# Proceedings of the EURING Analytical Meeting 2021

31 May-11 June 2021, Quebec City, Quebec, Canada

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# Introduction

The 12<sup>th</sup> EURING Analytical Meeting was held May 31 to June 11, 2021 and in several ways was unique in the 35 years of conferences. Of course, due to the COVID-19 pandemic, the meeting was the first conference held online. This was challenging for an international meeting because no matter the hour someone would need to be awake in the middle of the night to attend the meeting live. However, since most participants were from Europe and North America we held the meeting each day from 10am-2pm EDT, which allowed most participants to attend during daylight hours.

Another challenge was how to document the contributions to the conference. A survey of listserve members indicated about a 50:50 split on whether to have a published proceedings of the presentations. In addition, the rapidly changing business of scientific publications and the pressure within academia to publish in high impact-factor journals led us to decide to forego a one-volume published proceedings. Instead, we collated a list of references and links to the publications that resulted from the contributions made at the EURING Analytical Meeting 2021.

In comparison with the first few conferences, the 2021 conference impressively shows the dramatic development in the statistical methods used to study population dynamics. If you look at the titles in the issue related to the first EURING conference (1986, Wageninen, Netherlands, (North, 1986)), most deal with survival estimation and movement analyses. In the course of the following six conferences, the session topics broadened and since 2003 (Radolfzell, Germany) the range of session topics have been similar. Session topics now include population dynamics, model fit and assumptions, multi-state/multi-event models, monitoring and conservation (Robinson & Gardner, 2019). In 2017 (Barcelona, Spain), contributions included topics on occupancy models and analyses of unmarked animals (Robinson & Gardner, 2019). At the 2021 conference, the focus shifted to integrated data analyses, for which we held two sessions because of the large number of contributions.

Pertti Saurola was the Honoured Speaker and he emphasized the importance of integrated data analysis, long-term field studies, and the collaboration between biologists and statisticians. Also, he communicated his enthusiasm for science and nature, a spirit that is embodied in the EURING community and this enthusiasm is reflected in the contributions of the EURING 2021 conference. With further development of individually based spatially-explicit capture-mark-recapture analyses presenters studied habitat use and species interactions. Technical development of animal movement models and of data acquisition give persistently deeper insight into ecological mechanisms of animal movement. Integral projection models are now increasingly used to understand evolutionary mechanisms of population dynamics and management and conservation is benefitting from the development and increasing experience in decision-theoretic methods. Survival estimation had been an important focus during the first six conferences (1986–2000) and at the 2021 conference, survival estimation was revived with papers on Bayesian estimation techniques, random effects, individual heterogeneity and how to account for misidentification of individuals.

With the session on the European-African Migration Atlas a milestone in the history of EURING was celebrated: the publication of all European bird ring recapture and recovery data since the beginning of bird ringing. This session shared new methods that have been developed to visualize and analyze bird movements over large distances.

Overall, the EURING 2021 meeting and the virtual proceedings give an overview of the current state-of-art modelling of population dynamics including traditional topics on survival estimation and the study of animal movement. We would like to thank two other people who were instrumental to the success of the conference. The support that Evan Cooch provided on the phidot.org website made soliciting and organizing abstracts very easy. Because he has automated so many aspects of before-the-meeting tasks we were able to focus on research

topics and recruiting speakers. Then when it came to hosting the conference, Marc Mazerolle seamlessly transitioned from an in-person to on-line format. He identified tools and techniques that worked very well for the organizers and participants. Without Evan and Marc all our efforts would have been for naught and so we greatly appreciate and thank them for their hard work.

Fränzi Korner-Nievergelt Duane Diefenbach Scientific Program Co-chairs

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# List of Publications

- Acker, P., Daunt, F., Wanless, S., Burthe, S.J., Newell, M., Harris, M.P., Gunn, C., Swann, R., Payo-Payo, A., & Reid, J.M. (2022) Hierarchical variation in phenotypic flexibility across timescales and associated survival selection shape the dynamics of partial seasonal migration. The American Naturalist, in press. <a href="https://doi.org/10.1086/722484">https://doi.org/10.1086/722484</a>
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# Abstracts (by session topic)

Building on the Eurasian-African Migration Atlas: towards robust quantitative analyses of avian movements

# The Eurasian African bird migration atlas – a starting point for a more quantitative understanding of avian movements

Spina, F., Baillie, S. R., Bairlein, F., Fiedler, W., Thorup, K.

This online Migration Atlas covers the huge geographical area represented by two continents, encompassing the flyways between Eurasia and Africa. Movements in time and space of 300 bird species are mapped and analysed drawing on data gathered by <a href="European Ringing Schemes">European Ringing Schemes</a> over more than a century and collated by the EURING databank.

Another unique feature of this Atlas is that it complements movement data provided by ring recoveries with detailed migration patterns of individual birds provided by tracking studies. Tracking data come via a dynamic data feed from <a href="Movebank">Movebank</a>, a platform hosted by the Max Planck Institute of Animal Behaviour. Movebank provides tools to help researchers and wildlife managers worldwide to manage, share, analyse and archive data on the movements of individual animals. For over 100 of the species covered by this Atlas, the online mapping tool overlays movement patterns based on ring recoveries, each of which documents only part of the migratory journey, with tracks from electronic devices, principally satellite transmitters, GPS-GSM tags or geolocators, providing the most complete information available on the migration routes of individual birds.

Thus, the Atlas brings together conventional ringing data - offering information from a large array of species, huge numbers of marked individuals, broad geographical scope, information on recovery causes, and long historical coverage - with detailed information on migratory movements from tracking data, from a smaller number of species and individuals and less extensive geographic scope. This complementarity represents a unique feature of the Atlas and a positive example that could be applied to different taxonomic groups.

The online species accounts included in the Atlas have the following elements (see Map Help for more detailed information on interpreting the maps):

Introductory text, photograph, and basic statistics.

Overall connectivity map and text (see analysis button) based on 8 ringing regions across Europe. A tracking layer can be displayed where available. Maps showing overall connectivity by age and sex are also provided. These maps show the main connectivity patterns that will often be important for conservation and management.

Connectivity by condition map and text showing connectivity patterns in relation to seven cause of recovery categories. The associated text explains how the observed recovery patterns are influenced by different recovery causes. This is important information for critical interpretation of the other maps.

Connectivity by month and by region map showing connectivity for one region at a time, with encounter locations colour coded by month. These maps and the associated text show how different populations are distributed at different times of year.

Seasonal movements maps and associated text shows bird movements throughout the annual cycle based on ten-day periods.

The Statistics section displays a range of graphs and tables describing the recovery data present in the Atlas database, including not only the mapped, distant recoveries (distant = at least 50 km between ringing and recovery encounters), but also local recoveries. This information will help users to understand and interpret the data presented.

Associated references cited in the text which can be viewed using the bibliography button.

The other main feature of this Atlas is the four research modules addressing different aspects of bird migration and relationships between birds and people. All are highly relevant

to international and flyway scale bird conservation. These research modules address the following topics:

- Historical changes in migration patterns
- Intentional killing of birds by man
- Migration seasons of hunted species
- Migratory connectivity within the European African migration system

Follow the above links to the individual research modules to read an overview or to download the full reports.

This Atlas has been produced in collaboration with the <u>Convention on Migratory Species (CMS)</u>, thus a key aim of the work is to inform the conservation of the migratory bird species covered here. In particular, the Atlas provides information to support the implementation and development of important international agreements managed by CMS, including those on the <u>Conservation of African-Eurasian Migratory Waterbirds (AEWA)</u>, the <u>Conservation of Albatrosses and Petrels (ACAP)</u>, the <u>Memorandum of Understanding on the Conservation of Migratory Birds of Prey in Africa and Eurasia (Raptors MoU) and the <u>African-Eurasian Migratory Landbirds Action Plan (AEMLAP)</u>. CMS needs such information for all of the species groups that it covers, and has an objective to create a Global of Atlas of Animal Migration (GAAM). This Atlas forms the first part of that initiative and we hope that the work presented here will provide an important contribution and tools towards this broader goal. The Executive Summary provides an overview of the key developments and findings produced by the Eurasian African Bird Migration Atlas project with particular emphasis on their relevance to the Conservation of Migratory Species.</u>

Spina, F., Baillie, S. R., Bairlein, F., Fiedler, W. and Thorup, K. (Eds) 2022. The Eurasian African Bird Migration Atlas. <a href="https://migrationatlas.org">https://migrationatlas.org</a>. EURING/CMS.

# Contributed talk 1

Patterns of migratory connectivity in the European-African migratory system as inferred by ring recovery analysis of the EURING database

Fattorini, N., Spina F., Rubolini, D., Ambrosini, R.

Understanding how individuals redistribute after migration assists in the conservation and management of mobile species, yet the eco-evolutionary drivers of migratory connectivity remain unclear. Taking advantage of an exceptionally large (~150,000 individuals, 83 species) and more-than-a-century long dataset of bird ringing encounters, we investigated determinants of avian migratory connectivity on both short- and long-distance migrants. Most species exhibited significant connectivity likely due to the large intraspecific variability in migration strategies, which often led to the identification of distinct migratory populations. Migratory connectivity was strongly predicted by geography, especially migration distance, but it was evolutionary labile and weakly influenced by biological traits due to flexibility in migratory behaviour. By unravelling determinants of migratory connectivity we improve knowledge about the resilience of migrants to ecological perturbations. Also, our population-level analysis provides a critical tool to inform transboundary conservation and management strategies by explicitly considering the large intraspecific variability of avian migration.

