydrogen isotopic variation in migratory bird tissues of known origin: implications for geographic assignment. Oecologia 152:449–457.

Lassau, S. A., and D. F. Hochuli. 2008. Testing predictions of beetle community patterns derived empirically using remote sensing. Diversity and Distributions 14:138-147.

Laughlin, A. J., C. M. Taylor, D. W. Bradley, D. Leclair, R. C. Clark, R. C, R. D. Dawson, P. O. Dunn, A. Horn, M. Leonard, D. R. Sheldon, D. Shutler, L. A. Whittingham, D. W. Winkler, and D. R. Norris. 2013. Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. The Auk 130:230-239.

Leu, M., and C. W. Thompson. 2002. The potential importance of migratory stopover sites as flight feather molt staging areas: a review for neotropical migrants. Biological Conservation 106:45–56.

Lindstrom, A., G. H. Visser, and S. Daan. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. Physiological Zoology 66:490–510.

Link, W. A. and J. R. Sauer. 2002. A hierarchical analysis of population change with application to Cerulean Warblers. Ecology 83:2832-2840.

Link, W. A. and J. R. Sauer. 2007. Seasonal components of avian population change: joint analysis of two large-scale monitoring programs. Ecology 88:49-55.

Link, W. A. and R. J. Barker. 2010. Bayesian inference with ecological applications. Academic Press, London, UK.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS-a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10:325–337.

Mann, K. K., A. W. Schumann, and T. A. Obreza. 2011. Delineating productivity zones in a citrus grove using citrus production, tree growth and temporally stable soil data. Precision Agriculture 12:457-472.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Meehan, T. D., J. T. Giermakowski, and P. M. Cryan. 2004. GIS-based model of stable hydrogen isotope ratios in North American growing-season precipitation for use in animal movement studies. Isotopes in Environmental and Health Studies 40:291–300.

Myneni, R. B., F. G. Hall, P. J. Sellers, and A. L. Marshak. 1995. The interpretation of spectral vegetation indexes. Geoscience and Remote Sensing, IEEE Transactions on 33:481–486.

Newton, I. 2011. Migration within the annual cycle: species, sex and age differences. Journal of Ornithology, 152:169-185.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society of London Series B: Biological Sciences 271: 59-64.

Nott, M. P., D. F. Desante, R. B. Siegel, and P. Pyle. 2002. Influences of the El Niño/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America. Global Ecology and Biogeography 11:333–342.

Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.

Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15–27.

Pyle, P. 1997. Identification Guide to North American Birds: A Compendium of Information on Identifying, Ageing, and Sexing Waterbirds, Diurnal Raptors, and Gallinaceous Birds in the Hand. Slate Creek Press, Bolinas, CA, USA.

Pyle, P., W. A. Leitner, L. Lozano-Angulo, F. Avilez-Teran, H. Swanson, E. G. Limón, and M. K. Chambers. 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. The Condor 111:583–590.

Quinlan, S. P., and D. J. Green, 2011. Variation in deuterium (δD) signatures of Yellow Warbler *Dendroica petechia* feathers grown on breeding and wintering grounds. Journal of Ornithology 152:93-101.

Renfrew, R. B., D. Kim, N. Perlut, J. Smith, J. Fox, and P. P. Marra. 2013. Phenological matching across hemispheres in a long-distance migratory bird. Diversity and Distributions 19:1008–1019.

Reudink, M. W., P. P. Marra, T. K. Kyser, P. T. Boag, K. M. Langin, and L. M. Ratcliffe. 2009a. Non-breeding season events influence sexual selection in a long-distance migratory bird. Proceedings of the Royal Society of London Series B: Biological Sciences 276:1619–1626.

Reudink, M. W., C. E. Studds, P. P. Marra, T. K. Kyser, and L. M. Ratcliffe. 2009b. Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American redstart *Setophaga ruticilla*. Journal of Avian Biology, 40:34-41.

Rising, J. D. and P. L. Williams. 1999. Bullock's Oriole (*Icterus bullockii*). in A. Poole and F. Gills editors, The Birds of North America, No. 416. The Birds of North America Inc., Philadelphia, PA, USA.

Robinson, W. D., M. S. Bowlin, I. Bisson, J. Shamoun-Baranes, K. Thorup, R. H. Diehl, T. H. Kunz, S Mabey, and D. W. Winkler. 2009. Integrating concepts and technologies to advance the study of bird migration. Frontiers in Ecology and the Environment 8:354-361.

Rohwer, S., and J. Manning. 1990. Differences in timing and number of molts for Baltimore and Bullock's orioles: Implications to hybrid fitness and theories of delayed plumage maturation. The Condor:125–140.

Rohwer, S., L. K. Butler, D. R. Froehlich, R. Greenberg, and P. P. Marra. 2005. Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. Pages 87-105 in R. Greenberg, and P. P. Marra, editors. Birds of Two Worlds: The Ecology and Evolution of Migration Johns Hopkins University Press, Baltimore, MD, USA.

Rubenstein, D. R., and K. A. Hobson. 2004. From birds to butterflies: animal movement patterns and stable isotopes. Trends in Ecology & Evolution 19:256–263.

Ryder, T. B., J. W. Fox, and P. P. Marra. 2011. Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geolocator and mark-recapture data. The Auk 128:448–453.

Saino, N., T. Szép, R. Ambrosini, M. Romano, and A. P. Moller. 2004. Ecological conditions during winter affect sexual selection and breeding in a migratory bird. Proceedings of the Royal Society of London Series B: Biological Sciences 271:681–686.

Sanz, J. J., J. Potti, J. Moreno, S. Merino, and O. Frías. 2003. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. Global Change Biology 9:461-472.

Sauer, J. R., and W. A. Link. 2011. Analysis of the North American breeding bird survey using hierarchical models. The Auk 128:87–98.

Seagle, S. W., and B. R. Sturtevant. 2005. Forest productivity predicts invertebrate biomass and ovenbird (*Seiurus aurocapillus*) reproduction in Appalachian landscapes. Ecology 86:1531-1539.

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology 79:2057-2070.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040–2042.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Smith, A. D., K. Donohue, and A. M. Dufty Jr. 2008. Intrafeather and intraindividual variation in the stable-hydrogen isotope (δD) content of raptor feathers. The Condor 110:500-506.

Studds, C. E., and P. P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86:2380–2385.

Studds, C. E., K. P. McFarland, Y. Aubry, C. C. Rimmer, K. A. Hobson, P. P. Marra, and L. I. Wassenaar. 2012. Stable-hydrogen isotope measures of natal dispersal reflect observed population declines in a threatened migratory songbird. Diversity and Distributions 18:919–930.

Stutchbury, B. J., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. Science 323:896–896.

Tøttrup, A. P., R. H. G. Klaassen, M. W. Kristensen, R. Strandberg, Y. Vardanis, Å. Lindström, C. Rahbek, T. Alerstam, and K. Thorup. 2012. Drought in Africa caused delayed arrival of European songbirds. Science 338:1307–1307.

Wang, Q., S. Adiku, J. Tenhunen, and A. Granier. 2005. On the relationship of NDVI with leaf area index in a deciduous forest site. Remote Sensing of Environment 94:244–255.

Wassenaar, L. I., and K. A. Hobson. 2000. Stable-carbon and hydrogen isotope ratios reveal breeding origins of red-winged blackbirds. Ecological Applications 10:911–916.

Wassenaar, L. I., and K. A. Hobson. 2003. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. Isotopes in Environmental and Health studies 39: 211-217.

Wassenaar, L. I. 2008. An Introduction to Light Stable Isotopes for Use in Terrestrial Animal Migration Studies. Pages 21-44 in K. A. Hobson, and L. I. Wassenaar, editors. Tracking animal migration with stable isotopes. Elsevier, London, UK.

Webster, M. S., P. P. Marra, R. Greenberg, and P. P. Marra. 2005. The importance of understanding migratory connectivity and seasonal interactions. Birds of two worlds: the ecology and evolution of migration. Johns Hopkins University Press, Baltimore, Maryland, USA:199–209.

Wilson, S., S. L. Ladeau, A. P. Tøttrup, P. P. Marra. 2011. Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. Ecology 92: 1789-1798.

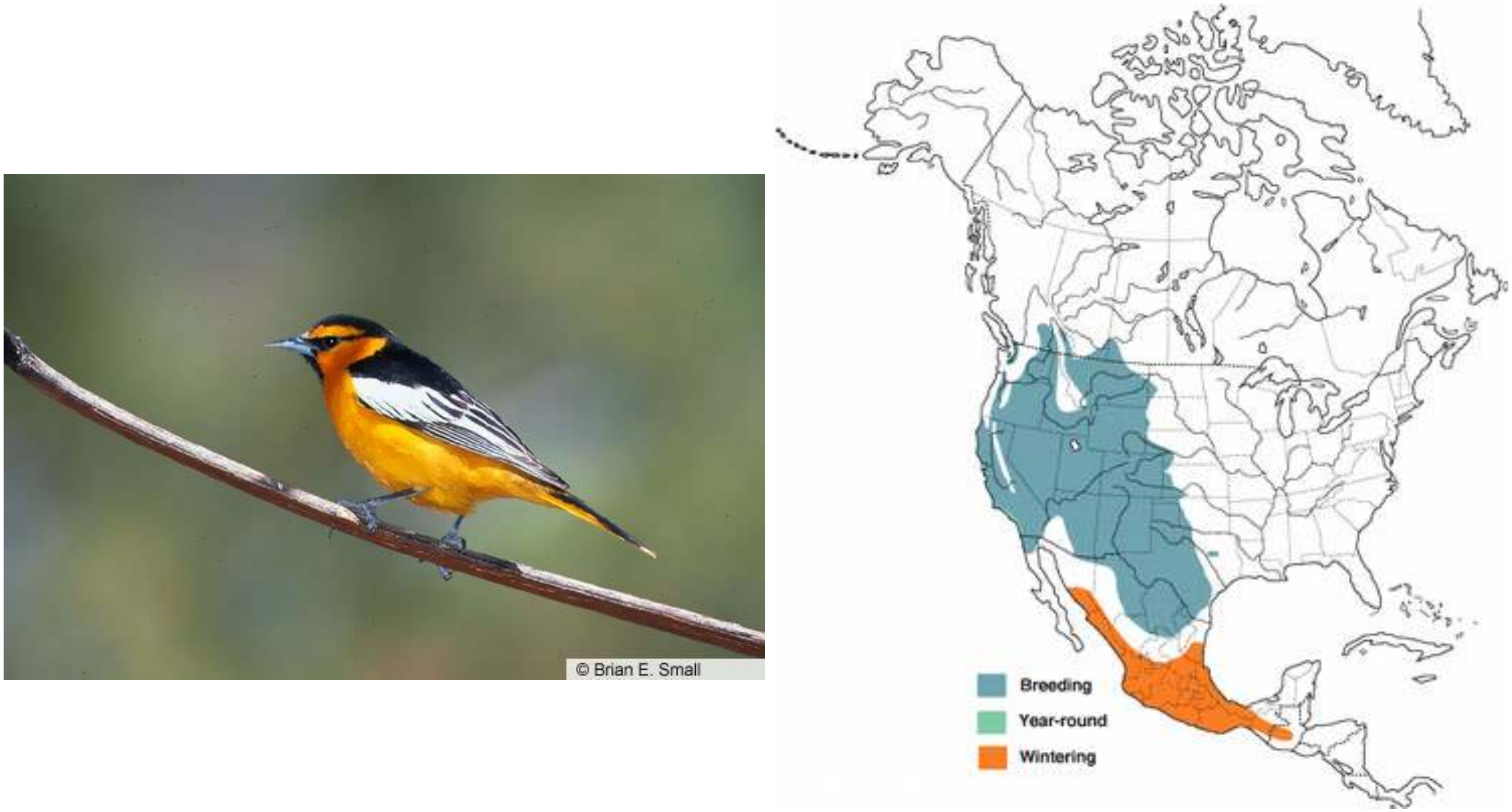

Figure 1.1: ASY Male Bullock's oriole (Left) (Image © Brian E. Small) Bullock's oriole range map (Right) (Rising and Williams 1999).

CHAPTER 2: INVESTIGATING MOULT-MIGRATION IN BULLOCK'S ORIOLES

Abstract

In contrast to the majority of migratory songbirds in Western North America, which moult on their breeding grounds, Bullock's oriole (*Icterus bullockii*) is one of a small number of species that appear to stop during fall migration to moult en-route to the wintering grounds. These birds seem to take advantage of food resources in the Mexican monsoon region, which may be more abundant compared to what is typically available on their breeding grounds during the same time period. We studied a population of Bullock's orioles at the northern extent of their breeding range in Kamloops, BC Canada. Using a combination of stable hydrogen isotope analysis and light-level geolocators, we found evidence to support the existence of moult-migration, with all birds appearing to make use of the Mexican monsoon region for moult in an extended stopover period during fall migration. Claw and feather samples showed differing hydrogen isotope signatures, indicating that moult was occurring away from the wintering grounds. Stable hydrogen isotope findings supported widespread occurrence of moult-migration in Bullock's orioles and were largely consistent across differing age groups and sexes, generally supporting a complete pre-basic moult in adults and at least partial moult in first-year orioles. Geolocator data were retrieved from three birds, two of which provided complete data. The two birds tracked throughout the annual cycle showed a prolonged stopover (73 & 80 days) in the Mexican monsoon region followed by a short migration to central and eastern Mexico for overwintering. All three birds showed variation in the duration and route of migration, as well as moult-stopover and overwintering sites. Our results confirm that this northern population of Bullock's orioles employ a moult-migration strategy and highlight the usefulness of combining stable isotope and geolocator studies. Our study also illustrates the importance of the Mexican monsoon region for Bullock's orioles and other western moult-migrants.

Introduction

Breeding, moult, and migration are three of the most energy intensive events in the life of migratory birds (Lindstrom et. al. 1993). As a result, they typically occur at different times. Most songbird species undergo a single complete moult, replacing all their feathers on or near their breeding grounds; some species have an additional, pre-alternate moult, consisting primarily of body feathers, on the wintering grounds (Pyle et al. 1997). The moult-migration strategy in which a small number of species interrupt fall migration to fully or partially moult en route at a stopover site is relatively rare (Newton 2011, Pyle et al. 2009). Understanding the ecological and evolutionary pressures that led to this unique strategy requires a thorough exploration of the prevalence of this behaviour among species, as well as intraspecific differences in the timing, extent, and pattern of migration and moult.