Fattorini, N., A. Costanzo, A. Romano, D. Rubolini, S. Baillie, F. Bairlein, F. Spina, R. Ambrosini. (2022). Eco-evolutionary drivers of avian migratory connectivity. bioRxiv 2022.07.04.497586; doi: <a href="https://doi.org/10.1101/2022.07.04.497586">https://doi.org/10.1101/2022.07.04.497586</a>

# Estimating migratory connectivity strength and pattern across data types

Hostetler, J. A. Division of Migratory Bird Management, US Fish and Wildlife Service, Laurel, MD. USA.

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Hallworth, M. T., Cary Institute for Ecosystem Studies, Millbrook, NY, USA; Vermont Center for Ecostudies, White River Junction, VT, USA.

Rushing, C. S., Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT, USA.

Contina, A., Department of Integrative Biology, University of Colorado Denver, Denver, CO, USA.

Bossu, C., Department of Biology, Colorado State University, Fort Collins, CO, USA.

Ruegg, K., Department of Biology, Colorado State University, Fort Collins, CO, USA.

#### Contributed talk 3

## Disentangling survival, migratory connectivity and observation in continuous space

Schirmer, S., Korner-Nievergelt, F., von Rönn J. A. C., Liebscher, V.

Spatial variation in survival has individual fitness consequences and influences population dynamics. Which space animals use during the annual cycle determines how they are affected by this spatial variability. Therefore, knowing spatial patterns of survival and space use is crucial to understand demography of migrating animals. Extracting information on survival and space use from observation data, in particular dead recovery data, requires explicitly identifying the observation process.

We build a fully stochastic model for animals marked in populations of origin, which were found dead in spatially discrete destination areas. The model acts on the population level and includes parameters for use of space, survival and recovery probability. It is based on the division coefficient and the multinomial reencounter model. We use a likelihood-based approach, derive Restricted Maximum Likelihood-like estimates for all parameters and prove their existence and uniqueness.

In a simulation study we demonstrate the performance of the model by using Bayesian estimators derived by the Markov chain Monte Carlo method. We obtain unbiased estimates for survival and recovery probability if the sample size is large enough. Moreover, we apply the model to real-world data of European robins *Erithacus rubecula* ringed at a stopover site. We obtain annual survival estimates for different spatially discrete non-breeding areas. Additionally, we can reproduce already known patterns of use of space for this species.

Schirmer, S., Korner-Nievergelt, F., C von Rönn, J. A., & Liebscher, V. (2022). Estimation in the multinomial reencounter model - Where do migrating animals go and how do they survive in their destination area? Journal of Theoretical Biology, 111108. https://doi.org/10.1016/j.jtbi.2022.111108

Schirmer, S. (2021). SaskiaSchirmer/CONSURE: First release of CONSURE (v1.0.0). Zenodo. https://doi.org/10.5281/zenodo.5468963

# Quantifying individual variation in migration versus residence within and among year: a dynamic-finite-mixture multi-state capture-recapture model

Acker, P., Daunt, F., Burthe, S. J., Reid, J. M.

Population responses to environmental variation ultimately depend on within-individual and among-individual variation in labile phenotypic traits that affect fitness, and resulting episodes of selection. Yet, complex patterns of individual phenotypic variation arising within and between time periods, and associated variation in selection, have not been fully conceptualised or quantified. We highlight how structured patterns of phenotypic variation in dichotomous threshold traits can theoretically arise and experience varying forms of selection, shaping overall phenotypic dynamics. We then fit novel multistate models to ten years of bandresighting data from European shags to quantify phenotypic variation and selection in a key threshold trait underlying spatio- seasonal population dynamics: seasonal migration versus residence. First, we demonstrate substantial among-individual variation alongside substantial between-year individual repeatability in within-year phenotypic variation ('flexibility'), with weak sexual dimorphism. Second, we demonstrate that between-year individual variation in withinyear phenotypes ('supraflexibility') is structured and directional, consistent with the threshold trait model. Third, we demonstrate strong survival selection on within- year phenotypes, and hence on flexibility, that varies across years and sexes, including episodes of disruptive selection representing costs of flexibility. By quantitatively combining these results, we show how supraflexibility and survival selection on migratory flexibility jointly shape population-wide phenotypic dynamics of seasonal movement.

Acker, P., Daunt, F., Wanless, S., Burthe, S.J., Newell, M., Harris, M.P., Gunn, C., Swann, R., Payo-Payo, A., & Reid, J.M. (2022) Hierarchical variation in phenotypic flexibility across timescales and associated survival selection shape the dynamics of partial seasonal migration. The American Naturalist, in press.

# Contributed talk 5

# Assessing the timing of migration progression based on ring recoveries

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Rubolini, D., Department of Environmental Science and Policy, University of Milan, Milan, Italy.

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Imperio, S., Area Avifauna Migratrice, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), Ozzano Emilia (BO), Italy.

Bairlein, F., Institute of Avian Research, Vogelwarte Helgoland, Helgoland, Germany.

# Spatially-explicit capture-mark-recapture analysis

# Keynote

# Spatial capture-recapture and a general framework for individual-based models of population dynamics

Chandler, R. Warnell School of Forestry and Natural Resources, University of Georgia, USA Gaya, H. Warnell School of Forestry and Natural Resources, University of Georgia, USA

#### Contributed Talk 1

## A Marked Poisson Process for Latent ID Spatial Capture-Recapture Models

van Dam-Bates, P. School of Mathematics and Statistics, University of St Andrews, St Andrews, Scotland

Borchers, D. School of Mathematics and Statistics, University of St Andrews, St Andrews, Scotland Papathomas, M. School of Mathematics and Statistics, University of St Andrews, St Andrews, Scotland

Stevenson, B. Department of Statistics, University of Auckland, Auckland, New Zealand Fewster, R. Department of Statistics, University of Auckland, Auckland, New Zealand

### Contributed Talk 2

# **Modeling Species Interactions Using Spatial Capture Recapture**

Heather Gaya, Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia, USA

Richard Chandler, Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia, USA

#### Contributed Talk 3

# **Spatial Capture-Recapture Density Estimation Using Acoustic Recording Units Without Individual Identification**

Augustine, Ben C. U.S. Geological Survey John Wesley Powell Center, Cornell Department of Natural Resources, Ithaca, New York, USA

Royle, J. Andrew. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA

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Fuller, Angela K. US Geological Survey, New York Cooperative Fish and Wildlife Research Unit, Department of Natural Resources, Cornell University, Ithaca, New York, USA

#### Contributed Talk 4

# Secondary Forest, Secondary Role: Density and Home Range Size Variation of Understory Birds in A Forest Mosaic

Amaral, B.R., Department of Ecosystem Sciences and Management, Pennsylvania State University, USA

Miller, D.A.W., Department of Ecosystem Sciences and Management, Pennsylvania State University, USA

Ferraz, G. Department of Ecology, Federal University of Rio Grande do Sul, Brazil

# Integral projection modelling

# Keynote

# Using IPMs to study the response of populations to a changing environment

Simmonds, E.

We are currently in a period of rapid environmental change, with populations across the globe experiencing alterations to the environments they experience. These changes have consequences for population dynamics and demography. Predicting how individual populations might respond has been a challenge, but one that can be (and has been) addressed with integral projection models. This plenary will synthesize the theoretical and applied advances in integral projection models over the past two decades, which have given new insights into how populations (often birds) could respond to environmental changes. The talk will finish with looking to the future and how integral project models can be used to best predict the fate of our biological populations.

Simmonds, E. G., Cole, E.F., Sheldon, B. C., Coulson, T. (2020) Phenological asynchrony: a ticking time-bomb for seemingly stable populations? Ecology Letters 23 (12), 1766-1775. https://onlinelibrary.wiley.com/doi/full/10.1111/ele.13603

Simmonds, E, G., Coulson, T. (2015) Analysis of phenotypic change in relation to climatic drivers in a population of Soay sheep Ovis aries. Oikos 124 (5), 543-552. https://onlinelibrary.wiley.com/doi/abs/10.1111/oik.01727

### Contributed talk 1

# The demographic causes of population change vary across four decades in a long-lived shorebird

Allen, A. M., Jongejans, E., Van de Pol, M., Ens, B. J., Frauendorf, M., Van der Sluijs, M., De Kroon, H.