Several western North American songbirds, including Bullock's oriole (*Icterus bullockii*), lazuli bunting (*Passerina amoena*), Lucy's warbler (*Vermivora luciae*), black-headed grosbeak (*Pheucticus melanocephalus*), western kingbird (*Tyrannus verticalis*), warbling vireo (*Vireo gilvus*), ash throated flycatcher (*Myiarchus cinerascens*), and western tanager (*Piranga ludoviciana*) all have a distinctive moult-migration strategy (Leu and Thompson 2002, Pyle et al. 2009, Rohwer et al. 2005). These species, termed moult-migrants, appear to forego a moult on the breeding grounds, instead interrupting migration to stop in the Southwestern US Southwest and Northwestern Mexico for their moult (Leu and Thompson 2002, Rohwer et al. 2005, Pyle et al. 2009), and timing stopover to coincide with an increase in food abundance following late summer monsoon rains (Rohwer and Manning 1990, Rohwer et al. 2005). Stopover sites such as that in the Mexican monsoon region may thus be crucial, as they provide abundant resources allowing birds to build up vital fat stores, and grow high quality plumage important for both flight and communication (Hutto 1998, Leu and Thompson 2002). However, it is unclear whether the monsoon region is important because it provides more abundant resources than are present on the breeding grounds or if it simply provides adequate resources for a long enough period of time for birds to complete their moult (Butler, 2013). Moulting site fidelity in Western North American moult-migrants appears to be low, with local environmental factors playing an important role in the spatial distribution of birds during the moult period. A study by Pyle et al. (2009) over two years demonstrated that during a wet year, moult-migrants spread out into more xeric regions, while in a drier year birds appeared to cluster around riparian areas. All of the western moult-migrants have been detected in the Mexican monsoon region, but not every combination of species, sex, and age group have been found undergoing moult in the area, making it unclear as to the general importance of this region and the generality of stopover moult behaviour (Pyle et al. 2009).

Until recently, it has been extremely difficult to track small migratory birds throughout the year. Currently, a useful technique for delineating location information and habitat use of migratory birds is stable-isotope analysis (Rubenstein and Hobson 2004). Isotopes are incorporated into growing animal tissue from the food and water they ingest, though some exchange of isotopes can also occur between tissue and the surrounding environment (Wassenar 2008). It is thus the ratio of non-exchangeable, stable isotopes in animal tissues that reflects both the environment in which the tissue was grown, and the diet of the individual (Wassenar 2008). Because tissues may be grown in different locations or temporally discrete periods, these analyses have been used to infer spatial and dietary information for a number of species, revealing patterns of migratory connectivity (Hobson et al. 2004), habitat use (Bearhop et al. 2004), and important carry-over effects (Marra et al. 1998). Stable-carbon isotope analysis of the claws of migrating black-throated blue warblers (*Dendroica caerulescens*) revealed that body condition is influenced by the habitat quality of their overwintering sites (Bearhop et al. 2004). Similarly, work on American redstarts (*Setophaga ruticilla*) demonstrated that birds overwintering in wetter tropical habitats, as inferred by stable-carbon isotope analysis, arrive on the breeding grounds earlier and in better condition, and ultimately experience higher reproductive success (Marra et al. 1998, Norris et al. 2004, Reudink et al. 2009a). Stable-hydrogen isotope ratios can provide a rough latitudinal approximation, as the ratio of deuterium to hydrogen increases with proximity to the equator (Hobson 2008). Using information from isoscape maps and stable hydrogen isotope analysis of animal tissues, we can determine the general area in which a bird has moulted in. For example, if a bird moults on their breeding grounds, feathers from individuals captured at overwintering sites can allow us to determine where the feather was initially grown, thus linking breeding and wintering populations (Wassenaar and Hobson 2000, Hobson 2008). Stable hydrogen isotope analysis has been used to link breeding and wintering grounds in Bicknell's thrush (*Catharus bicknelli*) (Hobson et al. 2004) and many other species (Wassenar and Hobson, 2000, Kelly et al. 2002, Rubenstein et al. 2002). A recent study by Quinlan and Green (2010) found that overwintering yellow warblers could be assigned to breeding grounds using stable hydrogen isotope analysis, but suggested that interannual variation in feathers grown on the wintering grounds, combined with weak gradients in precipitation isotopes make it difficult to assign winter habitat using isotope signatures and isoscape maps alone. In addition to linking wintering and breeding grounds, stable hydrogen isotope analysis has shown the range of natal dispersal in Bicknell's thrush and how that range has declined over time (Studds et al. 2012).

Although stable isotope analysis can prove useful spatial information gleaned from its use is limited. Naturally occurring stable isotopes can have similar ratios across expansive areas, and thus may show considerable variation within populations (Langin et al. 2007). On the other hand, Global Positioning System (GPS) tracking of individuals can provide incredibly detailed information about migratory routes; at present, however, these devices are still relatively heavy and thus are limited to use on larger birds (Bridge et al. 2011). Currently, geolocators are the only feasible option for tracking the timing and route of migration in smaller birds. (Bridge et al. 2011). Geolocators are small light sensors and data loggers that record time of day and ambient light levels using sunrise and sunset to determine the geographical location of the device (Bridge et al. 2011). Early work with geolocators revealed faster than expected migration speeds in purple martin (*Progne subis*) and wood thrush (*Hylocichla mustelina*) (Stuchbury et al. 2009). Recently, their use has exploded, and is providing new insights into the ecology of migratory birds. For example, geolocators haverevealed longer than expected migration and multiple over-wintering sites in veeries (*Catharus fuscescens*) (Heckscher et al. 2011). Migratory connectivity has also been estimated in gray catbirds showing different wintering sites for breeding populations in the Eastern and Mid-Western United States (Ryder et al. 2011). Differences in migratory routes, stopover locations, and wintering sites have also been detected in coastal and inland subspecies of Swainson's thrush (*Catharus ustulatus*) (Delmore et al. 2012). Geolocators, when combined with bird survey and weather data, revealed a potentially important stopover location for tree swallows (*Tachycineta bicolor*) (Laughlin et al. 2013). Combining use of geolocators with isotopic data, can be particularly informative. A comparison between geolocator and feather hydrogen isotope data in ovenbirds (*Seiurus aurocapilla*) demonstrated that the two techniques can support each other, but also showed that the use of isotopes alone could lead to incorrect interpretations of migratory connectivity (Hallworth et al. 2013). To date, only one study has examined moult-migration using stable hydrogen isotopes and geolocators. This study, of an eastern moult-migrant, the painted bunting, revealed differing moult-migration strategies for individuals of the same breeding population (Contina et al. 2013). No study has used geolocators to examine moult-migration in western songbirds.

Among western songbirds, Bullock's oriole is an ideal species to investigate moult-migration. Bullock's orioles are small (adults: 29-42g), colourful, icterid songbirds that breed as far north as the Southern Interior of British Columbia and overwinter as far south as Costa Rica. Bullock's orioles have a moderate to high rate of return to the breeding grounds rate 31-79% (Butcher 1991) and high breeding site fidelity averaging 111m between nesting sites from one year to the next, making them an ideal species on which to deploy geolocators (Rising and Williams 1999). With the exception of a population in southern California that is resident, adult, after second year (ASY) birds appear to leave their breeding areas prior to moulting, and undergo a complete pre-basic moult in the Mexican monsoon region before arriving in the wintering areas (Rising and Williams 1999). The completion of moult prior to arrival in the over-wintering areas suggests that, in this species at least, the phenomenon is not discretionary (Pyle et al. 2009).

Using stable hydrogen isotope analysis of tail feathers, breast feathers, and claws from all age and sex classes, combined with data from geolocators, we examined the prevalence and pattern of moult migration in Bullock's Orioles at the Northern extent of their range. We predicted that the flight and breast feathers of adult (ASY) orioles would show a stable hydrogen isotope ratio consistent with the monsoon region, indicating that moult-migration had taken place. Tail feathers for SY birds would likely show variation in moult location, as rectrices are initially grown in the nest, but SY birds may replace a variable number of tail feathers in the monsoon region (Pyle et al. 1997). Isotopically, breast feathers in SY birds should be consistent with moult in the monsoon region. We also predicted that claw samples would show more positive (more enriched in deuterium) hydrogen isotope signatures than feathers, consistent with wintering in Mexico or Central America, In addition, we expected the geolocator data to reflect the same pattern of moult stopover and the same general wintering region indicated by stable isotope data.

Methods

Field Methods

Our study sites were located in Kamloops, BC Canada (50.68 N 120.34 W) at the northern extent of the Bullock's oriole range. Using a combination of passive mist netting around oriole feeders and active targeting using mist nets, a decoy, and song playback, we caught a total of 45 birds over two field seasons; 31 in 2012 (18 ASY Males, 4 ASY Females, 2 SY Males, and 7 SY Females), and 20 in 2013 (10 ASY Males, 7 ASY Females, 2 SY Males, and 1 SY Females), including a total of 6 between-year recaptures (3 with geolocators). Each captured bird was banded with a Canadian Wildlife Service-issued aluminum band and a unique combination of colour bands for individual identification. From each bird, we acquired breast feathers, a tail feather, and a claw sample. Claw samples were collected within two weeks of the birds' arrival on the breeding ground to try to ensure hydrogen isotope signatures reflected winter conditions.

Stable Hydrogen Isotope Analysis

We conducted our stable hydrogen isotope analysis at the Smithsonian Institution OUSS/MCI Stable Isotope Mass Spectrometry Facility in Suitland, MD. We washed feather samples in a 2:1 chloroform-methanol solution, and then allowed them to dry and acclimate to the atmospheric conditions of the lab in a fume hood for over 72 hours prior to sample preparation and analyses. Approximately 0.30-0.40 mg of feather and claw samples were weighed and crushed in silver capsules. We then pyrolyzed these samples in a Thermo TC/EA elemental analyzer at 1,350 °C and analyzed then using a Thermo Delta V Advantage isotope ratio mass spectrometer. Isotope ratios reported (δ^2H) are relative to Vienna Standard Mean Ocean Water. Four standards were run for every 10 samples including the hydrogen standard International Atomic Energy Agency (IAEA-CH-7) and three additional standards

(KHS, CBS, Spectrum keratin). Measurements of the same feather were repeatable to within 3 ± 2 ‰ (mean ± SD, n = 10). Non-exchangeable δ^2H values were corrected to keratin standards following Wassenar and Hobson (2003). Predicted breeding ground (mean: 157 ± 10 ‰ SD) and moulting ground (mean: 77 ± 20 ‰ SD) feather isotope ratios were estimated using a precipitation isoscape map (Meehan et al. 2004) with a 50km buffer surrounding our study site in Kamloops, BC for the breeding ground. The Mexican monsoon region was delinated as described by Comrie and Glenn (1998). Moulting tissue isotope fractionation was estimated using the precipitation δ^2H to feather-tissue δ^2H fractionation equation for non-ground foraging Neotropical migrants from (Hobson et al. 2012). Predicted wintering ground (-76 to -45 ‰) feather isotope values were estimated using a feather isoscape map of Mexico (Hobson et al. 2009).

Geolocators

We deployed 1.2 g British Antarctic Survey (BAS) Mk10s geolocators on 17 ASY male Bullock's Orioles caught during the 2012 field season (mid-May to early-July), and were able to recover three in 2013. We attached the geolocators to birds via a leg loop harness made of Stretch Magic™, an elastic cord commonly used for bead crafts. Geolocators measure light intensity levels at one minute intervals and allow us to estimate the locations of birds at noon and midnight on given dates, based on changes in sunrise and sunset times. Of these three geolocators, two functioned for an entire annual cycle, while the other lost power during fall migration. We calibrated individual geolocators using recorded locations of the orioles while the birds were still on the breeding ground for a minimum of 11 days and a maximum of 14 days and using individual solar angles of -2.4, -2.5, and -3.1 degrees. Using the BASTrak suite of geolocator software, we downloaded, decompressed, and examined each individual light response curve in TransEdit2. We eliminated dates within 20 days of the spring and fall equinoxes, as latitudinal location estimates become extremely poor during these periods. We also eliminated dates in which an obvious shading event detected through examining the sunrise and sunset transition, or a significant amount of noise was occurred close to sunrise or sunset (18/416 + 3/72 + 76/383 = 97 of 871 days 11% of total). Because there is very little known about the behaviour of Bullock's orioles away from the breeding grounds, we used only the midnight location estimates during stationary phases off the breeding grounds, as the birds should be staying in one spot (i.e., not in flight) at this time (Rising and Williams 1998). As location was known during the breeding season, and the birds may be migrating during the night, we used both midnight and noon positions for these phases. We estimated error (range: 1 to 309km, latitude: 90 ± 63 SD, 88 ± 67 SD, 87 ± 69 SD km, longitude: 54 ± 42 SD, 69 ± 59 SD, 81 ± 71 SD km for birds 24, 22, and 41) in measurement while the birds were known to be on their breeding site in 2012. Stopover sites were determined if the stay was ≥ 14 days. Using ESRI's ArcGIS, we ran kernel density estimates (50%, 75%, and 90% of maximum density) with an output cell size of 1 km and a search radius of 309 km. These kernel density estimates were converted to polygons and mapped.

Statistical Analysis

We used mixed models with δ^2H as a response variable, tissue type and year as fixed effects, and band number as a random effect since some birds were present in both years. Where year was not significant, we eliminated it as a fixed effect and re-ran the models without it. When examining differences in δ^2H between male and female orioles, we separated age classes and built mixed models using sex and year as a main effect and individual as a random effect. Similarly, when we examined differences in δ^2H between ASY and SY orioles, we separated by sex and built mixed models using δ^2H as response variable, age and year as main effects and individual as a random effect. We also used paired t-tests to examine differences in δ^2H values in tissues within individuals within sex and age classes. Outliers were detected using 1.5*Inter Quartile Range (IQR) for all samples pooled.

Results

Comparisons among tissues

When we examined differences among tissues in ASY males (tail feathers, breast feathers, claws), we found that δ^2H signatures differed significantly among all tissue types (mixed model: n = 60, F = 14.58, p < 0.0001) (Figure 2.1). Two outlier claw samples had δ^2H signatures (96.6 and 99.6 ‰) that were consistent with a location south of the breeding grounds, but far north of the wintering grounds. This was potentially due to the birds either arriving in more northern latitudes earlier, or taking a longer time during spring migration, thus allowing the claws to begin incorporating the isotope signature of the higher latitude areas en route. Although the analyses reported below exclude these two unusual claw samples, results from each of the same tests containing the outliers are reported in Appendix A.