Understanding which factors cause populations to decline begins with identifying which parts of the life cycle, and which vital rates, have changed over time. However, in a world where humans are altering the environment both rapidly and in different ways, the demographic causes of decline likely vary over time. Identifying temporal variation in demographic causes of decline is crucial to assure that conservation actions target current and not past threats. However, this has rarely been studied as it requires long time series. Here we investigate how the demography of a long-lived shorebird (the Eurasian Oystercatcher Haematopus ostralegus) has changed in the past four decades, resulting in a shift from stable dynamics to strong declines (-9% per year), and recently back to a modest decline. Since individuals of this species are likely to respond differently to environmental change, we captured individual heterogeneity through three state variables: age, breeding status, and lay date (using integral projection models). Timing of egg-laying explained significant levels of variation in reproduction, with a parabolic relationship of maximal productivity near the average lay date. Reproduction explained most variation in population growth rates, largely due to poor nest success and hatchling survival. However, the demographic causes of decline have also been in flux over the last three decades: hatchling survival was low in the 2000s but improved in the 2010s, while adult survival declined in the 2000s and remains low today. Overall, the joint action of several key demographic variables explain the decline of the oystercatcher, and improvements in a single vital rate cannot halt the decline. Conservations actions will thus need to address threats occurring at different stages of the oystercatcher's life cycle. The dynamic nature of the threat landscape is further supported by the finding that the average individual no longer has the highest performance in the population, and emphasizes how

individual heterogeneity in vital rates can play an important role in modulating population growth rates. Our results indicate that understanding population decline in the current era requires disentangling demographic mechanisms, individual variability, and their changes over time.

Allen, Andrew M., Jongejans, Eelke, van de Pol, Martijn, Ens, Bruno J., Frauendorf, Magali, van der Sluijs, Martijn, and de Kroon, Hans (2022) The Demographic Causes of Population Change Vary across Four Decades in a Long-Lived Shorebird. Ecology 103(4): e3615. https://doi.org/10.1002/ecy.3615

#### Contributed talk 2

Integral projection modeling for Weddell seals: evaluating multi-decadal population dynamics and the importance of individual heterogeneity to population stability

MacDonals, K. R., Ecology Department, Montana State University, USA Paterson, J. T., Ecology Department, Montana State University, USA Rotella, J. J., Ecology Department, Montana State University, USA

# Building integral projection models with nonindependent vital rates

Fung, Y.L., Newman, K., King, R., de Valpine, P.

Population dynamics are functions of several demographic processes including survival, reproduction, somatic growth, and maturation. The rates or probabilities for these processes can vary by time, by location, and by individual. These processes can co-vary and interact to varying degrees, e.g., an animal can only reproduce when it is in a particular maturation state. Population dynamics models that treat the processes as independent may yield somewhat biased or imprecise parameter estimates, as well as predictions of population abundances or densities. However, commonly used integral projection models (IPMs) typically assume independence across these demographic processes. We examine several approaches for modelling between process dependence in IPMs and include cases where the processes covary as a function of time (temporal variation), co-vary within each individual (individual heterogeneity), and combinations of these (temporal variation and individual heterogeneity). We compare our methods to conventional IPMs, which treat vital rates independent, using simulations and a case study of Soay sheep (Ovis aries). In particular, our results indicate that correlation between vital rates can moderately affect variability of some population-level statistics. Therefore, including such dependent structures is generally advisable when fitting IPMs to ascertain whether or not such between vital rate dependencies exist, which in turn can have subsequent impact on population management or life-history evolution.

Fung, Y. L., Newman, K., King, R., & de Valpine, P. (2022). Building integral projection models with nonindependent vital rates. Ecology and Evolution, 12(3), e8682. <a href="https://doi.org/10.1002/ece3.8682">https://doi.org/10.1002/ece3.8682</a>

#### Contributed talk 4

Benefits and costs of male and female subordinates on the population dynamics of a cooperative breeding species

Chamiot-clerc Benoit Cohas Aurélie Plard Floriane

# **Animal Movement**

#### Keynote

# Big data empowers a new era of comparative animal movement analyses.

Kays, Roland, Smithsonian Tropical Research Institute, Balboa, Republic of Panama and North Carolina Museum of Natural Sciences, Raleigh, NC, USA and Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC, USA Ben Hirsch, Smithsonian Tropical Research Institute, Balboa, Republic of Panama and College of Science and Engineering, James Cook University, Townsville, QLD, Australia Damien Caillaud, Department of Anthropology, University of California, Davis, CA, USA Rafael Mares, Smithsonian Tropical Research Institute, Balboa, Republic of Panama and Department of Anthropology, University of California, Davis, CA, USA Shauhin Alavi, Department of Biology, University of Konstanz, Konstanz, Germany and Center for the Advanced Study of Collective Behavior, University of Konstanz, Konstanz, Germany

Rasmus Worsøe Havmøller, Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, Germany and Department of Biology, University of Konstanz, Konstanz, Germany and Center for the Advanced Study of Collective Behavior, University of Konstanz, Konstanz, Germany

Margaret Crofoot, Smithsonian Tropical Research Institute, Balboa, Republic of Panama and Department of Anthropology, University of California, Davis, CA, USA and Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior,

Konstanz, Germany and Department of Biology, University of Konstanz, Konstanz, Germany and Center for the Advanced Study of Collective Behavior, University of Konstanz, Konstanz, Germany

#### Contributed talk 1

### **Modeling Yearly Patterns in Golden Eagle Movement**

Eisenhauer, E. Department of Statistics, Penn State University, State College, PA, USA. Hanks, E. Department of Statistics, Penn State University, State College, PA, USA. Murphy, R. Eagle Environmental, Inc., Santa Fe, NM, USA.

#### Contributed talk 2

# **Empirical Natal And Breeding Dispersal Kernels for European Birds**

Fandos G., Talluto, M., Fiedler, W., Robinson, R., Thorup K., Zurell, D.

Dispersal is a key life-history trait for most species and essential to ensure connectivity and gene flow between populations and facilitate population viability in variable environments. Despite the increasing importance of range shifts due to global change, dispersal has proved difficult to quantify, limiting empirical understanding of this phenotypic trait and wider synthesis. Here we aim to estimate and compare empirical dispersal kernels for European breeding birds considering average dispersal, natal (before first breeding) and breeding dispersal (between subsequent breeding attempts), and test whether different dispersal properties are phylogenetically conserved. We standardised and analysed data from an extensive volunteer-based bird ring-recoveries database in Europe (EURING) by accounting for biases related to different censoring thresholds in reporting between countries and to migratory movements. Then, we fitted four widely used probability density functions in a Bayesian framework to compare and provide the best statistical descriptions of the average, the natal and the breeding dispersal kernels for each bird species.

The dispersal movements of the 234 European bird species analysed were statistically best explained by heavy-tailed kernels, meaning that while most individuals disperse over short distances, long-distance dispersal is a feature in almost all bird species. The overall phylogenetic signal in both median and long dispersal distances was low (Pagel's  $\lambda$  < 0.40), implying a high degree of taxonomic generality in our findings. As expected in birds, natal dispersal was 5 Km greater as an average than breeding dispersal for most species (88% species analysed). Our comprehensive analysis of empirical kernels indicates that long-distance dispersal is common among European breeding bird species and across life stages. The dispersal estimates offer a first guide to selecting appropriate dispersal kernels in range expansion studies and provide new avenues to improve our understanding of the mechanisms and rules underlying dispersal events.

Fandos, G., Talluto, M., Fiedler, W., Robinson, R. A., Thorup, K., Zurell, D. (2021) Standardised empirical dispersal kernels emphasise the pervasiveness of long-distance dispersal in European birds. bioRxiv 2021.11.08.467775; https://doi.org/10.1101/2021.11.08.467775

#### Contributed talk 3

# Hierarchical computing for hierarchical models in ecology

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Feuka, A.B., Dept. of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, USA

Hooten, M.B., U.S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, CO, USA; Dept. of Fish, Wildlife, and Conservation Biology, Colorado State University, USA; Dept. of Statistics, Colorado State University, USA

### Contributed talk 4

# **Guidance on Inferring Behavioral States From Animal Location Data**

Buderman, F. E., Gingery, T. M., Diefenbach, D. R., Gigliotti, L. C., Begley-Miller, D., McDill, M. M., Wallingford, B. D., Rosenberry, C. S., Drohan, P. D.

We are increasingly able to obtain fine-scale long-term animal movement data across multiple individuals. With the advent of modern tracking methods, we have also developed a suite of statistical methods that can be used to model metrics that describe space-use and movement. From an ecological standpoint, the goal is often to link a particular set of metrics or space-use patterns to unobserved, or latent, behaviors. Quantifying these behaviors can, in turn, be used to increase our understanding of events that are difficult to observe in the wild and incorporate these events into management and conservation plans. However, these latent behavioral states, and where and when a model suggests they occur, are rarely validated against independent observations. We discuss multiple case studies, centered on ungulates in Pennsylvania, in which various statistical methods for animal space-use and movement can result in erroneous inference on behavioral states. Our goal is to highlight the statistical underpinnings of commonly used space-use and movement models, how the statistical foundations are related to the obtainable inference, and caution against over-interpreting inferred latent states without auxiliary data. We suggest that researchers plan for data-collection that can help confirm statistical identification of behavioral states.

Buderman, F.E., T.M. Gingery, D.R. Diefenbach, L.C. Gigliotti, D. Begley-Miller, B.D. Wallingford, & C.R. Rosenberry. (2021) Caution is warranted when using animal space-use and movement to infer behavioral states. Movement Ecology 9:30.

Link: <a href="https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-021-00264-8">https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-021-00264-8</a>

# Honored Talk by Pertti Saurola, Finnish Museum of Natural History



# Life behind the numbers: 55 years among the owls. -- Why?

The reason why I have been interested in owls, particularly in the Ural Owl *Strix uralensis*, has been conservation. In Finland, the Ural Owl suffers from the lack of ideal natural nest-sites – large cavities and chimney-like stumps of big trees - which do not exist in commercial forests. In 1965, I started to provide nest-boxes for hole-nesting owls to compensate the losses caused by forestry.

Another reason why I have studied the Ural Owl has been science. The Ural Owl is an ideal species for population studies. The breeding female can be easily and safely trapped any time during the breeding season, even before egg laying. Trapping males is more difficult, but possible with experience and stamina. Because both sexes are strongly philopatric, it is possible to gather relevant and reliable long-term data of the same individuals. The Ural Owl is a generalist feeder and feeds on a wide variety of vertebrates, ranging from frogs and shrews to mammals and birds weighing up to several hundred grams. However, in Finland, the population dynamics of the Ural Owl has been highly dependent on 3–4-year cycles of microtines. My main goal has been to find out how different population parameters, such as age at first breeding, onset of egg-laying, clutch size, brood size, survival of different age-classes, recruitment, natal and breeding dispersal and lifetime reproduction, vary in relation to fluctuating environment. For comparison, I have collected similar data on the close relative, the Tawny Owl *Strix aluco*, a newcomer from the south.

The third reason to spend much of my lifetime with Ural Owls has been the privilege to have an opportunity to be legally in close contact with different individuals of such a fascinating species, which defends its offspring with a kamikaze-like fearlessness and fierceness. Over the decades, some individuals have become my "old friends" and even been given anthropomorphic names like *Mama of Yltiö*, *Papa of Hyypiö*, etc. For the general public, the most interesting part of my study has been information about "divorces" and polygamy based on the real lives of owls. My presentation will be a mixture of memories through the decades and selected facts of the life of the Ural Owl and Tawny Owl.

Saurola, P. & Francis, C.M. 2018: Towards Integrated Population Monitoring based on the fieldwork of volunteer ringers: Productivity, Survival and Population Change of Tawny and Ural Owls (Strix aluco and Strix uralensis) in Finland. – Bird Study 65, NO, S1, S63–S76.

Vrecez, A., Saurola, P., Avotins, A., Kocijancic, S. & Sulkava, S. 2018: Comparative breeding diet study of the Ural Owl Strix uralensis over species range in Europe using nestbox monitoring data. – Bird Study 65, NO, S1, S85–S95.

# Data Integration and Population Analysis

### Keynote

# Addressing data integration challenges to link ecological processes across scales

Zipkin, E., Zylstra, E. R., Wright, A. D., Saunders, S. P., Finley, A. O., Dietze, M. C., Itter, M. S., Tingley, M. W.

Data integration is a statistical modeling approach that incorporates multiple data sources within a unified analytical framework. Macrosystems ecology — the study of ecological phenomena at broad scales, including interactions across scales — increasingly employs data integration techniques to expand the spatiotemporal scope of research and inferences, increase the precision of parameter estimates, and account for multiple sources of uncertainty in estimates of multiscale processes. We highlight four common analytical challenges to data integration in macrosystems ecology research: data scale mismatches, unbalanced data, sampling biases, and model development and assessment. We explain each problem, discuss current approaches to address the issue, and describe potential areas of research to overcome these hurdles. Use of data integration techniques has increased rapidly in recent years, and given the inferential value of such approaches, we expect continued development and wider application across ecological disciplines, especially in macrosystems ecology.

Zipkin, E.F., Zylstra, E.R., Wright, A.D., Saunders, S.P., Finley, A.O., Dietze, M.C., Itter, M.S., Tingley, M.W., 2021. Addressing data integration challenges to link ecological processes across scales. Frontiers in Ecology and the Environment 19 (1), 30–38. https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/fee.2290

### Contributed talk 1

# A semi-spatial integrated population model to assess population dynamics of a recolonizing species

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Gardner, B., School of Environmental and Forest Sciences, University of Washington, Seattle, WA.

Maletzke, B. T., Washington Department of Fish and Wildlife, Olympia, WA.

Bassing, S. B., School of Environmental and Forest Sciences, University of Washington, Seattle, WA.

Long, R. A., Woodland Park Zoo, Seattle, WA.

Ransom, J. I. National Park Service, North Cascades National Park Service Complex, Sedro Woolley, WA.

Shipley, L. A. School of the Environment, Washington State University, Pullman, WA. Thornton, D. H. School of the Environment, Washington State University, Pullman, WA. Coverse, S. J., U,S. Geological Survey, Washington Cooperative Fish and Wildlife Research Unit, School of Environmental and Forest Sciences & School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA.

# How accurate are integrated population models in estimating the contribution of immigration to changes in population growth?

Paquet, M., Knape, J., Arlt, D., Forslund, P., Pärt, T., Flagstad, Ø., Jones, C., Nicoll, M., Norris, K., Pemberton, J., Sand, H., Svensson, L., Tatayah, V., Wabakken, P., Wikenros, C., Åkesson, M., Low, M.

Estimating the contribution of demographic parameters to changes in population growth is essential for understanding how populations are fluctuating. Integrated Population Models (IPMs) offer the possibility to estimate contributions of additional demographic parameters, for which no data have been explicitly collected: often immigration. Such parameters are often found to be the main driver of population growth. Accuracy in the estimation of their temporal variation, and consequently their contribution to changes in population growth rate, has however not been investigated. To quantify the magnitude and cause of potential biases when estimating the contribution of immigration using IPMs, we use both empirical and simulated data. We used data from wild populations with known immigration (Soay Sheep Ovis aries and Mauritius Kestrel Falco punctatus with zero and Scandinavian Wolf Canis lupus with near-zero immigration), implementing IPMs that estimate the effect of immigration. We also used simulated data from controlled scenarios to examine the origin of bias and its magnitude depending on IPM parametrization, the level of temporal variation in immigration, and sample size. IPMs strongly overestimated the contribution of immigration to changes in population growth in the wild populations, where the true number of immigrants was zero or near-zero (depending on IPM formulation: Sheep 4.5-32.9%, Kestrel 19.7-97.8%, Wolf 89.7-99.6%), and in scenarios when immigration was simulated with zero temporal variation. Although the estimation of immigration in the simulation study became more accurate with increasing temporal variation and sample size, it was often not possible to distinguish between an accurate estimation from data with high temporal variation versus an overestimation from data with low temporal variation. To minimise the risk of overestimating the contribution of immigration (or any additional parameter) in IPMs, we recommend to: (i) look for evidence of variation in immigration before investigating its contribution to population growth, (ii) model a simulated dataset for comparison to the real dataset, and (iii) use explicit data on immigration where possible. We provide details on what evidence to look for and how to run a simulation study to help researchers identify when estimates from additional parameters are likely to be accurate.

Paquet, M., Knape, J., Arlt, D., Forslund, P., Pärt, T., Flagstad, Ø., Jones, C. G., Nicoll, M. A. C., Norris, K., Pemberton, J. M., Sand, H., Svensson, L., Tatayah, V., Wabakken, P., Wikenros, C., Åkesson, M., & Low, M. (2021) Integrated population models poorly estimate the demographic contribution of immigration. Methods in Ecology and Evolution, 00, 1–12. <a href="https://doi.org/10.1111/2041-210X.13667">https://doi.org/10.1111/2041-210X.13667</a>

### Contributed talk 3

Using multispecies integrated population model to understand interspecific competition: A case study on Great tits and Blue tits

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# Multi-population analysis reveals spatial consistency in drivers of population dynamics of a declining migratory bird

Nater, C. R., Burgess, M. D., Coffey, P., Harris, B., Lander, F., Price, D., Reed. M., Robinson, R.

Many migratory species are in decline across their geographical ranges. Single-population studies can provide important insights into drivers at a local scale, but effective conservation requires multi-population perspectives. This is challenging because relevant data are often hard to consolidate, and state-of-the-art analytical tools are typically tailored to specific datasets

We capitalized on a recent data harmonization initiative (SPI-Birds) and linked it to a generalized modeling framework to identify the demographic and environmental drivers of large-scale population decline in migratory pied flycatchers (Ficedula hypoleuca) breeding across Britain.

We implemented a generalized integrated population model (IPM) to estimate age-specific vital rates, including their dependency on environmental conditions, and total and breeding population size of pied flycatchers using long-term (34-64 years) monitoring data from seven locations representative of the British breeding range. We then quantified the relative contributions of different vital rates and population structure to changes in short- and long-term population growth rate using transient life table response experiments (LTREs).

Substantial covariation in population sizes across breeding locations suggested that change was the result of large-scale drivers. This was supported by LTRE analyses, which attributed past changes in short-term population growth rates and long-term population trends primarily to variation in annual survival and dispersal dynamics, which largely act during migration and/or non-breeding season. Contributions of variation in local reproductive parameters were small in comparison, despite sensitivity to local temperature and rainfall within the breeding period. We show that both short- and longer-term population changes of British-breeding pied flycatchers are likely linked to factors acting during migration and in non-breeding areas, where future research should be prioritized. We illustrate the potential of multi-population analyses for informing management at (inter)national scales and highlight the importance of data standardization, generalized and accessible analytical tools, and reproducible workflows to achieve them.