We detected no year effects in any model, thus all results are shown with the effect of year removed from the model. Claws exhibited the highest δ^2H values (n = 6, mean ± SD = -58 ± 4), followed by breast (n = 28, mean ± SD = -71 ± 12) and tail (n = 26, mean ± SD = -79 ± 10). Pairwise comparisons revealed that breast feathers and tail feathers differed significantly (breast and tail (n_{breast} = 28, n_{tail} = 26, F = 22.45, p <0.0001), as did tail feathers and claw (n_{claw} = 6, n_{tail} = 26, F = 14.58, p < 0.0001), though there was no difference between breast feathers and claws (n_{breast} = 28, n_{claw} = 6, F = 3.51, p = 0.09). Matched-pairs t-tests for ASY male orioles revealed similar trends within individuals: breast and tail feathers differed significantly (n = 26, t = -4.41, p = 0.0002), while there was no difference between breast feathers and claws (n = 6, t = 1.41, p = 0.22). Tail feathers and claws showed significant differences when the 2 outlier claw samples were excluded (n = 6, t = -3.15, p = 0.03), but were not significantly different when the outlier claw samples were included (n = 8, t = -1.28, p = 0.24). In addition, we found a significant association between δ^2H for breast and tail feathers (n = 26 F = 12.41, p = 0.0002). However, there was no relationship between δ^2H for claws and tail (n = 10, F= 0.0038, p =0.95) or claws and breast (n = 10, F = 0.31, p = 0.59). ASY breast (-72.6 ± 12.4 SD ‰) and tail (-82.6 ± 16.3 SD ‰) feathers are comparable to the predicted value of the moulting grounds (mean: 77 ± 20 ‰ SD). Excluding the two outlier samples, claw samples (range -49.3 to -72.5 ‰; mean: -59.1 ± 7.3 ‰ SD) fell within the predicted range (-76 to -45 ‰) for the wintering grounds.

Due to the time-sensitive nature of collecting claw samples, we were unable to collect an adequate number of claw samples from females or SY males. However, when we examined differences between tail and breast feathers within individuals, SY males had higher but non-significant δ^2H values in breast feathers compared to the δ^2H values in tail feathers (mean breast: -70 ± SD = 19; mean tail: -116 ± SD 33; n = 4, t = -2.29, p = 0.11), though the sample size was extremely limited (SY male n = 4) (Figure 2.2). We found no differences between tail and breast feathers in either ASY females (n = 8, mean breast: -82 ± SD = 5, mean tail: -90 ± SD = 26; n = 8, t = -1.05, p = 0.33) or SY females (n = 5, mean breast: -61 ± SD = 11, mean tail:-70 ± SD = 13; n = 5, t = -1.58, p = 0.19) (Figure 2.2). The difference between δ^2H for breast and tail of ASY female feathers approached significance (n = 8 F = 4.49, p = 0.07).

Comparing δ^2H among Age and Sex classes

We examined the δ^2H values of breast and tail feathers, making comparisons between ASY and SY birds for both sexes. For male orioles, we found no significant difference between the breast feathers of SY and ASY birds (mixed model: n_{total} = 32, n_{ASY} = 28, n_{SY} = 4, F = 0.13, p =0.73), but did find a significant difference between the age classes with respect to tail feathers (mixed model: n_{total} = 30, n_{ASY} = 26, n_{SY} = 4, F = 22.13, $p < 0.0001$) (Figure 2.3). Conversely, we found that the δ^2H values of breast feathers for ASY females were more negative than those of SY females (n_{total} = 16, n_{ASY} = 8, n_{SY} = 8, F = 10.51, p = 0.0006), but that there was no no significant difference between the age classes with respect to tail feathers (n_{total} = 14, n_{ASY} = 9, n_{SY} = 5, F = 0.31, p = 0.59) (Figure 2.3). We found a significant year effect for the model comparing tail feathers in female orioles (F = 9.77, p = 0.01). Comparing sexes in the ASY age class, δ^2H values were not significantly different for either breast (mixed model: n_{total} = 36, n_{Female} = 8, n_{Male} = 28, F = 3.04, p = 0.09), or tail feathers (mixed model: n_{total} = 34, n_{Female} = 8, n_{Male} = 26, F = 0.26, p = 0.61). Additionally, there was no difference between the sexes for SY birds with respect to the δ^2H values of breast feathers (mixed model: n_{total} = 12, n_{Female} = 8, n_{Male} = 4, F = 0.07, p = 0.79), but there was a significant difference for tail feathers: SY males exhibited more negative tail feather signatures than did SY females (mixed model: n_{total} = 9, n_{Female} = 5, n_{Male} = 4, F = 5.95, p = 0.05).

Geolocators

We tracked the full annual cycle of two birds and part of the fall migration of another (Figure 2.4). All three birds left the breeding grounds in mid to late July 2012 (Birds 24 and 41 on July 18th and Bird 22 on July 26th). Birds 22 and 24 arrived in the monsoon region in August 2nd and 5th, and left in October 18th and 21st apparently stopping over in in Central and Eastern Mexico, respectively. Spring migration towards the breeding ground began on April 26th (Bird 24) and 23rd (Bird 22) of 2013, with the two birds arriving on the breeding grounds on May 19th (Bird 24) and 17th (Bird 22). The location of the long stopover during fall migration and the location of the over-wintering areas are within the expected ranges of δ^2H values for our sample set. The remaining bird (Bird 41) appeared to stopover in the Nevada-Idaho-Oregon area for 2 weeks before continuing south towards the moulting area. As a result, the rate of Bird 41's fall migration was much slower than that of the other two birds; in fact, Bird 41 was just leaving this 2-week stopover 10-13 days after the other two had reached the Mexican monsoon region. This last geolocator appears to have lost power while the bird was moving south through Arizona.

Discussion

Our results from geolocators (Figure 2.4) and stable isotope analysis of multiple tissues from all sexes and ages of Bullock's orioles are consistent with obligatory moult migration in Bullock's orioles breeding at the northern extent of the range. Northern Bullock's orioles appear to migrate to the Mexican monsoon region for a stopover-moult before heading to the wintering grounds, as has been suggested previously based on captures of moulting orioles in the Mexican monsoon region (Rohwer and Manning 1990, Pyle et al. 1997, Rising and Williams 1999, Pyle et al. 2009). The results obtained from two geolocators clearly show that the birds made a long stopover (approximately 73 and 80 days respectively) in the Mexican monsoon region before they moved on to the wintering sites. This stopover is long enough for a complete moult to take place in other migratory songbirds (de la Hera et al. 2009). While two of the geolocators showed similar fall migration patterns, the third geolocator revealed that the bird approached the edge of the expected moult region two weeks later than the others due to a stopover during southward migration. This two-week stopover is too short for a complete moult, but may have provided resources necessary to continue migration. Although the geolocator failed en route, the bird arrived the subsequent year within a day of its previous arrival. Migratory pathways differed between individuals, with birds appearing to utilize both the Pacific and Central Flyways.

Our isotope data also support the previously cited reports that ASY Bullock's orioles moult en-route to the wintering grounds and this pattern appeared consistent across all ASY males and females. Isotopic results and field observations (Pillar unpublished data) demonstrate that moult is not taking place on or near the breeding grounds (expected feather δ^2H mean = 156.7 ± 10.1 SD ‰ for the breeding grounds, observed ASY breast feather mean = -72.6 ± 12.4 SD ‰, observed ASY tail feather mean = -82.6 ± 16.3 SD ‰). In addition, substantial variation in feather isotopic signatures likely indicates that there is a broad range of moult locations within the Mexican monsoon region, and may support previous findings of low moult-site fidelity in western North American moult-migrants (Pyle et al. 2009). Significant differences in claws which are constantly growing, and feathers which are grown on the moult site also suggest that the location of the moult site differs from that of the overwintering site for ASY males, providing further evidence of moult-migration rather than an over-winter moult. ASY and SY male birds did not show significant differences in δ^2H of breast feathers, but did in tail feathers, with SY tail feather signatures being much more negative than that of the ASY males. The δ^2H signature for two of the four SY male tail feathers fell within the range of expected breeding range signatures, suggesting these feathers were grown on the breeding grounds, as predicted. However, the other two SY males had tail feather signatures consistent with ASY birds, suggesting moult in the monsoon region. Though unexpected, this result is consistent with the suggestion that juvenile birds moult a variable number of rectrices (0-12) in the monsoon region (Pyle et al. 1997). Female SY birds had significantly less negative δ^2H signatures in breast feathers and a non-significant difference in tail feathers when compared to ASY females. The breast feather signatures may indicate that a small number of hatch-year females are completing their moult on the wintering grounds or further south than the other individuals in our study. SY breast feathers (of both males and females) and SY female tail feathers were consistent with moult-migration in the Mexican monsoon region, suggesting that this region is critical for all age and sex classes of Bullock's orioles.

Perhaps surprisingly, we found differences in the average isotopic signatures of tail and breast feathers in ASY males. However, the significant correlation between the tail and breast feathers of individual birds suggests that the feathers were likely grown in the same general location, and differences between tissues were likely due to isotopic fractionation rather than being the result of the feathers being grown in two different. When compared to their body feathers, the flight feathers of Wilson's warblers (*Wilsonia pusilla*) have more negative (9.6 ‰ difference) δ^2H signatures (Kelly et al. 2002). In addition, merlin (*Falco columbarius*), red-tailed hawks (*Buteo jamaicensis*), and sharp-shinned hawks (*Accipiter striatus*) all have been shown to have more negative δ^2H signatures in flight feathers than covert feathers (Smith et al., 2008). It is possible that isotopic fractionation can explain the differences we observed between claw and feather samples. However, while a strong within-individual correlation was found between breast and tail feather δ^2H signatures, no such relationship was detected for breast feathers and claws or claws and tail feathers. Thus, we suggest it is unlikely that the claws were grown in the same location as the feathers.

Our study is the first to examine moult-migration in western songbirds by tracking individuals throughout the annual cycle. Earlier studies on Bullock's orioles indicated moult-migration was occurring, but had not confirmed how widespread the phenomenon was, or provided any details of possible intraspecific differences in moult strategies (Rising and Williams 1999, Pyle et al. 2009). From our results, it appears clear that moult-migration in the Mexican monsoon region is a common, potentially obligatory, strategy in Bullock's orioles breeding at the northern extent of the range. While many studies have investigated breeding origins, wintering locations, and migratory connectivity in songbirds using stable hydrogen isotope analysis, to our knowledge, there has been only one other study (Contina, 2013) that used hydrogen isotope analysis and geolocators to identify moulting sites. As several other western songbirds seem to employ this same moult-migration strategy (Pyle et al. 2009), investigating patterns of moult and migration in these other species would give us a broader understanding of evolution of this unique life history.

Literature cited

Bearhop, S., G. M. Hilton, S. C. Votier, and S. Waldron. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:S215–S218.

Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. Hartl, R. Kays, J. F. Kelly, and W. D. Robinson. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. BioScience 61:689–698.

van den Brink, B., R. G. Bijlsma, and T. M. Van der Have. 2000. European Swallows *Hirundo rustica* in Botswana during three non-breeding seasons: the effects of rainfall on moult. Ostrich 71:198-204.

Butcher, G. S. 1991. Mate choice in female northern orioles with a consideration of the role of the black male coloration in female choice. The Condor 93:82-88.

Comrie, A. C., and E. C. Glenn. 1998. Principal components-based regionalization of precipitation regimes across the southwest United States and northern Mexico, with an application to monsoon precipitation variability. Climate Research 10:201-215.

Contina, A., E. S. Bridge, N. E. Seavy, J. M. Duckles, and J. F. Kelly. 2013. Using geologgers to investigate bimodal isotope patterns in Painted Buntings (Passerina ciris). The Auk 130:265–272.

Delmore, K. E., J. W. Fox, and D. E. Irwin. 2012. Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. Proceedings of the Royal Society London Series B: Biological Sciences 279:4582-4589.

Hallworth, M. T., C. E. Studds, T. S. Sillett, and P. P. Marra. 2013. Do archival light-level geolocators and stable hydrogen isotopes provide comparable estimates of breeding-ground origin? The Auk 130:273-282.

Heckscher, C. M., S. M. Taylor, J. W. Fox, and V. Afanasyev. 2011. Veery (*Catharus fuscescens)* wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. The Auk 128:531–542.

de la Hera, I., J. A. Díaz, J. Pérez-Tris, and J. Luis Tellería. 2009. A comparative study of migratory behaviour and body mass as determinants of moult duration in passerines. Journal of Avian Biology 40:461–465.

Hobson, K. A., Y. Aubry, and L. I. Wassenaar. 2004. Migratory connectivity in Bicknell's Thrush: Locating missing populations with hydrogen isotopes. The Condor, 106:905-909.

Hobson K. A. 2008. Isotopic Methods to Track Animal Movements. Pages 45-78 in K. A. Hobson, and L. I. Wassenaar, editors. Tracking animal migration with stable isotopes. Elsevier, London, UK.

Hobson, K. A., S. L. Van Wilgenburg, K. Larson, and L. I. Wassenaar. 2009. A feather hydrogen isoscape for Mexico. Journal of Geochemical Exploration 102:167–174.

Hobson, K. A., S. L. Van Wilgenburg, L. I. Wassenaar, and K. Larson. 2012. Linking hydrogen (δ2H) isotopes in feathers and precipitation: sources of variance and consequences for assignment to isoscapes. PLoS One 7:e35137.

Hutto, R. L. 1998. On the importance of stopover sites to migrating birds. The Auk 115:823-825.

Kelly, J. F., V. Atudorei, Z. D. Sharp, and D. M. Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia 130:216–221.

Langin, K. M., M. W. Reudink, P. P. Marra, D. R. Norris, T. K. Kyser, and L. M. Ratcliffe. 2007. Hydrogen isotopic variation in migratory bird tissues of known origin: implications for geographic assignment. Oecologia 152:449–457.