Nater, C. R., Burgess, M. D., Coffey, P., Harris, B., Lander, F., Price, D., Reed, M., Robinson, R. A. (2022, April 21). Multi-population analysis reveals spatial consistency in drivers of population dynamics of a declining migratory bird. *EcoEvoRxiv*. https://doi.org/10.32942/osf.io/5ru9f

### Contributed talk 5

Integrated population model for Ferruginous hawk and Golden eagle in Wyoming, USA, to assist with a long-term, state-wide monitoring plan

Sanderlin, J. S., USDA Forest Service, Rocky Mountain Research Station, Flagstaff, Arizona, IJSA

Wallace, Z. P., Wyoming Natural Diversity Database, University of Wyoming, Laramie, Wyoming, USA

Olson, L., USDA Forest Service, Rocky Mountain Research Station, Missoula, Montana, USA

Squires, J., USDA Forest Service, Rocky Mountain Research Station, Missoula, Montana, USA

# Integrating tracking and resight data enables unbiased inferences about migratory connectivity and winter range survival from archival tags

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Sharp, A., Department of Wildland Resources and the Ecology Center, Utah State University, 5230 Old Main Hill, Logan, UT 84322

Ruiz-Gutierrez, V., Cornell Lab of Ornithology, Cornell University, Ithaca, NY

Freeman, M. C., U.S. Geological Survey, Patuxent Wildlife Research Center, Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, USA

Sykes, P. W., U.S. Geological Survey, Patuxent Wildlife Research Center, Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, USA

Sillet, T. S., Smithsonian Migratory Bird Center, National Zoological Park, Washington, DC, USA

#### Contributed talk 7

# Spatial integrated models foster complementarity between monitoring programs in producing large-scale ecological indicators

Lauret, V., Labach, H., Turek, D., Authier, M., Gimenez, O.

Obtaining relevant information about large-scale population dynamics from a single monitoring program is challenging, and often several sources of data, possibly heterogeneous, need to be integrated. In this context, spatial integrated models combine multiple data types into a single analysis to quantify population dynamics of a targeted population. Using available information at different spatial or temporal scales, spatial integrated models have the potential to produce detailed ecological estimates that would be difficult to obtain if data were analyzed separately. So far, these models are available for open populations to estimate demographic parameters (survival, recruitment), therefore requiring data collected in long-term monitoring programs. However, we often need to quantify population abundance and density in closed populations. Adapting the method developed by Chandler et al. (2018), we showcase the implementation of spatial integrated models to closed populations. We analyzed spatial capture-recapture data together with distance-sampling data to estimate abundance and density. Focusing on the Mediterranean bottlenose dolphins Tursiops truncatus as a case study, we combined 21,464 km of at-sea photo-identification surveys collecting spatial capturerecapture data with 24,624 km of aerial line-transect following a distance-sampling protocol. We compared the performances of the spatial integrated model, with that of the distance sampling model, and the spatial capture-recapture model separated. We discussed the benefits of using a spatial integrated model in the context of the assessment of French Mediterranean bottlenose dolphin conservation status to inform continental scale public policies. Spatial integrated models are widely applicable and relevant to conservation research and biodiversity assessment at large spatial scales.

Chandler RB, Hepinstall-Cymerman J, Merker S, Abernathy-Conners H, Cooper RJ. 2018. Characterizing spatio-temporal variation in survival and recruitment with integrated population models. The Auk 135:409–426.

Lauret, V., Labach, H., Turek, D., Laran, S., & Gimenez, O. (2021). Spatial integrated models foster complementarity between monitoring programs in producing large-scale ecological indicators. DOI: 10.1101/2021.02.01.429097, *Under review*.

# Integrating data types to estimate spatial patterns of avian migration across the Western Hemisphere

Meehan, T. D., Saunders, S. P., DeLuca, W. V., Michel, N. L., Grand, J., Deppe J. L., Jimenez, M. F., Knight, E. J., Seavy, N. E., Smith, M. A., Taylor, L., Witko. C., Akresh, M. E., Barber, D. R., Bayne E. M., Beasley, J. C., Belant J. L., Bierregaard, R. O., Bildstein, K. L., Boves, T. J., Brzorad, J. N., Campbell, S. P., Celis-Murillo, A., Cooke, H. A., Domenech, R., Goodrich, L., Gow, E. A., Haines, A., Hallworth, M. T., Hill, J. M., Holland, A. E., Jennings, S., Kays, R., King, D. T., Mackenzie, S. A., Marra, P. P., McCabe, R. A., McFarland, K. P., McGrady, M. J., Melcer, R. Jr., Norris, D. R., Norvell, R. E., Rhodes, O. E. Jr., Rimmer, C. C., Scarpignato, A. L., Shreading, A., Watson, J. L., Wilsey, C. B.

For many avian species, spatial migration patterns remain largely undescribed, especially across hemispheric extents. Recent advancements in tracking technologies and highresolution species distribution models (i.e., eBird Status and Trends products) provide new insights into migratory bird movements and offer a promising opportunity for integrating independent data sources to describe avian migration. Here, we present a three-stage modeling framework for estimating spatial patterns of avian migration. First, we integrate tracking and band re-encounter data to quantify migratory connectivity, defined as the relative proportions of individuals migrating between breeding and nonbreeding regions. Next, we use estimated connectivity proportions along with eBird occurrence probabilities to produce probabilistic least-cost path (LCP) indices. In a final step, we use generalized additive mixed models (GAMMs) both to evaluate the ability of LCP indices to accurately predict (i.e., as a covariate) observed locations derived from tracking and band re-encounter datasets versus pseudo-absence locations during migratory periods, and to create a fully integrated (i.e., eBird occurrence, LCP, and tracking/band re-encounter data) spatial prediction index for mapping species-specific seasonal migrations. To illustrate this approach, we apply this framework to describe seasonal migrations of 12 bird species across the Western Hemisphere during preand post-breeding migratory periods (i.e., spring and fall, respectively). We found that including LCP indices with eBird occurrence in GAMMs generally improved the ability to accurately predict observed migratory locations, when compared to models with eBird occurrence alone. Using three performance metrics, the eBird + LCP model demonstrated equivalent or superior fit relative to the eBird-only model for 22 of 24 species-season GAMMs. In particular, the integrated index filled in spatial gaps for species with over-water movements and those that migrated over land where there were few eBird sightings, and thus, low predictive ability of eBird occurrence probabilities (e.g., Amazonian rainforest in South America). This methodology of combining individual-based seasonal movement data with temporally dynamic species distribution models provides a comprehensive approach for integrating multiple data types to describe broad-scale spatial patterns of animal movement. Further development and customization of this approach will continue to advance knowledge about the full annual cycle and conservation of migratory birds.

Meehan, T.D., Saunders, S.P., DeLuca, W.V., Michel, N.L., Grand, J., Deppe, J.L., Jimenez, M.F., Knight, E.J., Seavy, N.E., Smith, M.A., Taylor, L., Witko, C., Akresh, M.E., Barber, D.R., Bayne, E.M., Beasley, J.C., Belant, J.L., Bierregaard, R.O., Bildstein, K.L., Boves, T.J., Brzorad, J.N., Campbell, S.P., Celis-Murillo, A., Cooke, H.A., Domenech, R., Goodrich, L., Gow, E.A., Haines, A., Hallworth, M.T., Hill, J.M., Holland, A.E., Jennings, S., Kays, R., King, D.T., Mackenzie, S.A., Marra, P.P., McCabe, R.A., McFarland, K.P., McGrady, M.J., Melcer, R., Norris, D.R., Norvell, R.E., Rhodes, O.E., Rimmer, C.C., Scarpignato, A.L., Shreading, A., Watson, J.L., Wilsey, C.B., 2022. Integrating data types to estimate spatial patterns of avian migration across the Western Hemisphere. Ecological Applications. https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/eap.2679

# Integrating demographic and epidemiological data improves dispersal quantification

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# Population management

# Keynote

# A decision analytical framework for guiding demographic estimation

Michael C. Runge, U.S. Geological Survey, Eastern Ecological Science Center at the Patuxent Research Refuge, Laurel MD, USA

Anna M. Tucker, U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Iowa State University, Ames, IA, USA

#### Contributed talk 1

# Integrating Understanding to Inform Management, Research and Monitoring

Yackulic, C.B., Runge, M.

Over the period 2014–2016, the number of nonnative brown trout (Salmo trutta) captured during routine monitoring in the Lees Ferry reach of the Colorado River, downstream of Glen Canyon Dam, began increasing. Management agencies and stakeholders have questioned whether the increase in brown trout in the Lees Ferry reach represents a threat to the endangered humpback chub *Gila cypha*, to the rainbow trout *Oncorhynchus mykiss* sport fishery, or to other resources of concern. In this report, we evaluate the evidence for the expansion of brown trout in the Lees Ferry reach, consider a range of causal hypotheses for this expansion, examine the likely efficacy of several potential management interventions to reduce brown trout, and analyze the effects of those interventions on other resources of concern.

The brown trout population at Lees Ferry historically consisted of a small number of large fish supported by low levels of immigration from downstream reaches. This population is now showing signs of sustained successful reproduction and is on the cusp of recruiting locally hatched fish into the spawning class, based on analysis with a new integrated population model. The proximate causes of this change in status are a large pulse of immigration in the fall of 2014 and higher reproductive rates in 2015–2017. The ultimate causes of this change are not clear. The pulse of immigrants from downstream reaches in fall 2014 may have been induced by three sequential high-flow releases from the dam in November of 2012–2014, but may also have been the result of a unique set of circumstances unrelated to dam operations. The increase in reproduction may have been the result of any number of changes, including an Allee effect, warmer water temperatures, a decrease in competition from rainbow trout, or

fall high-flow releases. Correlations over space and time among predictor variables do not allow us to make a clear inference about the cause of the changes. Under a null causal model, and without any changes to management, we predict there is a 36-percent chance the brown trout population at Lees Ferry will not show sustained growth, and will remain around a mean size of 5,800 adults, near its current size; in contrast, we predict there is a 64-percent chance that the population has a positive intrinsic growth rate and will increase 3–10 fold over the next 20 years. A humpback chub population model linked to the brown trout model suggests an increase of brown trout of this magnitude could lead to declines in the minimum adult humpback chub population over the same time period. Forecasts of rainbow trout abundance, however, suggest that increased abundance of brown trout in the Lees Ferry reach does not pose a threat to the rainbow trout fishery there.

There are interventions that may be effective in moderating the growth of the brown trout population in the Lees Ferry reach of the Colorado River. Across causal hypotheses, we predict that removal strategies (for example, a concerted electrofishing effort or an incentivized take program targeted at large brown trout) could reduce brown trout abundance by approximately 50 percent relative to status quo management. Reductions in the frequency or a change in the seasonal timing of high-flow releases from Glen Canyon Dam could be even more effective, but only under the causal hypotheses that involve effects of such releases on immigration or reproduction. Brown trout management flows— dam releases designed to strand young fish at a vulnerable stage—may be able to reduce brown trout abundance to some degree, but are not forecast to be the most effective strategy under any causal hypothesis.

We predict that the alternative management interventions would have effects on other resource goals as well, and the pattern of these effects differs across causal hypotheses. The removal strategies would incur direct costs (on the order of \$7 million over 20 years) and the mechanical removal strategy is unethical from the perspective of several tribes. The strategies that involve reducing the frequency of high-flow releases from Glen Canyon Dam would decrease the ability to transport and store sediment in the ecosystem, potentially undermining goals associated with sandbar building, recreation, and riparian vegetation, but would increase hydropower revenue. Trout management flows would reduce hydropower revenue. From the standpoint of humpback chub, the alternative strategies largely follow the effect on brown trout; when brown trout abundance is reduced, predation pressure decreases, and humpback chub viability is predicted to increase, but the variation in predicted chub viability is not large across strategies or causal hypotheses.

To design a response to brown trout, management agencies will need to navigate both the tradeoffs among resources goals and the uncertainty in the causes of the brown trout expansion. Continued monitoring, possibly coupled with new research or experimental management actions that better inform demographic and ecological dynamics, can help to reduce the causal uncertainty.

Runge, M.C., Yackulic, C.B., Bair, L.S., Kennedy, T.A., Valdez, R.A., Ellsworth, C., Kershner J.L., Rogers, R.S., Trammell, M.A., and Young, K.L., 2018, Brown trout in the Lees Ferry reach of the Colorado River—Evaluation of causal hypotheses and potential interventions: U.S. Geological Survey Open-File Report 2018–1069, 83 p., https://doi.org/10.3133/ofr20181069.

Bayesian population models can be exceedingly slow due, in part, to the choice to simulate discrete latent states. Here, we discuss an alternative approach to discrete latent states, marginalization, that forms the basis of maximum likelihood population models and is much faster. Our manuscript has two goals: (1) to introduce readers unfamiliar with marginalization to the concept and provide worked examples and (2) to address topics associated with marginalization that have not been previously synthesized and are relevant to both Bayesian

and maximum likelihood models. We begin by explaining marginalization using a Cormack-Jolly-Seber model. Next, we apply marginalization to multistate capture-recapture, community occupancy, and integrated population models and briefly discuss random effects, priors, and pseudo-R2. Then, we focus on recovery of discrete latent states, defining different types of conditional probabilities and showing how quantities such as population abundance or species richness can be estimated in marginalized code. Last, we show that occupancy and siteabundance models with auto-covariates can be fit with marginalized code with minimal impact on parameter estimates. Marginalized code was anywhere from five to >1,000 times faster than discrete code and differences in inferences were minimal. Discrete latent states and fully conditional approaches provide the best estimates of conditional probabilities for a given site or individual. However, estimates for parameters and derived quantities such as species richness and abundance are minimally affected by marginalization. In the case of abundance, marginalized code is both quicker and has lower bias than an N-augmentation approach. Understanding how marginalization works shrinks the divide between Bayesian and maximum likelihood approaches to population models. Some models that have only been presented in a Bayesian framework can easily be fit in maximum likelihood. On the other hand, factors such as informative priors, random effects, or pseudo-R2 values may motivate a Bayesian approach in some applications. An understanding of marginalization allows users to minimize the speed that is sacrificed when switching from a maximum likelihood approach. Widespread application of marginalization in Bayesian population models will facilitate more thorough simulation studies, comparisons of alternative model structures, and faster learning.

Yackulic, C. B. Dodrill, M., Dzul, M., Sanderlin, J. S., and Reid, J. A.. 2020. A need for speed in Bayesian population models: a practical guide to marginalizing and recovering discrete latent states. Ecological Applications 30(5):e02112. 10.1002/eap.2112 https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2112

### Contributed talk 2

### Data analysis and modeling for endangered species listing decisions

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Beisler W., U.S. Fish and Wildlife Service, National Conservation Training Center, Shepherdstown, WV, USA

Angeli N., U.S. Virgin Islands Division of Fish and Wildlife, St. Croix, U.S. Virgin Islands, USA Rivenbark E., U.S. Fish and Wildlife Service, Ecological Services, Athens, GA, USA

The US Fish and Wildlife Service (USFWS) has initiated a re-envisioned approach for providing decision makers with the best available science and synthesis of that information, called the Species Status Assessment (SSA), for endangered species decision making. The SSA report is a descriptive document that provides decision makers with an assessment of the current and predicted future status of a species. These analyses support all manner of decisions under the US Endangered Species Act, such as listing, reclassification, and recovery planning but have been widely applied to listing determinations. Novel scientific analysis and predictive modeling in SSAs could be an important part of rooting conservation decisions in current data and cutting edge analytical and modeling techniques. Ideally assessing current status uses analysis of available data to estimate demographic parameters such as abundance, trend, survival and the future condition analysis uses the results of that analysis to make predictions about population and species trajectories. Here, we describe an analysis of available presence absence data to assess the current condition of eastern black rail across its range in a dynamic occupancy analysis and how we used the results of that analysis to develop a site occupancy projection model where the model parameters (initial occupancy, site persistence, colonization) were linked to environmental covariates, such as land management and land cover change (sea-level rise, development, etc.). Occupancy probability and site colonization were low in all analysis units, and site persistence was also low, suggesting low resiliency and

redundancy currently. Extinction probability was high for all analysis units in all simulated scenarios except one with significant effort to preserve existing habitat, suggesting low future resiliency and redundancy. With the results of these data analyses and predictive models, the USFWS concluded that protections of the Endangered Species Act were warranted for this subspecies.

McGowan CP, Angeli NF, Beisler WA, Snyder C, Rankin NM, Woodrow JO, Wilson JK, Rivenbark E, Schwarzer A, Hand CE, Anthony R. Linking monitoring and data analysis to predictions and decisions for the range-wide eastern black rail status assessment. Endangered Species Research. 2020 Oct 8;43:209-22.

## Contributed talk 3

Hierarchical Models to Link Occupancy And Habitat Dynamics To Management Decisions: Recovering Endangered Florida Scrub And Scrub-Jays

Eaton, M.J., Breininger, D.R., Nichols, J.D., Fackler, P.L.

Quantifying the contribution of habitat dynamics relative to intrinsic population processes in regulating species persistence remains an ongoing challenge in ecological and applied conservation. Understanding these drivers and their relationship is essential for managing habitat-dependent species, especially those that specialize in transitional habitats. Limitations in the ability of natural disturbance to mediate transitional habitat dynamics have resulted in a decline in early- and mid-successional vegetation structure and prompted the need for aggressive habitat management to replace natural perturbations and increase habitat structural complexity. We describe a collaborative effort with a group of independent land managers to design an adaptive management program for restoring an imperiled ecosystem and recovering declining populations of an endemic habitat specialist. We developed a set of integrated, hierarchical models to estimate management-mediated transition rates among vegetation classes in two dominant scrub communities and the species response (local colonization and extinction probabilities) as a function of habitat state. Models were fit using a long-term data set of habitat and occupancy observations from 361 Florida scrub-jay territories across two Florida counties. Occupancy model results correspond closely to previous approaches of estimating differential survival and reproductive success associated with habitat conditions, with highest colonization and lowest extinction rates estimated for those habitat states found to have the highest rates of survival and reproduction. In addition to offering an innovative approach for jointly modeling habitat and species population dynamics, the program we describe will also be of interest from a management perspective by providing guidance for developing collaborative, adaptive management frameworks from the ground up. We engaged land managers via workshops to specify objectives and desired state-variable conditions, identify management alternatives, and elicit consensus opinions on model parameters. Treating expert opinions as pseudo-observations to define Dirichlet priors allowed us to make use of existing management knowledge. Formal learning was then accumulated by updating transition probability estimates as management activities were implemented over the study period. We believe this adaptive management framework provides a useful approach for increasing our understanding of complex ecological relationships and hope that it will be adopted by others who have interest in informing management and conservation efforts.