Laughlin, A. J., C. M. Taylor, D. W. Bradley, D. Leclair, R. C. Clark, R. C, R. D. Dawson, P. O. Dunn, A. Horn, M. Leonard, D. R. Sheldon, D. Shutler, L. A. Whittingham, D. W. Winkler, and D. R. Norris. 2013. Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. The Auk 130:230-239.

Leu, M., and C. W. Thompson. 2002. The potential importance of migratory stopover sites as flight feather molt staging areas: a review for neotropical migrants. Biological Conservation, 106:45-56.

Lindstrom, A., G. H. Visser, and S. Daan. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. Physiological Zoology 66:490–510.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Meehan, T. D., J. T. Giermakowski, and P. M. Cryan. 2004. GIS-based model of stable hydrogen isotope ratios in North American growing-season precipitation for use in animal movement studies. Isotopes in Environmental and Health Studies 40:291–300.

Newton, I. 2011. Migration within the annual cycle: species, sex and age differences. Journal of Ornithology, 152:169-185.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society of London Series B: Biological Sciences 271: 59-64.

Pyle, P. 1997. Identification Guide to North American Birds: A Compendium of Information on Identifying, Ageing, and Sexing Waterbirds, Diurnal Raptors, and Gallinaceous Birds in the Hand. Slate Creek Press, Bolinas, CA, USA.

Pyle, P., W. A. Leitner, L. Lozano-Angulo, F. Avilez-Teran, H. Swanson, E. G. Limón, and M. K. Chambers. 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. The Condor 111:583–590.

Quinlan, S. P., and D. J. Green, 2011. Variation in deuterium (δD) signatures of Yellow Warbler *Dendroica petechia* feathers grown on breeding and wintering grounds. Journal of Ornithology 152:93-101.

Renfrew, R. B., D. Kim, N. Perlut, J. Smith, J. Fox, and P. P. Marra. 2013. Phenological matching across hemispheres in a long-distance migratory bird. Diversity and Distributions 19:1008–1019.

Reudink, M. W., P. P. Marra, T. K. Kyser, P. T. Boag, K. M. Langin, and L. M. Ratcliffe. 2009a. Non-breeding season events influence sexual selection in a long-distance migratory bird. Proceedings of the Royal Society of London Series B: Biological Sciences 276:1619–1626.

Rising, J. D. and P. L. Williams. 1999. Bullock's Oriole (*Icterus bullockii*). in A. Poole and F. Gills editors, The Birds of North America, No. 416. The Birds of North America Inc., Philadelphia, PA, USA.

Rohwer, S., and J. Manning. 1990. Differences in timing and number of molts for Baltimore and Bullock's orioles: Implications to hybrid fitness and theories of delayed plumage maturation. Condor:125–140.

Rohwer, S., L. K. Butler, D. R. Froehlich, R. Greenberg, and P. P. Marra. 2005. Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. Pages 87-105 in R. Greenberg, and P. P. Marra, editors. Birds of Two Worlds: The Ecology and Evolution of Migration Johns Hopkins University Press, Baltimore, MD, USA.

Rubenstein, D. R., and K. A. Hobson. 2004. From birds to butterflies: animal movement patterns and stable isotopes. Trends in Ecology & Evolution 19:256–263.

Ryder, T. B., J. W. Fox, and P. P. Marra. 2011. Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geolocator and mark-recapture data. The Auk 128:448–453.

Smith, A. D., K. Donohue, and A. M. Dufty Jr. 2008. Intrafeather and intraindividual variation in the stable-hydrogen isotope (δD) content of raptor feathers. The Condor 110:500-506.

Studds, C. E., K. P. McFarland, Y. Aubry, C. C. Rimmer, K. A. Hobson, P. P. Marra, and L. I. Wassenaar. 2012. Stable-hydrogen isotope measures of natal dispersal reflect observed population declines in a threatened migratory songbird. Diversity and Distributions 18:919–930.

Stutchbury, B. J., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. Science 323:896–896.

Wassenaar, L. I., and K. A. Hobson. 2000. Stable-carbon and hydrogen isotope ratios reveal breeding origins of red-winged blackbirds. Ecological Applications 10:911–916.

Wassenaar, L. I., and K. A. Hobson. 2003. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. Isotopes in Environmental and Health Studies 39: 211-217.

Wassenaar, L. I. 2008. An Introduction to Light Stable Isotopes for Use in Terrestrial Animal Migration Studies. Pages 21-44 in K. A. Hobson, and L. I. Wassenaar, editors. Tracking animal migration with stable isotopes. Elsevier, London, UK.

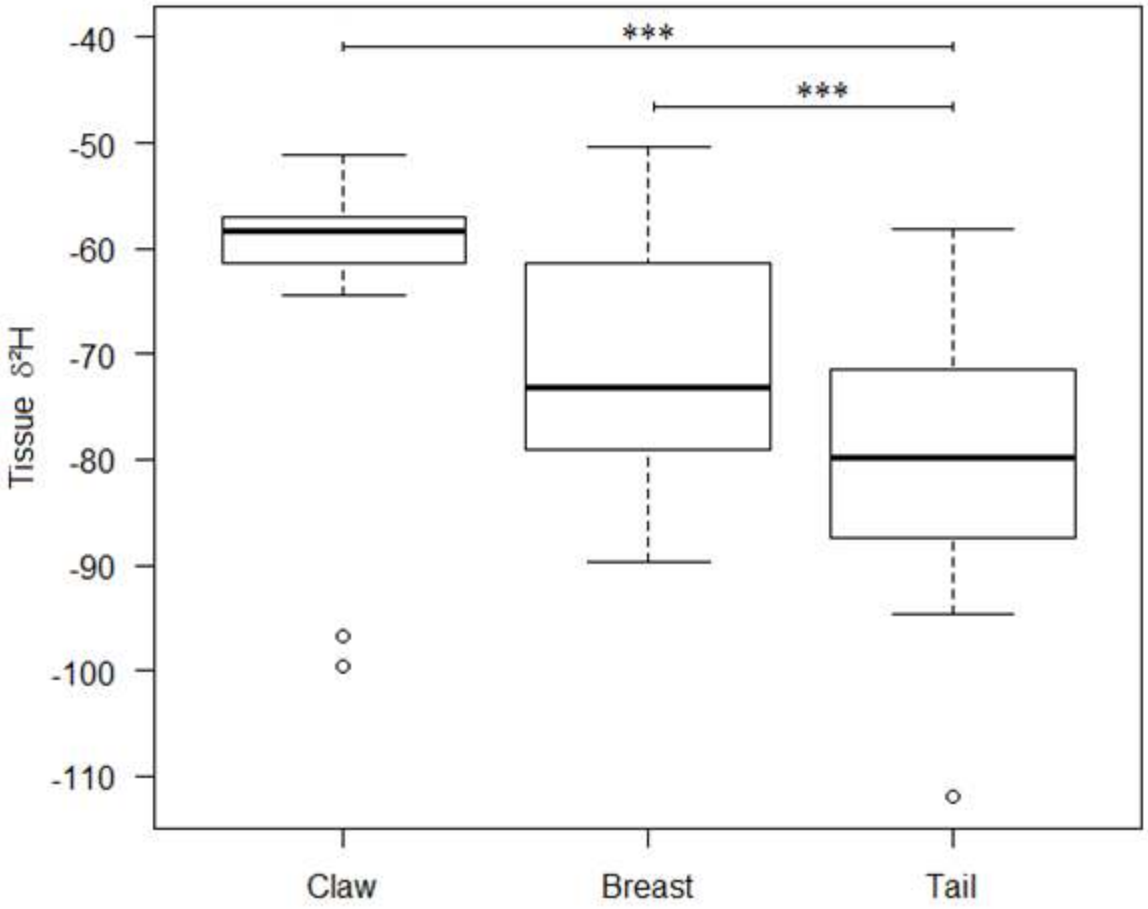

Figure 2.1: ASY Male Bullock's oriole δ^{2}H values by tissue type. Significance: * $0.05 \geq p > 0.01$, ** $0.01 \geq p < 0.001$, *** $0.001 \geq p > 0.0001$, **** $0.0001 \geq p$

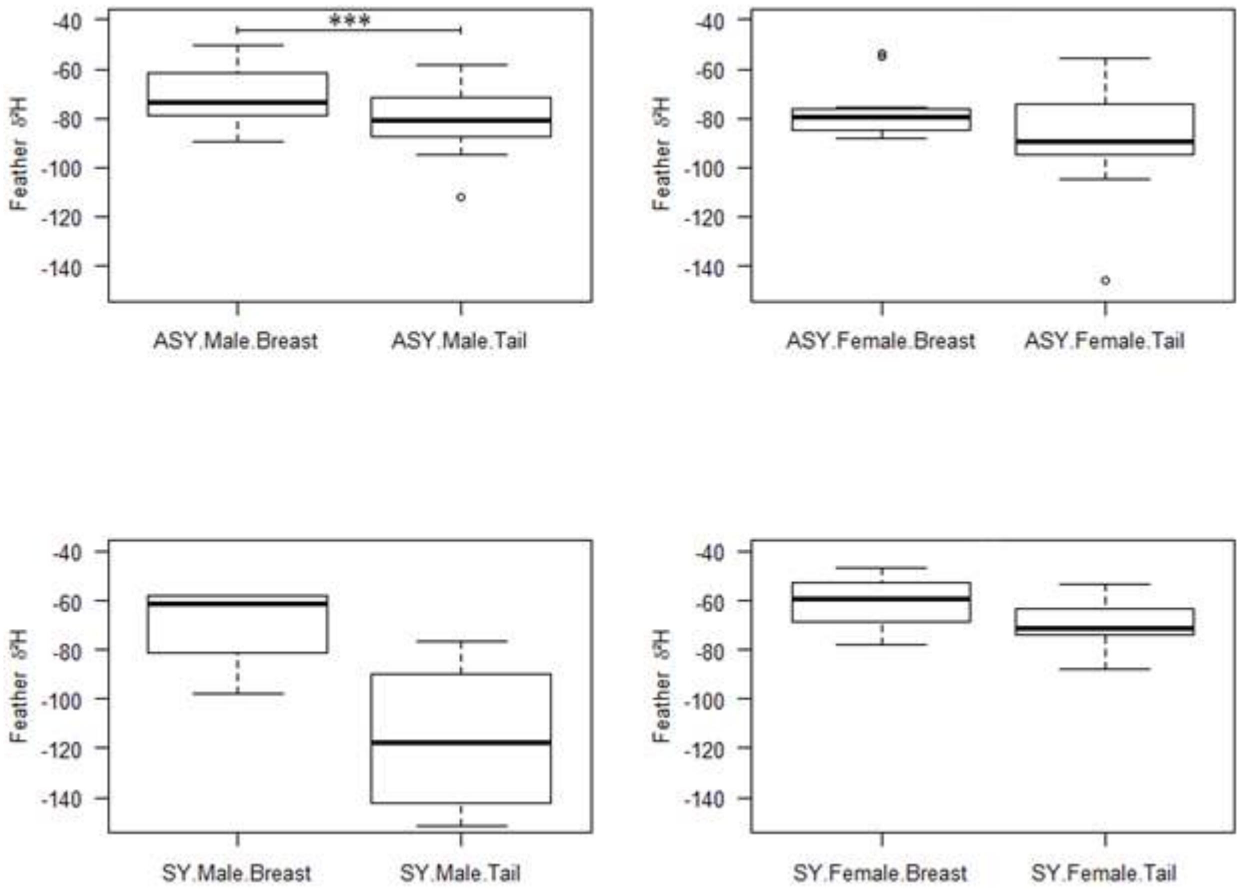

Figure 2.2: Comparison between δ^2H values in breast and tail feathers of each age and sex class of Bullock's oriole. Significance: * $0.05 \geq p > 0.01$, ** $0.01 \geq p < 0.001$, *** $0.001 \geq p > 0.0001$, **** $0.0001 \geq p$

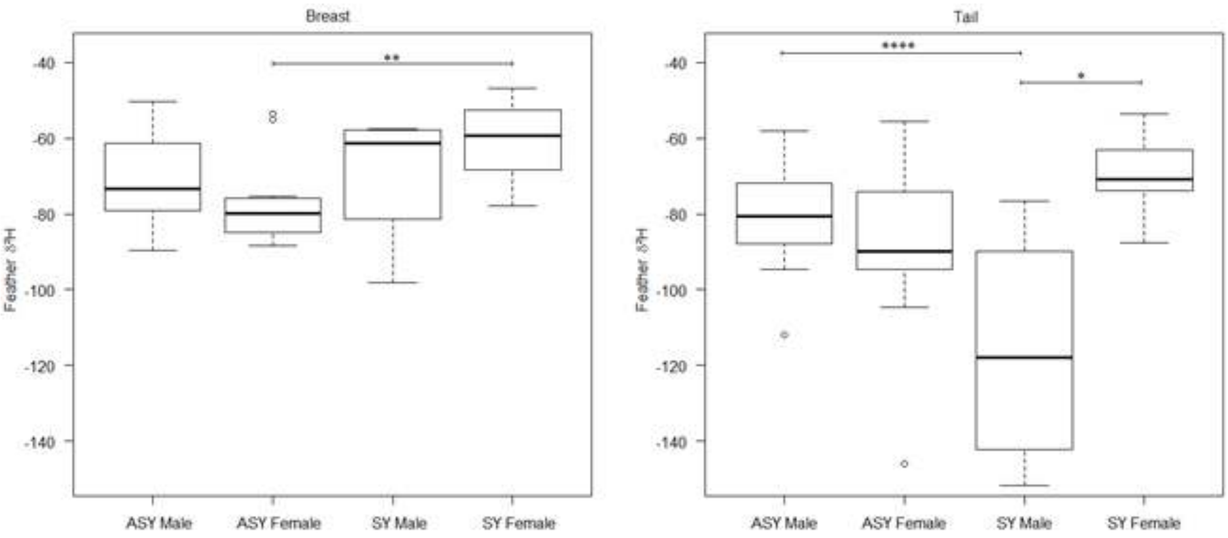

Figure 2.3: Differing δ^2H values among breast feathers (left) and tail feathers (right) for each age and sex class. Significance: * $0.05 \geq p > 0.01$, ** $0.01 \geq p < 0.001$, *** $0.001 \geq p > 0.0001$, **** $0.0001 \geq p$