Eaton MJ, DR Breininger, JD Nichols, PL Fackler, S McGee, M Smurl, D DeMeyer, J Baker, MB Zodervan (2021) Integrated hierarchical models to inform management of transitional habitat and the recovery of a habitat specialist, Ecosphere 12 (1), e03306. https://doi.org/10.1002/ecs2.3306

# Integrated Simulations of Demography, Monitoring And Decisions for Conservation of Endangered Species

Canessa, Stefano. Institute of Zoology, Zoological Society London, England

# Survival estimation

Keynote

Models for survival: from  $\varphi_{ta}$  to  $\varphi_{fc}$  and everything in between

Matechou, E., Statistical Ecology, Kent School of Mathematics, Statistics and Actuarial Science, University of Kent, U.K.

#### Contributed talk 1

Large Data and (Not Even Very) Complex Ecological Models: When Worlds Collide

King, R., Sarzo, B., Elvira, V.

We consider the challenges that arise when fitting complex ecological models to "large" data sets. In particular, we focus on random effect models which are commonly used to describe individual heterogeneity, often present in ecological populations under study. In general, these models lead to a likelihood that is expressible only as an analytically intractable integral. Common techniques for fitting such models to data include, for example, the use of numerical approximations for the integral, or a Bayesian data augmentation approach. However, as the size of the data set increases (i.e. the number of individuals increases), these computational tools may become computationally infeasible. We present an efficient Bayesian model-fitting approach, whereby we initially sample from the posterior distribution of a smaller subsample of the data, before correcting this sample to obtain estimates of the posterior distribution of the full dataset, using an importance sampling approach. We consider several practical issues, including the subsampling mechanism, computational efficiencies (including the ability to parallelise the algorithm) and combining subsampling estimates using multiple subsampled datasets. We demonstrate the approach in relation to individual heterogeneity capturerecapture models. We initially demonstrate the feasibility of the approach via simulated data before considering a challenging real dataset of approximately 30,000 guillemots, and obtain posterior estimates in substantially reduced computational time.

# https://arxiv.org/abs/2205.07261

#### Contributed talk 2

# Laplace approximations for capture-recapture models in the presences of individual heterogeneity

Herliansyah, R., School of Mathematics, University of Edinburgh, James Clerk Maxwell Building, The King's Buildings, Peter Guthrie Tait Road, Edinburgh, UK/ School of Statistics, Institut Teknologi Kalimantan, Balikpapan, Indonesia

King, R., School of Mathematics, University of Edinburgh, James Clerk Maxwell Building, The King's Buildings, Peter Guthrie Tait Road, Edinburgh, UK.

King, S., School of Mathematics, University of Edinburgh, James Clerk Maxwell Building, The King's Buildings, Peter Guthrie Tait Road, Edinburgh, UK.

Capture—recapture studies are common for collecting data on wildlife populations. Populations in such studies are often subject to different forms of heterogeneity that may influence their associated demographic rates. We focus on the most challenging of these relating to individual heterogeneity. We consider (i) continuous time-varying individual covariates and (ii) individual random effects. In general, the associated likelihood is not available in closed form but only expressible as an analytically intractable integral. The integration is specified over (i) the unknown individual covariate values (if an individual is not observed, its associated covariate value is also unknown) and (ii) the unobserved random effect terms. Previous approaches to dealing with these issues include numerical integration and Bayesian data augmentation techniques. However, as the number of individuals observed and/or capture occasions increases, these methods can become computationally expensive. We propose a new and efficient approach that approximates the analytically intractable integral in the likelihood via a Laplace approximation. We find that for the situations considered, the Laplace approximation performs as well as, or better, than alternative approaches, yet is substantially more efficient.

Herliansyah, R., King, R. and King, S. E. (2022) "Laplace Approximations for Individual Heterogeneity Capture-recapture Models" – Journal of Agricultural, Biological, and Environmental Statistics – in press. <a href="https://link.springer.com/article/10.1007/s13253-022-00486-2">https://link.springer.com/article/10.1007/s13253-022-00486-2</a>

#### Contributed talk 3

Misidentification errors in reencounters result in biased estimates of survival from CJS models: evidence and a possible solution using the robust design

Rakhimberdiev, E., Karagicheva, J., Saveliev, A., Loonstra, A.H.J., Verhoeven, M.A., Hooijmeijer, J.C.E.W., Schaub, M., Piersma, T.

Misidentification of marked individuals is unavoidable in most studies of wild animal populations. Models commonly used for the estimation of survival from such capture—recapture data ignore misidentification errors potentially resulting in biased parameter estimates. With a simulation study, we show that ignoring misidentification in Cormack—Jolly—Seber (CJS) models results in systematic positive biases in the estimates of survival and in spurious declines of survival over time.

We developed an extended robust design capture mark-resight (RDM) model that includes correct identification parameters to get unbiased survival estimates when resighting histories are prone to misidentification. The model assumes that resightings occur repeatedly within a season, which in practice is often the case when resightings of colour-marked individuals are collected. We implemented the RDM model in a state-space formulation and also an approximate, but computationally faster, model (RDMa) in JAGS and evaluated their performances using simulated and empirical capture-resight data on black-tailed godwits Limosa limosa.

The CJS models applied to simulated data under an imperfect identification scenario data produced strongly positively biased estimates of survival. For a range of degrees of correct identification probabilities, the RDM model provided unbiased and accurate estimates of survival, reencounter and correct-identification probabilities. The RDMa model performed well for large datasets (>25 individuals), with high resighting (>0.3) and high correct identification (>0.7) probabilities. For the empirical data, the CJS model estimated average juvenile survival at 0.997% and adult survival at 0.939% and also detected a strong decline in adult survival over time at a rate of  $-0.14 \pm 0.029$ . In contrast, the RDMa model estimated a probability of correct identification of 0.94, annual juvenile survival at 0.234%, adult at 0.834% and less strong decline over time ( $-0.046 \pm 0.016$ ).

We conclude that estimates of survival probabilities obtained from data that include misidentification errors and analysed with standard CJS model are unlikely to be correct. The bias in survival increases with the magnitude of misidentification errors, which is inevitable as datasets become longer. Since misidentification due to tag misreads is common in empirical

data, we recommend the use of the here presented RDM model to provide unbiased parameter estimates.

Rakhimberdiev, E., Karagicheva, J., Saveliev, A., Loonstra, A. H. J., Verhoeven, M. A., Hooijmeijer, J. C. E. W., Schaub, M., Piersma, T. (2022) Misidentification errors in reencounters result in biased estimates of survival probability from CJS models: Evidence and a solution using the robust design. Methods in Ecology and Evolution 13: 1106-1118. https://doi.org/10.1111/2041-210X.13825

#### Contributed talk 4

Using multievent recovery and auxillary resighting data to improve inference from multistate mark-recapture studies

Kendall W.L., U. S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado, USA.

White, G.C., Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA.

Langtimm, C.A., U. S. Geological Survey, Wetland and Aquatic Research Center, Gainesville, Florida, USA.

#### Posters

## Bayesian inference for models of moult duration and timing in birds

Boersch-Supan, P. H., Hanmer, H., Robinson, R. A.,

Feather replacement during moult is an energetically demanding stage of birds' annual cycles. Despite this, moult remains a neglected field of study in ornithology. This may in part be because the analysis of moult observations requires non-standard statistical techniques. We present moultmcmc an R package implementing Bayesian inference for models of avian moult phenology using fast Hamiltonian Monte Carlo sampling. Our package expands on existing maximum likelihood methods by accommodating repeat measures data, and by facilitating the joint analysis of different moult data types. We describe the theory behind moult phenology models and demonstrate their application using simulated and real world data. The moultmcmc package provides an interface for modelling moult phenology data from typical real world datasets and thereby further facilitates the uptake of appropriate statistical methods for these data.

Boersch-Supan, P.H., Hanmer, H.J. & Robinson, R.A. (2022) Bayesian inference for models of moult duration and timing in birds. arXiv:2205.12120. <a href="https://doi.org/10.48550/arXiv.2205.12120">https://doi.org/10.48550/arXiv.2205.12120</a>

### An analytical approach to improve comparative studies of survival rates

Brusa, J. L., Rotella, J. J., Banner, K. M., Hutchins, P. R.