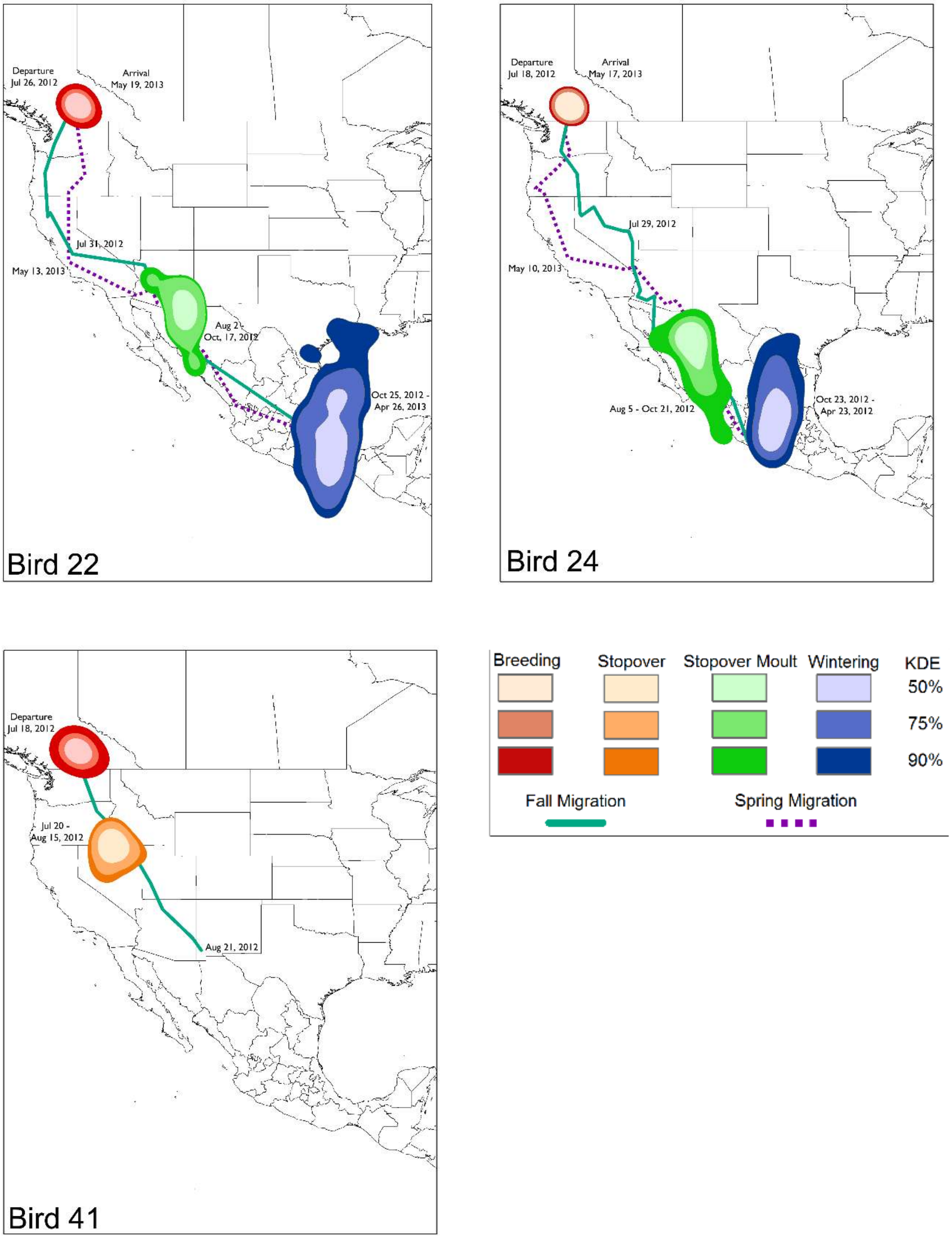

Figure 2.4: Geolocator data displayed as Kernel Density estimates at the 50%, 75%, and 90% levels. Red represents the breeding grounds, orange a stopover, green the moult-stopover, and blue the overwinter location. The solid line represents fall migration while the dashed line represents spring migration.

CHAPTER 3: EXAMINING ENVIRONMENTAL INFLUENCES ON BULLOCK’S ORIOLE BREEDING ABUNDANCE USING A FULL ANNUAL CYCLE APPROACH.

Abstract

Environmental factors affect migratory bird populations in every phase of their annual cycle and have significant impacts on breeding success and survival. The breeding bird survey provides a long-term database for examining population trends in North American birds, allowing us to examine large-scale environmental factors that influence population abundance. We examined plant productivity as measured by NDVI (Normalized Difference Vegetation Index) over a 25-year period from 1982 – 2006 in bird conservation regions (BCR) that overlapped Bullock’s oriole breeding, moult, and wintering ranges to ask whether plant productivity in one year influences population abundance in the subsequent breeding season. Bullock’s orioles have a rare moult-migration strategy, with a stopover moult in the Mexican monsoon region, which necessitates examining each stationary phase of the bird’s annual cycle in order to understand the impacts of environmental factors on population abundance. Our results show increased breeding abundance in three BCRs (Great Basin, Coastal California and Shortgrass Prairies) following years with high NDVI values. We detected no response of breeding abundance to high NDVI values in the moulting region in the previous year. Both negative and positive breeding abundance responses were detected from plant productivity in overwintering regions prior to breeding season. Our results demonstrate that primary productivity on both breeding grounds and overwintering sites can have an impact on breeding bird abundance the following season. Given the potential influence of climate change and local habitat loss, these findings have important implications for the future migratory bird populations.

Introduction

Throughout the annual cycle, numerous biotic and abiotic factors can interact to influence variation in breeding success and survival in animals. For migratory birds, studying these interactions can be challenging due to the vast distances individuals travel in a year. Most studies have focused on birds on their breeding grounds, at migratory banding stations, or occasionally on their wintering grounds, but relatively little is known about how these phases of the annual cycle interact to influence individual and population level processes (Bowlin et al. 2010, Marra et al. 1998, Webster et al. 2005). A more comprehensive, annual-cycle approach to the study of migratory birds, which integrates these phases of breeding, moult, migration, and over-wintering, is necessary to understand the interactions between them (Marra et al. 1998, Bowlin et al. 2010, Newton 2011). Breeding, moult and migration are the most energetically demanding events in a bird's life (Newton 2011). Although conditions during the breeding (Sillett et al. 2000), migration (Sillett ad Holmes, 2002), and wintering periods (Sillett et al. 2000, Saino et al. 2004, Wilson et al. 2011, Tøttrup et al. 2012) have all been shown to have strong impacts on survival, little is known about the potential effect of the critical moult period on population dynamics.

Variation in climatic conditions and the influence of this variation on resource availability can have important effects on individuals throughout the annual cycle. For example, spring migration of individual red-backed shrikes (*Lanius collurio*) and thrush nightingales (*Lanius luscinia*) is delayed by the need for a longer stopover period, induced by drought conditions in eastern Africa (Tøttrup et al. 2012). Resource availability can be measured in a number of different ways, including the use of remotely sensed measures of plant productivity such as NDVI. Green vegetation absorbs visible light and reflects infrared light, leading to high NDVI values (Pettorelli 2011). In bobolinks (*Dolichonyx oryzivorus*), declines in primary productivity, as measured by NDVI, appears to lead to early departure for fall migration and movement from one stopover site to another (Renfrew et al. 2013). Similarly, greater plant cover is positively related to diurnal body mass gain during migration stopover for forest dwelling willow warblers (*Phylloscopus trochilus*) and Eurasian redstarts (*Phoenicurus phoenicurus*) (Ktitorov et al. 2008). Thus, plant productivity appears to be critical for both migratory and sedentary individuals and can be measured both directly (i.e., in the field), as well as indirectly, through the use of metrics such as NDVI obtained by remotely sensed satellite data.

Although climatic conditions and plant productivity may influence individuals immediately and directly, these effects may also carry-over to subsequent seasons. Carry-over effects occur when conditions in one phase of the annual cycle have a significant effect on the animal in a subsequent phase; these effects are thought to be especially strong among migratory species, and may have a significant impact on their life history and evolution (Inger et al. 2010). For example, environmental conditions on over-wintering territories can carry over to have an impact on arrival dates (Marra et al. 1998, Reudink et al. 2009a) and reproductive success in the following season (Saino et al. 2004, Reudink et al. 2009a). Annual variability in amount of rainfall in the wintering range of American redstarts is associated with changes in both the physical condition of individuals and the timing of their spring migration departure (Studds and Marra 2005). In the case of birds that utilize stopover sites to moult during migration (i.e. moult-migrants), it is possible that these types of carry-over effects are likely to be contingent on both the over-wintering environment and the condition of the stop-over moult location.

In addition to individual-level effects of climate and environmental conditions, large-scale climate patterns can have major impacts on population-level dynamics. For example, the El Nino Southern Oscillation (ENSO) influences rainfall patterns and temperature and thus food availability for black-throated blue warblers (*Dendroica caerulescens*) wintering in Jamaica, leading to lower survival rates in drier, El Nino years (Sillett et al. 2000). Climate indices for ENSO and other large-scale cyclical climatic events have also been shown to account for the majority of variability in reproductive success of 10 other migratory bird species (Nott et al. 2002). Temperature trends have affected populations of yellow-billed cuckoos (*Coccyzus americanus*), with greater numbers of birds following cooler years (Anders and Post 2006). In addition, Saino et al. (2004) and Wilson et al. (2011) demonstrated that plant productivity, as measured by NDVI, is a significant driver of population trends in both barn swallows (*Hirundo rustica*) and American redstarts (*Setophaga ruticilla*). In both species, years with low NDVI on the wintering grounds resulted in a significant decrease in abundance during the subsequent breeding season (Saino et al. 2004, Wilson et al. 2011).

Although a vast majority of migratory songbirds have two stationary phases during the annual cycle, a small number of western North American songbirds, including Bullock's orioles (*Icterus bullockii*), have an interesting migratory strategy that includes a prolonged stationary moult period in the Mexican monsoon region (Pyle et al. 2009). Rather than undergoing a partial or complete post-breeding moult on the breeding grounds, birds that employ this strategy make use of a stopover moult location while en route to their wintering grounds (Rising and Williams 1999, Newton2011). These moult-migrants generally stop in the Southwestern United States and Northwestern Mexico during the late summer through early fall, apparently timing moult to coincide with an increase in food abundance in these areas, resulting from a dramatic increase in plant productivity during and following late summer monsoon rains (Rohwer and Manning 1990, Rohwer et al. 2005, Pyle et al. 2009). Because moult and migration are energetically costly, these stopover sites may be crucial, allowing birds to build up important fat stores, and grow high quality plumage necessary for both flight and communication (Hutto 1998, and Leu and Thompson 2002). To our knowledge, no research to date has investigated environmental conditions during each stationary phase of the annual cycle to explore population-level effects of environmental variability on moult-migrants.

Using publically available Breeding Bird Survey (BBS) and environmental data (i.e., NDVI), we ask whether environmental variation during the 3 distinct stationary phases of the annual cycle influences Bullock's oriole breeding abundance in subsequent years. Bullock's orioles breed in riparian areas of Western North America from Northern Mexico to the Southern Interior of British Columbia. After Second Year (ASY) Bullock's oriole's undergo an entire pre-basic moult while en route to their over-wintering grounds in the fall, replacing all of their feathers (Rohwer and Manning 1990, Pyle 1997, Rising and Williams 1999, Chapter 2). With the exception of some individuals that are resident in southern California, orioles winter from Western Mexico to as far south as Costa Rica, with the core of the wintering range being in Central and Eastern Mexico (Rising and Williams 1999), though details of migratory connectivity are currently unknown.

We examined if plant productivity, as measured by NDVI, during each of the stationary components of the annual cycle (i.e., breeding, moulting, wintering), can act as a driver of Bullock's oriole breeding bird abundance the following year. We predicted that increased productivity in the monsoon region would be positively related to breeding bird abundance in the subsequent year. Similarly, we predicted positive relationships between the NDVI in oriole breeding and over-wintering regions and abundance in the next breeding season. Because the Mexican monsoon region appears to be important to a number of moult-migrant songbirds (Rohwer et al. 2005, Pyle et al. 2009), variation in resource availability may have important implications for all of these species.

Methodology

Survey Data

We obtained range-wide Breeding Bird Survey data for Bullock's orioles from 1982 to 2006 and classified data by Bird Conservation Regions (BCRs). BCRs capture a combination of geophysical and environmental conditions within a specified area (Commission for Environmental Cooperation 1997), and are a useful way to delineate regions within which individuals would be exposed to broadly similar habitat and climatic conditions. Bullock's orioles are present on BBS routes in 17 BCRs across western North America, but many have only small amounts of data, either because the BCR has few BBS routes or because it is located on the periphery of the species' range. We therefore limited our analysis to 6 BCRs (5, 9, 10, 16, 18 and 32), which represent the core of the breeding range and contained 80% (n=35,020) of the Bullock's orioles detected over the 24 years used in this analysis. Within these 6 BCRs (hereafter defined as 'strata'), many BBS routes only had data for a small number of years or had very few Bullock's oriole detections. To limit the influence of these routes, we further restricted the analysis to routes that had been surveyed for 14 or more of the 24 years and where 2 or more Bullock's orioles were recorded on average across all years.

Normalized Difference Vegetation Index

We obtained bimonthly Normalized Difference Vegetation Index (NDVI) data from the GIMMS (Global Inventory Mapping and Mapping Studies) remotely sensed raster image dataset for a 25 year period from 1982 to 2006 (Carroll et al. 2004). The NDVI is calculated as (NIR-Red)/(NIR+Red) with NIR and Red equal to the amount of near-infrared and red light reflected by a surface and recorded by remote sensing (Jensen 2007, Pettorelli et al. 2011). The NDVI is positively correlated with several measures of plant productivity including photosynthetic capacity, leaf area index, canopy extent and carbon assimilation (Myneni et al. 1995, Hicke et al. 2002, Wang et al. 2005, Pettorelli et al. 2011). As a measure of plant productivity, the NDVI is often used in wildlife studies as an index of resource abundance, and variation in that abundance, over time or space (Pettoretti et al. 2005, Boone et al. 2006, Wilson et al. 2011, Tøttrup et al. 2012). Our interest was to examine how annual variation in plant productivity, as measured by the NDVI, during the breeding, moult and winter periods influenced BBS abundance on the breeding grounds in the following season.

Bullock's orioles exhibit strong breeding site fidelity among years (mean adult dispersal of 111m; Rising and Williams 1999) and therefore strata-level measures of productivity during the breeding season in year t-1 were predicted to influence abundance in the following breeding season through positive effects on reproductive output. The onset of breeding for Bullock's orioles is delayed with increasing latitude and decreasing longitude (i.e. more northern and eastern populations within the range breed later, Rising and Williams 1999). To accommodate this in our measure of productivity during the pre-breeding and breeding periods, we used NDVI values averaged from April 1 – June 30 for BCRs 5, 9, 10, 16 and 18, and March 15 – June 15 in BCR 32. Using ESRI's ArcGIS (Zonal Statistics) we extracted NDVI values from the raster image dataset for each Bird Conservation Region (BCR) where values intersected with BCRs and the known Bullock's oriole range. In each area, we used only NDVI values flagged as good and not those where data was missing, values were the result of possibly snow reflectance, or values were retrieved from spline interpolation or average seasonal profile.

Identification of the optimal temporal and spatial window for the moult and winter periods is more difficult because individuals are not directly monitored and their presence in an area during these periods must be inferred through other methods. We delineated the monsoon region as described by Comrie and Glenn (1998). NDVI values for this moult region were limited to the majority of the species' moult period (mid-July through mid-October) as described in Rising and Williams (1999). The wintering range was delineated using information from Bullock's oriole range maps, and extracted NDVI values were temporally limited to values that fell outside the known moult migration, and prior to the start of spring migration (December through March). Wintering regions were defined by aggregating BCRs with a high degree of correlation in NDVI values.

The NDVI was standardized prior to analysis and because of absolute differences in the average NDVI across western North America, we standardized it within each strata. Breeding season primary productivity was very low during the 1999 La Niña event, particularly in the Great Basin and Coastal California strata (standardized NDVI values = -3.19 and -3.01 respectively). Because of the potential for strong influence of this single year anomaly we ran models with and without BBS abundance data from 2000 to examine how this year affected the beta coefficient and we report both in the results text for these three strata.

Statistical Analysis

Population change for Bullock's Orioles was modeled with a hierarchical, over-dispersed Poisson regression and analyzed under a Bayesian framework with Markov Chain Monte Carlo (MCMC) methods in WinBUGS 1.4.3 (Lunn et al. 2000). Each count $C_{i,j,t}$ for stratum i, observer-route combination j and year t was modeled as a Poisson random variable with mean $\lambda_{i,j,t}$ defined as a log-linear relation to the predictor variables, which include process and sampling components:

$$[1] \quad \log(\lambda_{i,j,t}) = \alpha_i + \beta_{1,i}*\text{year} + \beta_{2,i}*\text{breed NDVI}_{t-1} + \beta_{3,i}*\text{moult NDVI}_{t-1} + \beta_{4,i}*\text{winter NDVI1}_t + \beta_{5,i}*\text{winter NDVI2}_t + \beta_6*\text{start-up}_{j,t} + \text{observer-route}_{j,t} + \varepsilon_{i,j,t}$$

The model includes strata-specific estimates for average BBS abundance (α_i), temporal trend (β_1), and the NDVI-based estimates of productivity for the breeding period in year t-1 (β_2), moulting period in year t-1 (β_3) and the two proposed wintering regions in year t (β_4 and β_5). Betas 1-5 were assigned flat, normal distributions with mean 0 and variance 10^3. Parameter estimates at the stratum-level need to incorporate sources of variation in the data associated with routes and observers (Link and Sauer 2002, 2007) and observer-route combinations were treated as normal random variables. Observers also differ in their experience at identifying species on BBS routes, particularly between their first year and all subsequent years (Link and Sauer 2007). We incorporated these start-up effects by assigning a 1 if that count ($C_{i,j,t}$) was the first year of service for that individual and a 0 otherwise. Beta 6 (β_6) represents this first year influence in the model and was assigned a flat, normal distribution with mean 0 and variance 10^3. The component $\varepsilon_{i,j,t}$ helps accommodate over-dispersion that is common in count data such as the BBS. Because of our interest in the effects of an annually-varying covariate, we did not include the variance of year effects as is typically done for the analysis of temporal trends using BBS data (Sauer and Link 2011). Variance associated with observer-route combinations (σ^2_ω) and over-dispersion (σ^2_ε) were assumed to be constant across strata and assigned vague inverse-gamma prior distributions with shape and scale parameters = 0.001.

We ran three Markov chains for the model, each for 50,000 iterations, and examined convergence through individual parameter history plots, Gelman-Rubin diagnostics, and the estimation of MC error/SD for each parameter (Gelman et al. 2004, Link and Barker 2010). The chains typically converged within 1,000 iterations but we discarded the first 10,000 iterations as a burn-in before drawing samples from the posterior distribution. We examined the temporal trend and NDVI influence in each period by examining the median estimate along with 90 and 95% credible intervals (CI) for β_1 and $\beta_{2\text{-}5}$ respectively. Parameters were interpreted as significant when 90% or 95% CIs excluded zero. Posterior predictive checks were used to examine the fit of the model (Gelman et al. 2004). This measure involves drawing replicate samples of data from the posterior distribution and comparing the fit of the observed data to the replicate data that conforms to the assumptions of the model. The model fit was examined graphically by plotting the observed and replicate distributions, and quantitatively by calculating a test statistic. For each value of the observed (y) and replicated (y^{rep}) data, a test quantity is calculated based on (Gelman et al. 2004):

$$P_B = \Pr(T(y^{rep}, \theta) \geq T(y,\theta|y)$$

A model that fits the data should have a similar number of cases where the replicate data exceeds the observed data and vice versa, generating a probability closer to 0.5. Models with values nearer to the extremes of 0 or 1 indicate data that differ considerably from the replicate distribution based on the assumed model.

In our examination of the relationship between NDVI and BBS abundance, we initially ran a full model with breeding, moult and both winter regions, and examined β_2 through β_5 for each strata. If there were no significant relationships with 90 or 95% certainty, we removed that variable and ran a reduced model. This reduced model was then used to predict the expected change in BBS abundance in relation to a 1-unit change in the standardized NDVI for those strata in which the effect was significant for a period of the annual cycle. The predicted stratum-specific abundance in relation to NDVI was specified as a derived parameter in the model following Sauer and Link (2011) as:

$$[2] \quad Ni,t = \exp(\alpha_i + \beta_{1,i}{*}year_{t\text{-}mid} + \beta_{2,i}{*}breed\ NDVI_{t-1} + \beta_{3,i}{*}moult\ NDVI_{t-1} + \beta_{4,i}{*}winter1\ NDVI_t + \beta_{5,i}{*}winter2\ NDVI_t + 0.5{*}\sigma^2_{\omega} + 0.5{*}\sigma^2_{\varepsilon})$$

The estimate of how BBS abundance varied in relation to a change in the NDVI involved a comparison of the predictions from two models that differed in one unit of the standardized NDVI during that period while holding other variables constant. We set the NDVI beta parameters for the other periods equal to 0, which is equivalent to average productivity in those regions. We used the mid-point (t-mid = year 12) of the time series for each strata to incorporate temporal trends. Variance components for observer-route effects and over-dispersion were included to improve estimates of mean abundance from the log-normal distribution (Sauer and Link 2011).

We also considered the power to detect a significant relationship at 95% certainty between the NDVI and subsequent BBS abundance. This analysis was performed for each strata in relation to NDVI in the breeding, moult and winter regions. Power was measured by taking the lower credible interval half-widths (2.5%) of the posterior distribution for β_2

through β_5 and using these values with equation [2] to predict the change in abundance for a 1 unit change in the NDVI. These are the values that would be required for the credible intervals to exclude zero, assuming a positive effect of the NDVI in each period of the annual cycle, and thus provided a measure of the extent to which the NDVI would need to influence BBS abundance to declare a the existence of a significant effect in the face of other sampling and process variation.

Results

Survey Data

We included BBS data from 161 routes across 6 strata with 24,689 individual orioles recorded between 1983 and 2006. Bullock's oriole abundance was highest in Coastal California (BCR32), Shortgrass Prairie (BCR 18), and Great Basin (BCR9), and was lower in the Northern Pacific Rainforest (BCR5), Northern Rockies (BCR10 and Southern Rockies-Colorado Plateau (BCR16, Table 1). The species was also less abundant in the latter three strata and as such, the proportion of BBS routes that met our minimum criteria was lower, particularly for the Northern Rockies (8.4% of routes) and Southern Rockies-Colorado Plateau (11.5%). While the trends here are broadly similar to those reported for the entirety of each strata (i.e., Bird Conservation Region, Sauer et al. 2011), it is important to note that these are based only on those BBS routes used in this analysis and patterns may differ from those in each stratum as a whole.

Population model results

We initially examined model fit, variance components and first-year effects based on the full model (eq. 1 above). The Bayesian goodness-of-fit test on this model yielded a p-value of 0.28, suggesting a reasonable fit, although with a tendency for higher variance than expected in the count data (also evident in plots of the observed versus replicated counts). The Bayesian goodness-of-fit test without the over-dispersion parameter yielded a p-value of 0.19 indicating that the parameter helped account for additional variance in the count data.

Variance associated with the observer-route effect was 0.902 (posterior SD = 0.039) and for the over-dispersion parameter was 0.331 (posterior SD = 0.012). The first-year effect was negative (β_6 = -0.139, 95%CI: -0.238, -0.040) indicating that BBS observers tend to underestimate the abundance of Bullock's orioles in their first year of service. Trends were significantly negative with 95% certainty in the two coastal strata (Coastal California, Northern Pacific Rainforest) and not significant in the four interior strata (Table 3.1).

Our full model included 4 NDVI covariates for the breeding season, moulting period and the Gulf coast and Pacific regions. There was no evidence that productivity in the moulting region or Pacific wintering Pacific region influenced subsequent abundance for any breeding strata (90 and 95% credible intervals for all strata overlapped zero). Therefore, our examination of the effect of breeding season productivity was conducted using a reduced model with β_3 and β_4 removed. Breeding season productivity resulted in significantly greater abundance in the following year with 90 or 95% certainty for the Great Basin, Shortgrass Prairie and Coastal California (Table 3.2, Figure 3.1). For the Great Basin, this interpretation was based on the analysis without data from 2000, which followed the 1999 La Niña event, when breeding season plant productivity was very low. The estimated coefficient for the Great Basin was 0.057 (90% CI: 0.004, 0.102) without BBS data for the year 2000 and 0.006 with 2000 included (90% CI: -0.030, 0.042). This difference indicates that Bullock's oriole abundance was higher than expected in 2000 given the low primary productivity in 1999. There was less influence of the La Niña event on the slope for Coastal California (β_2 = 0.052 with 2000 vs 0.040 without 2000) or Shortgrass Prairie (β_2 = 0.053 with 2000 vs 0.045 without 2000) and in both cases, the response from 1999 to 2000 was more similar to the pattern across all years. The predicted % change in BBS abundance in response to a 1 unit change in the standardized breeding season NDVI was 5.8 (95% CI: -0.5, 12.6) in the Great Basin, 4.6 (95% CI: -0.3, 9.8) in Shortgrass Prairie and 5.3 (95% CI: 1.2, 9.6) in Coastal California. There were no significant relationships between breeding season NDVI and subsequent BBS abundance in the other three strata (Table 3.2). Northern Pacific Rainforest and Northern Rockies actually had negative coefficients, but the credible intervals were wide with low precision in these strata.

The only significant relationship during the non-breeding period was a response to the NDVI in wintering area of Gulf coast of Mexico. However, we found opposing effects with the Great Basin, which displayed a positive response to the winter NDVI with 90% certainty and Coastal California, which exhibited a negative response to those same conditions with 95% certainty (Table 3.2). Predictions based on these responses while holding other covariates constant indicate that a 1 unit increase in the standardized NDVI on the wintering grounds would result in a 3.3% change (95% CI: -0.6, 7.5) in BBS abundance in the Great Basin and a -3.7% change (95% CI: -7.2, -0.1) in Coastal California.

Our examination of precision considered what percent change in abundance would be needed in response to a 1 unit change in the NDVI for the 95% intervals of the coefficients to exclude zero. For the effect of prior breeding season productivity, the percent change in abundance required for the Great Basin, Coastal California and Shortgrass Prairies ranged from 4.40 to 4.84%, where as it was higher for the other three strata, in which abundance is lower (ranging from 7.60 to 8.16, Table 3.3). The pattern among strata was similar for the non-breeding periods but precision was typically lower (Table 3.3).

Discussion

Understanding how animal populations respond to large scale changes in climate has proven difficult, especially for migratory animals that inhabit areas separated by hundreds, if not thousands, of kilometers during different times of the year and are thus subject to different climatic events. The Breeding Bird Survey is an important long-term dataset that allows us to investigate trends in breeding bird populations. By linking BBS information with data from remotely sensed estimates of primary productivity, we can begin to understand how the effects of climate and subsequent green up, which occur at different locations during temporally distinct periods, can influence breeding bird population trends. Our analysis suggests that over the past 25 years, population fluctuations in several regions across the Bullock’s oriole breeding range are closely linked to changes in plant productivity during the preceding breeding season. Contrary to our predictions, we did not observe any effects of variation in moulting area (monsoon region) productivity on breeding bird abundance, and the effects of variation in productivity on the Gulf coast region wintering grounds showed opposing effects for Bullock's orioles in two strata.

Our results indicate that breeding abundance of Bullock's orioles in some regions is positively influenced by an increase in plant productivity in the previous breeding season. Specifically, we detected a significant increase in abundance in response to an increase in primary productivity in the Coastal Californian, Shortgrass Prairie, and Great Basin BCRs. Increased productivity may help with the energy demands associated with breeding, feeding nestlings, and subsequent migration. There are two non-exclusive hypotheses that may explain the pattern we observed. First, nestling productivity may be low during years of low productivity, due to reduced food availability during breeding, resulting in reduced recruitment the following season (Holmes et al. 1992). Species richness and abundance of insects (Haddad et al. 2001), grassland arthropod abundance (Siemann 1998), and beetle abundance (Lassau and Hochuli, 2008) are all positively linked to plant productivity. In addition, increases in arthropod abundance (Lepidoptera larvae) during the breeding season have been demonstrated to lead to increased reproductive success in the same year season for a number of species (Holmes et al. 1986). In a study of stonechats (*Saxicola dacotiae)* endemic to a semi-arid island in the Canary Islands, reproductive investment and clutch size were linked to increased arthropod abundance, which was in turn related to earlier rainfall (Illera and Diaz 2006). Similarly, forest productivity was positively related to insect abundance, which in turn was strongly positively related to fledgling success in ovenbirds (*Seiurus aurocapilla*) (Seagle and Sturtevant 2005).