Although survival rates are a central component of life-history strategies of large vertebrate species, very few comparative studies investigating life-history traits have included survival rates. The paucity of these studies could have resulted from challenges associated with obtaining a reliable dataset or incorporating information on the probability scale. The few studies that have included survival rates or some metric of survival (e.g., life span) tend to

ignore measurement error. This talk focuses on a technique to overcome the challenges of incorporating information on the probability scale and measurement error in comparative analyses. The approach uses Bayesian phylogenetically controlled regression with the flexibility to incorporate uncertainty in estimated survival rates and quantitative life-history traits as well as genetic similarity among species (with uncertainty). As with any comparative analysis, this approach makes several assumptions regarding the generalizability and comparability of empirical data from separate studies. The model is versatile in that it can be applied to any species group of interest and include any life-history traits as covariates. The utility of the model is demonstrated using both simulated and real data from pinnipeds, which is an excellent taxonomic group for comparative analyses. However, survival rate data for pinnipeds are scarce, and talk also emphasizes the importance of generating high-quality estimates of age-specific survival rates and information on other life-history traits that reasonably characterize a species. Overcoming these challenges will be necessary for addressing important questions related to broader ecological life-history patterns and how survival-reproduction tradeoffs might shape evolutionary histories of extant taxa.

Brusa, J. L., J. J. Rotella, K. M. Banner, and P. R. Hutchins. 2021. Challenges and opportunities for comparative studies of survival rates: An example with male pinnipeds. Ecology and Evolution 11: 7980-7999. DOI: 10.1002.ece3.7627 https://onlinelibrary.wiley.com/doi/full/10.1002/ece3.7627

# Irrigation drives declines in farmland bird populations

Cabodevilla, X., Wright, A. D., Villanua, D., Arroyo, B., & Zipkin, E. F.

Assessing the effects of agricultural intensification on biodiversity is critical for developing effective management plans for farmland conservation. Among other factors, the direct and indirect impacts of irrigation on wildlife have yet to be thoroughly studied despite significant increases in the surface area of irrigated farmlands since the mid-twentieth century (currently greater than 300 million hectares worldwide). Here, we evaluate the impact of irrigation on bird species occurrence patterns using a BACI (Before-After Control-Impact) design. Our study occurs in a 100 km2 area with rainfed agriculture in the Mediterranean region of northern Spain. We analysed a 13-year dataset comprised of the 47 most common bird species in the region using a multi-species hierarchical occurrence model. We examined how the implementation of irrigation in a rain-fed farmland area altered the local bird community, identifying which species were negatively or positively impacted by changes to the local ecosystem. The implementation of irrigation had an overall negative impact on the bird community, with occurrence rates of most species (55%) decreasing and only a small fraction (11%) increasing after the onset of irrigation, leading to an overall reduction in site-level species richness. Irrigation had the most detrimental impact on farmland birds (including steppe birds, which are of high conservation concern), but also had negative effects on forest, shrubland, and non-specialist bird species that occur frequently in rainfed agricultural environments. The observed negative impacts on bird occurrences are likely due to the loss of nesting and foraging habitat arising from shifts in crops and/or loss of fallow lands associated with irrigation. The fact that only a few species responded positively to the implementation of irrigation suggests that in the long-term irrigation may lead to substantial negative changes in local bird communities, with less diversity and a lack of ecologically-important farmland species. Irrigation schemes should thus be implemented carefully, avoiding areas with high species richness or high densities of endangered species. In cases where irrigation cannot be avoided, promoting diverse agrosystems, avoiding monocultures, and including interspersed rainfed crops and fallow lands may help to mitigate negative effects on local bird communities and their ecosystems.

Cabodevilla, X., Wright, A. D., Villanua, D., Arroyo, B., & Zipkin, E. F. (2022). The implementation of irrigation leads to declines in farmland birds. Agriculture, Ecosystems & Environment, 323, 107701. https://doi.org/10.1016/j.agee.2021.107701

# Point count offsets for population sizes of north american landbirds

Edwards, B. P. M., Smith, A. C., Sólymos, P., Robinson, B., Stralberg, D., Grinde, A., Murray, Harmer, T., Pasher, J., Gillespie, C., Gahbauer, M., Niemi, G., Iles, D., Michel, N., Docherty, T., Zlonis, E.

Bird monitoring in North America over several decades has led to millions of structured and semistructured bird observations to be freely available in databases. One such survey, the North American Breeding Bird Survey (BBS), has provided the basis for estimates of both trends and population sizes for North American landbirds. However, there are a number of spatial gaps on several levels that exist in the BBS. QPAD is a detectability function that can translate counts of birds from any survey type into estimates of true density, allowing for disparate surveys to be integrated. The integration of multiple data sets can allow these data and spatial gaps to be \_lled for better estimates of status, trends, and population sizes. Here, we introduce NA-POPS: Point Count O\_sets for Population Sizes of North American Landbirds, a large-scale, multi-agency project that was created to curate as many bird count observations as possible to generate an open-source database of detectability functions for all North American landbirds. As of this study, NA-POPS has collected over 6 million data points spanning 246 projects from across North America. This has allowed for the generation of detectability functions for over 300 species of landbirds so far. We describe the methods used to curate these data and generate these detectability functions, as well as describe the openaccess nature of the resulting database. We also describe our vision for use cases of the opensource detectability functions to improve population size estimates of North American landbirds.

Link to project webpage: <a href="https://na-pops.org/">https://na-pops.org/</a>

# Including a spatial predictive process in band recovery models improves inference for Lincoln estimates of animal abundance

Gonnerman, Matthew, Linden, Daniel W., Shea, Stephanie A., Sullivan, Kelsey, Kamath, Pauline, Blomberg, Erik

Abundance estimation is a critical component of conservation planning, particularly for exploited species where managers set regulations to restrict harvest based on current population size. An increasingly common approach for abundance estimation is through integrated population modeling (IPM), which uses multiple data sources in a joint likelihood to estimate abundance and additional demographic parameters. Lincoln estimators are one commonly used IPM component for harvested species, which combine information on the rate and total number of individuals harvested within an integrated band-recovery framework to estimate abundance at large scales. A major assumption of the Lincoln estimator is that banding and recoveries are representative of the whole population, which may be violated if major sources of spatial heterogeneity in survival or harvest rates are not incorporated into the model. We developed an approach to account for spatial variation in harvest rates using a spatial predictive process, which we incorporated into a Lincoln estimator IPM. We simulated data under different configurations of sample sizes, harvest rates, and sources of spatial heterogeneity in harvest rate to assess potential model bias in parameter estimates. We then applied the model to data collected from a field study of wild turkeys (Meleagris gallapavo) to estimate local and statewide abundance in Maine, USA. We found that the band recovery model that incorporated a spatial predictive process consistently provided estimates of adult

and juvenile abundance with low bias across a variety of spatial configurations of harvest rate and sampling intensities. When applied to data collected on wild turkeys, a model that did not incorporate spatial heterogeneity underestimated the harvest rate in some subregions. Consistent with simulation results, this led to overestimation of both local and statewide abundance. Our work demonstrates that a spatial predictive process is a viable mechanism to account for spatial variation in harvest rates and limit bias in abundance estimates. This approach could be extended to large-scale band recovery data sets and has applicability for the estimation of population parameters in other ecological models as well.

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# Spatially-autocorrelated detection probability in spatial capture-recapture

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Spatial capture-recapture (SCR) models are increasingly popular for analyzing wildlife monitoring data. SCR can account for spatial heterogeneity in detection that arises from individual space use (detection kernel), variation in the sampling process, and the distribution of individuals (density). However, unexplained and unmodeled spatial heterogeneity in detectability may remain due to cryptic factors, both intrinsic and extrinsic to the study system. This is the case, for example, when covariates coding for variable effort and detection probability in general are incomplete or entirely lacking.

We identify how the magnitude and configuration of unmodeled, spatially variable detection probability influence SCR parameter estimates.

We simulated SCR data with spatially variable and autocorrelated detection probability. We then fitted an SCR model ignoring this variation to the simulated data and assessed the impact of model misspecification on inferences.

Highly-autocorrelated spatial heterogeneity in detection probability (Moran's I = 0.85-0.96), modulated by the magnitude of the unmodeled heterogeneity, can lead to pronounced negative bias (up to 65%, or about 44-fold decrease compared to the reference scenario), reduction in precision (249% or 2.5-fold) and coverage probability of the 95% credible intervals associated with abundance estimates to 0. Conversely, at low levels of spatial autocorrelation (median Moran's I = 0), even severe unmodeled heterogeneity in detection probability did not lead to pronounced bias and only caused slight reductions in precision and coverage of abundance estimates.

Unknown and unmodeled variation in detection probability is liable to be the norm, rather than the exception, in SCR studies. We encourage practitioners to consider the impact that spatial autocorrelation in detectability has on their inferences and urge the development of SCR methods that can take structured, unknown or partially unknown spatial variability in detection probability into account.

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### A review of spatial capture-recapture: Ecological insights, limitations, and prospects

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First described by Efford (2004), spatial capture—recapture (SCR) has become a popular tool in ecology. Like traditional capture—recapture, SCR methods account for imperfect detection when estimating ecological parameters. In addition, SCR methods use the information inherent in the spatial configuration of individual detections, thereby allowing spatially explicit estimation of population parameters, such as abundance, survival, and recruitment. Paired with advances in noninvasive survey methods, SCR has been applied to a wide range of species across different habitats, allowing for population- and landscape-level inferences with direct consequences for conservation and management. I conduct a literature review of SCR studies published since the first description of the method and provide an overview of their scope in terms of the ecological questions answered with this tool, taxonomic groups targeted, geography, spatio-temporal extent of analyses, and data collection methods. In addition, I review approaches for analytical implementation and provide an overview of parameters targeted by SCR studies and conclude with current limitations and future directions in SCR methods.

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