A second hypothesis, is that reduced plant productivity may lead to lowered physical condition of hatchlings and/or adults, reducing the likelihood of surviving fall migration. For example, studies have demonstrated that American redstarts that winter in wetter mangrove forests have higher quality plumage than those in drier and less productive scrub environments (Reudink et al. 2009b). In addition, declining productivity during breeding season appears to have had a negative influence on individual European pied flycatcher (*Ficedula hypoleuca*) fitness and reproductive success in populations around the Mediterranean (Sanz et. al., 2003).

Our study found significant effects of breeding season productivity on subsequent abundance of Bullock's orioles in only three of the six strata. The three strata where no significant effects were observed all have lower breeding abundance in general, and one possibility is thus that we had limited potential to detect an effect. While our analysis of precision showed that this was true to some extent, and that a greater change in abundance would be needed in response to the NDVI, the coefficients for these three strata were near zero or even negative. It is also possible that other limiting factors, such as predation or habitat availability, have a greater influence on reproductive output and we were thus unable to detect a signal from the previous year's plant productivity. Further study of the link between annual climate, plant productivity and the reproductive output of Bullock's orioles is needed to better understand why only some regions of the breeding range show this link between BBS abundance and the NDVI in the previous breeding season.

In our models, responses to productivity in the over-wintering regions showed mixed results, with coastal California showing a negative response to increased productivity in the Mexican Gulf coast region. Conversely, the Great Basin region showed a positive response to increased productivity in the Mexican Gulf coast region. While positive responses to winter NDVI have been detected previously (Saino et al. 2004, Wilson et al. 2011), a negative relationship between winter conditions and breeding abundance is difficult to explain. High NDVI on the African overwintering grounds had a positive influence on the reproductive success of European barn swallows (*Hirundo rustica*) (Saino et al. 2004). Similarly, in American redstarts, productivity in the Caribbean showed positive relationships with breeding abundances for eastern populations, whereas western populations were not significantly influenced by winter conditions in Western Mexico (Wilson et al. 2011). In this case, knowledge of American redstart migratory connectivity and overwintering behaviour was valuable in determining the mechanism behind the interaction between winter conditions and breeding abundance. In the case of Bullock's Orioles, we lack a clear understanding of migratory connectivity between breeding and wintering populations, making it difficult to draw conclusions from these findings. The opposing breeding abundance response to the NDVI in the Gulf Coast region for Coastal California (negative) and the Great Basin (positive) may have been related to some other influence, such as changes in predation or habitat loss in these regions, that had subsequent effects on Bullock's orioles from these regions and the NDVI in the Gulf Coast region may thus simply have been correlated with this influence. Further study into migratory connectivity and winter habitat use, potentially using geolocators on multiple oriole populations, would be required to make conclusions about whether the relationships detected between overwintering NDVI and breeding abundance in the next season are spurious or represent a real biological phenomena.

Contrary to our predictions, we did not detect an influence of monsoon region plant productivity on breeding abundance in the following year. As with the wintering grounds, we do not have a full picture of where the birds from a specific breeding population moult, which hinders our ability to detect the impact of conditions in the moult region on breeding populations. Our results in Chapter 2 indicate that birds from the same breeding population may moult in different locations within the Mexican monsoon region, which makes it difficult to link breeding birds to their moult locations. However, Comrie and Glenn (1998) demonstrated strong autocorrelation in temperature and rainfall across the entire Mexican monsoon region which may suggest birds moulting throughout the area may experience similar environmental conditions. Moult-migrants using the Mexican monsoon region are thought to take advantage of resources that are not available on the breeding grounds, which experience drying out over the course of the summer (Pyle et al. 2009). The consistent productivity in the monsoon region may suggest that the region provides sufficient resources over the period to support a successful moult and before the relatively short migration from the moulting region to the over-wintering region. Thus, we may not have detected any influence of conditions in the moulting grounds on breeding abundance simply because environmental conditions consistently provide abundant, high quality resources, which is likely necessary for the evolution of this unique migratory strategy (Rohwer and Manning 1990, Rohwer et al. 2005, Pyle et al. 2009).

Because the environment in which moult takes place is important and the acquisition of high quality plumage for both flight and mate attraction, rainfall and productivity during moult may still have important consequences for the reproductive success of individuals. Bullock’s orioles appear to moult over a fairly broad area; they have been observed moulting in Arizona, Sonora, and Sinaloa (Pyle et al. 2009), suggesting that the microsite variation may be important. The quality of carotenoid-based ornamental plumage in Bullock’s orioles is dependent upon pigments obtained through the diet and therefore is likely linked to the quality of habitat and the availability of food in the area in which moult takes place. Future work examining whether the productivity of the moulting grounds, or timing of arrival in the area, influences the feather colour of individual orioles would provide further insight into how these environmental factors influence reproductive success at both an individual and population level. A logical future step for this study would be to run a similar analysis on other moult-migrant songbirds from Western North America, examining differences and similarities among western moult-migrants. By using an inclusive approach, which takes into account breeding, stopover, and overwintering regions, we can gain a more complete understanding of how climatic factors influence migratory bird populations, and thus be better equipped to deal with the potential conservation challenges associated with climate change.

Literature cited

Anders, A. D., and E. Post. 2006. Distribution-wide effects of climate on population densities of a declining migratory landbird. Journal of Animal Ecology 75:221-227.

Boone, R. B., S. J. Thirgood, and J. G. C. Hopcraft. 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. Ecology 87:1987–1994.

Bowlin, M. S., I.-A. Bisson, J. Shamoun-Baranes, J. D. Reichard, N. Sapir, P. P. Marra, T. H. Kunz, D. S. Wilcove, A. Hedenström, and C. G. Guglielmo. 2010. Grand challenges in migration biology. Integrative and Comparative Biology 50:261–279.

Carroll, M.L., C.M. DiMiceli, R.A. Sohlberg, and J.R.G. Townshend. 2004. 250m MODIS Normalized Difference Vegetation Index, 250ndvi28920033435, Collection 4, University of Maryland, College Park, Maryland, Day 289, 2003.

Commission for Environmental Cooperation (Montréal, Q., and Secretariat. 1997. Ecological regions of North America: toward a common perspective. The Commission.

Comrie, A. C., and E. C. Glenn. 1998. Principal components-based regionalization of precipitation regimes across the southwest United States and northern Mexico, with an application to monsoon precipitation variability. Climate Research 10:201–215.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. M. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. The American Naturalist 158:17-35.

Hicke, J. A., G. P. Asner, J. T. Randerson, C. Tucker, S. Los, R. Birdsey, J. C. Jenkins, and C. Field. 2002. Trends in North American net primary productivity derived from satellite observations, 1982–1998. Global Biogeochemical Cycles 16:2–1–2–14.

Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecological Monographs 56:201-220.

Holmes, R. T., T. W. Sherry, P. P. Marra, and K. E. Petit. 1992. Multiple brooding and productivity of a Neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. The Auk 109:321-333.

Hutto, R. L. 1998. On the importance of stopover sites to migrating birds. The Auk 115:823-825.

Illera, J. C., and M. Díaz. 2006. Reproduction in an endemic bird of a semiarid island: a food-mediated process. Journal of Avian Biology 37:447-456.

Inger, R., X. A. Harrison, G. D. Ruxton, J. Newton, K. Colhoun, G. A. Gudmundsson, G. McElwaine, M. Pickford, D. Hodgson, and S. Bearhop. 2010. Carry-over effects reveal reproductive costs in a long-distance migrant. Journal of Animal Ecology 79:974–982.

Jensen J. R. (2007) Remote sensing of the environment: an earth resource perspective, 2nd edition. Prentice Hall, Upper Saddle River, NJ, USA

Ktitorov, P., F. Bairlein, and M. Dubinin. 2008. The importance of landscape context for songbirds on migration: body mass gain is related to habitat cover. Landscape Ecology 23:169–179.

Lassau, S. A., and D. F. Hochuli. 2008. Testing predictions of beetle community patterns derived empirically using remote sensing. Diversity and Distributions 14:138-147.

Leu, M., and C. W. Thompson. 2002. The potential importance of migratory stopover sites as flight feather molt staging areas: a review for neotropical migrants. Biological Conservation 106:45–56.

Link, W. A. and J. R. Sauer. 2002. A hierarchical analysis of population change with application to Cerulean Warblers. Ecology 83:2832-2840.

Link, W. A. and J. R. Sauer. 2007. Seasonal components of avian population change: joint analysis of two large-scale monitoring programs. Ecology 88:49-55.

Link, W. A. and R. J. Barker. 2010. Bayesian inference with ecological applications. Academic Press, London, UK.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS-a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10:325–337.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Myneni, R. B., F. G. Hall, P. J. Sellers, and A. L. Marshak. 1995. The interpretation of spectral vegetation indexes. Geoscience and Remote Sensing, IEEE Transactions on 33:481–486.

Newton, I. 2011. Migration within the annual cycle: species, sex and age differences. Journal of Ornithology 152:169–185.

Nott, M. P., D. F. Desante, R. B. Siegel, and P. Pyle. 2002. Influences of the El Niño/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America. Global Ecology and Biogeography 11:333–342.

Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.

Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15–27.

Pyle, P. 1997. Identification Guide to North American Birds: A Compendium of Information on Identifying, Ageing, and Sexing Waterbirds, Diurnal Raptors, and Gallinaceous Birds in the Hand. Slate Creek Press, Bolinas, CA, USA.

Pyle, P., W. A. Leitner, L. Lozano-Angulo, F. Avilez-Teran, H. Swanson, E. G. Limón, and M. K. Chambers. 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. The Condor 111:583–590.

Rising, J. D. and P. L. Williams. 1999. Bullock's Oriole (*Icterus bullockii*). in A. Poole and F. Gills editors, The Birds of North America, No. 416. The Birds of North America Inc., Philadelphia, PA, USA.

Renfrew, R. B., D. Kim, N. Perlut, J. Smith, J. Fox, and P. P. Marra. 2013. Phenological matching across hemispheres in a long-distance migratory bird. Diversity and Distributions 19:1008–1019.

Reudink, M. W., P. P. Marra, T. K. Kyser, P. T. Boag, K. M. Langin, and L. M. Ratcliffe. 2009a. Non-breeding season events influence sexual selection in a long-distance migratory bird. Proceedings of the Royal Society of London Series B: Biological Sciences 276:1619-1626.

Reudink, M. W., C. E. Studds, P. P. Marra, T. K. Kyser, and L. M. Ratcliffe. 2009b. Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American redstart *Setophaga ruticilla*. Journal of Avian Biology, 40:34-41.

Rohwer, S., and J. Manning. 1990. Differences in timing and number of molts for Baltimore and Bullock's orioles: Implications to hybrid fitness and theories of delayed plumage maturation. The Condor:125–140.

Rohwer, S., L. K. Butler, D. R. Froehlich, R. Greenberg, and P. P. Marra. 2005. Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. Pages 87-105 in R. Greenberg, and P. P. Marra, editors. Birds of Two Worlds: The Ecology and Evolution of Migration Johns Hopkins University Press, Baltimore, MD, USA.

Saino, N., T. Szép, R. Ambrosini, M. Romano, and A. P. Moller. 2004. Ecological conditions during winter affect sexual selection and breeding in a migratory bird. Proceedings of the Royal Society of London Series B: Biological Sciences 271:681–686.

Sanz, J. J., J. Potti, J. Moreno, S. Merino, and O. Frías. 2003. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. Global Change Biology 9:461-472.

Sauer, J. R., and W. A. Link. 2011. Analysis of the North American breeding bird survey using hierarchical models. The Auk 128:87–98.

Seagle, S. W., and B. R. Sturtevant. 2005. Forest productivity predicts invertebrate biomass and ovenbird (*Seiurus aurocapillus*) reproduction in Appalachian landscapes. Ecology 86:1531-1539.

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology 79:2057-2070.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040–2042.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Studds, C. E., and P. P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86:2380–2385.

Tøttrup, A. P., R. H. G. Klaassen, M. W. Kristensen, R. Strandberg, Y. Vardanis, Å. Lindström, C. Rahbek, T. Alerstam, and K. Thorup. 2012. Drought in Africa caused delayed arrival of European songbirds. Science 338:1307–1307.

Wang, Q., S. Adiku, J. Tenhunen, and A. Granier. 2005. On the relationship of NDVI with leaf area index in a deciduous forest site. Remote Sensing of Environment 94:244–255.

Webster, M. S., P. P. Marra, R. Greenberg, and P. P. Marra. 2005. The importance of understanding migratory connectivity and seasonal interactions. Birds of two worlds: the ecology and evolution of migration. Johns Hopkins University Press, Baltimore, Maryland, USA:199–209.

Wilson, S., S. L. Ladeau, A. P. Tøttrup, P. P. Marra. 2011. Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. Ecology 92: 1789-1798.

Table 3.1: Sample size, abundance per route and temporal trend (1983-2006) for Bullock's orioles in the six strata used in this analysis. Columns under "Stratum" are the total number of routes and the average number of Bullock's orioles detected per route for all routes in the Stratum. Columns under "Analysis" are those values for the routes that met our minimum criteria and used in this analysis (surveys in ≥14 of 24 years and mean of > 2 Bullock's oriole detections per year). Trends were determined from the model and are only based on the routes used in this analysis.

BCR	Stratum Name	Stratum		Analysis		Trend
		N routes	BUOR/route	N routes	BUOR/route	
5	Northern Pacific Rainforest	82	2.1	18	5.7	-1.59 (-3.17. -0.02)
9	Great Basin	204	3.4	45	6.8	-0.27 (-1.17, 0.68)
10	Northern Rockies	143	1.6	12	7.3	0.15 (-1.76, 2.07)
16	Southern Rockies - Colorado Plateau	130	1.7	15	4.2	-0.83 (-2.53, 0.85)
18	Shortgrass Prairie	112	4.0	31	6.3	-0.10 (-1.29, 1.09)
32	Coastal California	104	9.8	40	11.5	-1.67 (-2.57, -0.75)

Table 3.2: Beta coefficients for the reduced model showing effects of NDVI on the breeding grounds and wintering area 2 on abundance on Breeding Bird Survey routes in the following year. [1]The Breed NDVI$_{t-1}$ coefficient for the Great Basin is from a model without data from 2000 since the 1999 La Niña event resulted in a low NDVI value that had considerable influence on the slope (see text). ** = 95% certainty, * = 90% certainty.

Strata	Breed NDVI$_{t-1}$	Winter 2 NDVI$_t$
Northern Pacific Rainforest	-0.040 (-0.117, 0.037)	-0.014 (-0.082, 0.053)
Great Basin[1]	0.057 (-0.005, 0.118)*	0.032 (-0.006, 0.072)
Northern Rockies	-0.037(-0.114, 0.040)	0.018 (-0.059, 0.094)
Southern Rockies / Colorado Plateau	0.007 (-0.065, 0.078)	0.010 (-0.065, 0.085)
Shortgrass Prairie	0.045 (-0.004, 0.093)*	0.018 (-0.032, 0.068)
Coastal California	0.051 (0.012, 0.091)**	-0.037 (-0.075, -0.001)**

Table 3.3: Percent change in BBS abundance needed to declare a significant response to a 1 unit change in the standardized NDVI for each period of the annual cycle in each strata. The percent change in the table is based on the lower credible interval half-width and is thus an indication of the power to detect a positive response.

Strata	Breed NVI_{t-1}	Moult $NDVI_{t-1}$	Winter 1 $NDVI_t$	Winter 2 $NDVI_t$
Northern Pacific Rainforest	8.08	8.20	8.73	7.36
Great Basin[1]	4.40	4.97	5.67	4.51
Northern Rockies	8.16	9.27	10.47	8.17
Southern Rockies / Colorado Plateau	7.60	9.02	9.88	8.11
Shortgrass Prairie	4.84	5.86	6.37	5.37
Coastal California	4.51	4.98	5.71	3.98

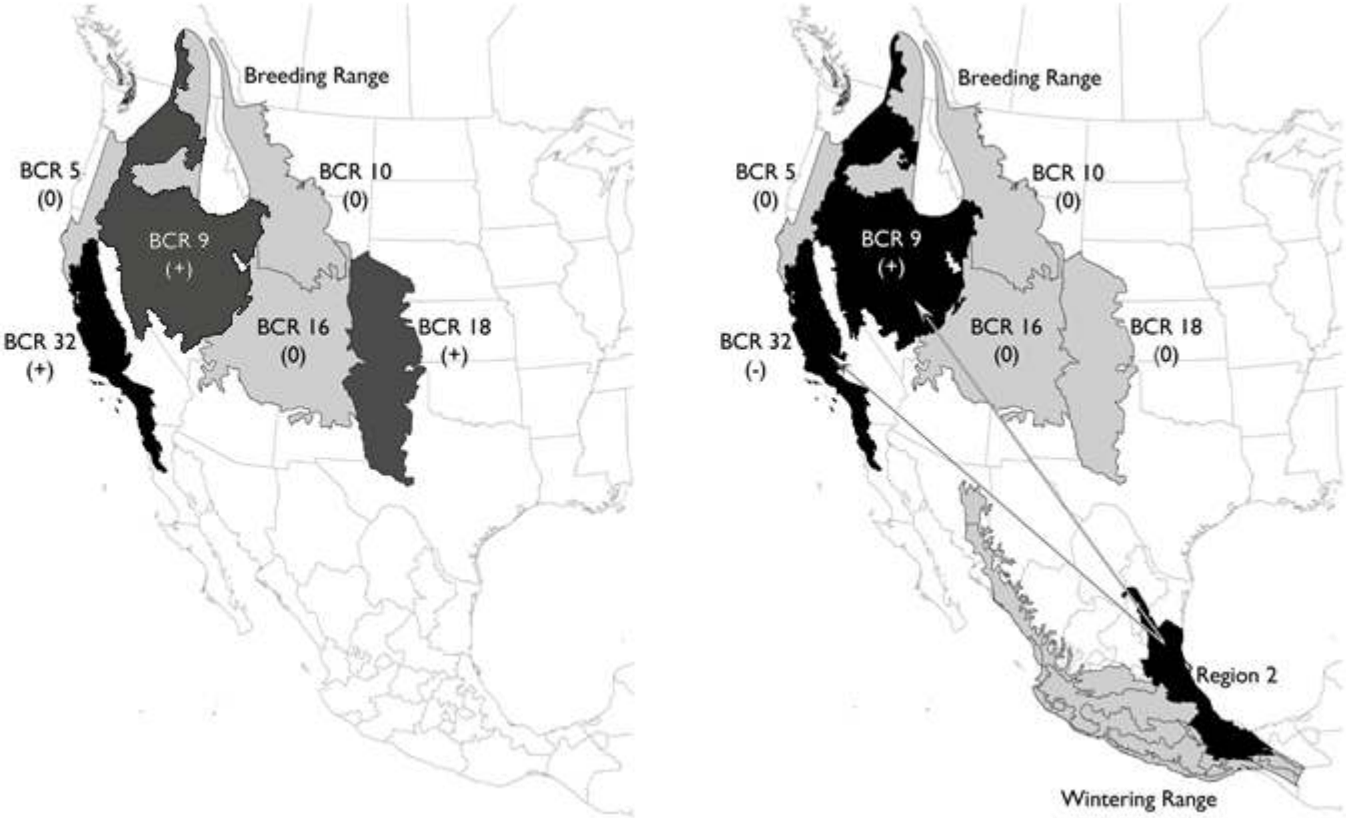

Figure 3.1: Left – Bullock's oriole breeding abundance response to NDVI in the same Bird Conservation Region (BCR) Right – Bullock's oriole breeding abundance response to NDVI in Region 2 of the wintering Range. Black indicates a significant response at ≥ 95% certainty, dark grey indicates a significant response at 90% certainty, light grey indicates no significant response.

CHAPTER 4: CONCLUSION

The goal of this study was to investigate moult-migration and the influence of primary productivity throughout the annual cycle on Bullock's orioles. Our results provide very strong evidence that Bullock's orioles from the population around Kamloops, BC, make use of the Mexican monsoon region to moult before moving to Central and Eastern Mexico to winter. The moult-migration strategy appears to be consistent across all age and sex classes. Geolocators show that the route of migration and the location of moulting and overwintering sites of individuals can vary greatly within the same population. Multiple short term stopover sites may also be used on the way to the moult location. I have also shown that primary productivity in breeding areas, and possibly wintering areas, can influence oriole breeding abundances in the following breeding season.

Limitations for techniques and future studies

A more comprehensive stable hydrogen isotope sampling in Mexico and Central America could greatly improve location estimates. I addition, our isotope analysis of feathers from multiple feather tracts adds further evidence that hydrogen isotope fractionation within different feather tracts, and is consistent with findings from Kelly et al. (2002) and Smith et al. (2008). The issue of tissue fractionation within individuals should be taken into account in future isotope studies as sampling only a single feather type, or assuming that different feather types would have the same isotope fractionation could result in erroneous conclusions on the location of moult.

Stable hydrogen isotope analysis and the use of geolocators are complementary techniques that can help to investigate migration of bird species that have less common moulting strategies. The use of both feather and claw material for isotope analysis allowed us to provide strong evidence of separate moulting and overwintering locations. While only two of the recovered geolocators tracked birds for an entire annual cycle, they also clearly demonstrated moult migration, with birds making use of the Mexican monsoon region. Taken together, these complementary analyses provided stronger evidence than could have been provided by one technique alone. With questions remaining about how widespread the occurrence of moult-migration is among birds currently considered to be moult-migrants (Pyle et al. 2009), I believe both of these techniques can offer valuable insight. In Bullock's orioles, the use of isotopes provides compelling evidence for obligate moult-migration across age/sex classes.

The BBS and long term remote sensing datasets are often publically available. Our study is a good example of how these data, and similar datasets, may be used to address questions of how bird populations change over time. In addition, the study highlights inexpensive methods by which one can examine environmental factors affecting birds throughout their entire annual cycle without requiring the resources necessary to conduct studies at each stationary phase. While field studies during each phase would be ideal, in their absence, approaches such as the one used here can help us gain a more comprehensive view of a bird throughout the annual cycle.

Implications for environmental management and potential conservation

Although Bullock's orioles are currently classified as a species of least concern, they do face a potential threat from habitat loss and climate change. Geolocators revealed some interesting facts about our study population of Bullock's orioles. From a sample of only 3 birds from the same breeding population, I found different uses of migratory flyways, the potential use of short stopover sites during fall migration, and different moulting and wintering sites. This makes it very different to identify important habitats for future protection. Given that the birds cluster together during breeding, have extremely high breeding site fidelity, and that plant productivity appears to be important, the best use of resources in protecting these birds, and potentially other moult-migrants, may be on the breeding grounds and the preservation of riparian habitats in which they nest and breed. While the conclusions I can draw from over-wintering results is limited by questions of migratory connectivity, the potential influence of habitat quality on breeding abundance suggests the area provides important resources necessary for successful spring migration and subsequent breeding. Additionally several other species make use of the same moult migration strategy and moulting location. These birds will no doubt have differing sensitivities to changes in the Mexican monsoon region. While I did not detect a significant contribution to breeding abundance from plant productivity, this does not necessarily mean it has no bearing on these birds' success. The area in which moult takes place has been shown to be of important in the acquisition of high quality ornamental plumage which has implications for both sexual and social selection. Presently, work examining how the moulting environment affects colouration of our study population of Bullock's orioles is currently underway. This study has demonstrated that (1) all age and sex classes of Bullock's orioles use the Mexican monsoon region for moult during migration, (2) that individuals from the same breeding population moult and winter in different locations, suggesting weak migratory connectivity, and (3) that plant productivity especially during breeding influences oriole breeding abundance the following season.

Literature cited

Kelly, J. F., V. Atudorei, Z. D. Sharp, and D. M. Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia 130:216–221.

Pyle, P., W. A. Leitner, L. Lozano-Angulo, F. Avilez-Teran, H. Swanson, E. G. Limón, and M. K. Chambers. 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. The Condor 111:583–590.

Smith, A. D., K. Donohue, and A. M. Dufty Jr. 2008. Intrafeather and intraindividual variation in the stable-hydrogen isotope (δD) content of raptor feathers. The Condor 110:500-506.

APPENDIX A

Appendix Table A.1: Differences among tissues. Mixed-effects models for ASY male Bullock's orioles (all, outliers included). Models "A" include both Year and Tissue (δ^2H) as a fixed effects, models "B" are run without Year when the effect was not significant. Bird ID is included as a random effect to address birds recaptured in 2013.

Model	Fixed effect(s)	F	p	Tissues	n	mean	SD
A	Year	1.60	0.21	**Breast**	28	-71	12
	Tissue	7.23	0.0002	**Claw**	8	-68	19
				Tail	27	-80	12
B	Tissue	7.25	0.0002				
A	Year	1.56	0.22	**Claw**	8	-68	19
	Tissue	4.24	0.05	**Tail**	27	-80	12
B	Tissue	4.12	0.05				
A	Year	3.22	0.08	**Breast**	28	-71	12
	Tissue	0.0009	0.98	**Claw**	8	-68	19
B	Tissue	0.0008	0.93				
A	Year	0.47	0.5	**Breast**	28	-71	12
	Tissue	21.94	<0.0001	**Tail**	27	-80	12
B	Tissue	22.45	<0.0001				

Appendix Table A.2: Differences among tissues with outliers removed. Mixed-effects models for ASY male Bullock's orioles (outliers removed). Models "A" include both Year and Tissue as a (δ^2H) fixed effects, models "B" are run without Year where the effect is insignificant. Bird ID is included as a random effect to address birds recaptured in 2013.

Model	Fixed effect(s)	F	p	Tissues	n	mean	SD
A	Year	0.42	0.52	**Breast**	**28**	**-71**	**12**
	Tissue	13.93	<0.0001	**Claw**	6	-58	4
				Tail	26	-78	10
B	Tissue	14.58	<0.0001				
A	Year	0.34	0.56	**Claw**	6	-58	4
	Tissue	18.02	0.0003	**Tail**	26	-78	10
B	Tissue	19.45	0.0002				
A	Year	2.09	0.17	**Breast**	28	-71	12
	Tissue	3.17	0.11	**Claw**	6	-58	4
B	Tissue	3.51	0.09				
A	Year	0.69	0.41	**Breast**	28	-71	12
	Tissue	17.80	0.0002	**Tail**	26	-78	10
B	Tissue	18.43	0.0002				

Appendix Table A.3: Matched Pairs t-test comparing tissue (δ^2H) types within each age and sex class.

Age/Sex	Matched Pair	n	t	p
ASY ♂	**Breast/Claw (all)**	8	-0.23	0.82
	Breast/Claw (outliers removed)	6	-1.41	0.22
ASY ♂	**Tail/Claw (all)**	8	-1.28	0.24
	Tail/Claw (outliers removed)	6	-3.15	0.03
ASY ♂	**Breast/Tail (all)**	27	-4.68	<0.0001
	Breast/Tail (outliers removed)	6	-4.41	0.0002
SY ♂	**Breast/Tail**	4	-2.29	0.11
ASY ♀	**Breast/Tail (all)**	10	-1.45	0.18
	Breast/Tail (outliers removed)	8	-1.05	0.33
SY ♀	**Breast/Tail**	5	-1.58	0.19

Appendix Table A.4 Relationships between feather types. Mixed-effects models comparing breast and tail feather δ^2H for male and female birds. Models "A" include both Year and Tissue (δ^2H) as a fixed effects, models "B" are run without Year where the effect is insignificant. Bird ID is included as a random effect to address birds recaptured in 2013.

Model	**Fixed effect(s)**	**n**	**F**	**p**
A	♂ Breast/Tail (all)	**26**		
	Year		0.05	0.82
	Tissue		12.69	0.002
B	Tissue		16.52	0.0004
A	♂ Breast/Tail (outliers removed)	**26**		
	Year		0.79	0.4
	Tissue		7.34	0.01
B	Tissue		12.41	0.002
A	♀ Breast/Tail	**8**		
	Year		0.01	0.92
	Tissue		2.55	0.16
B	Tissue		4.49	0.07