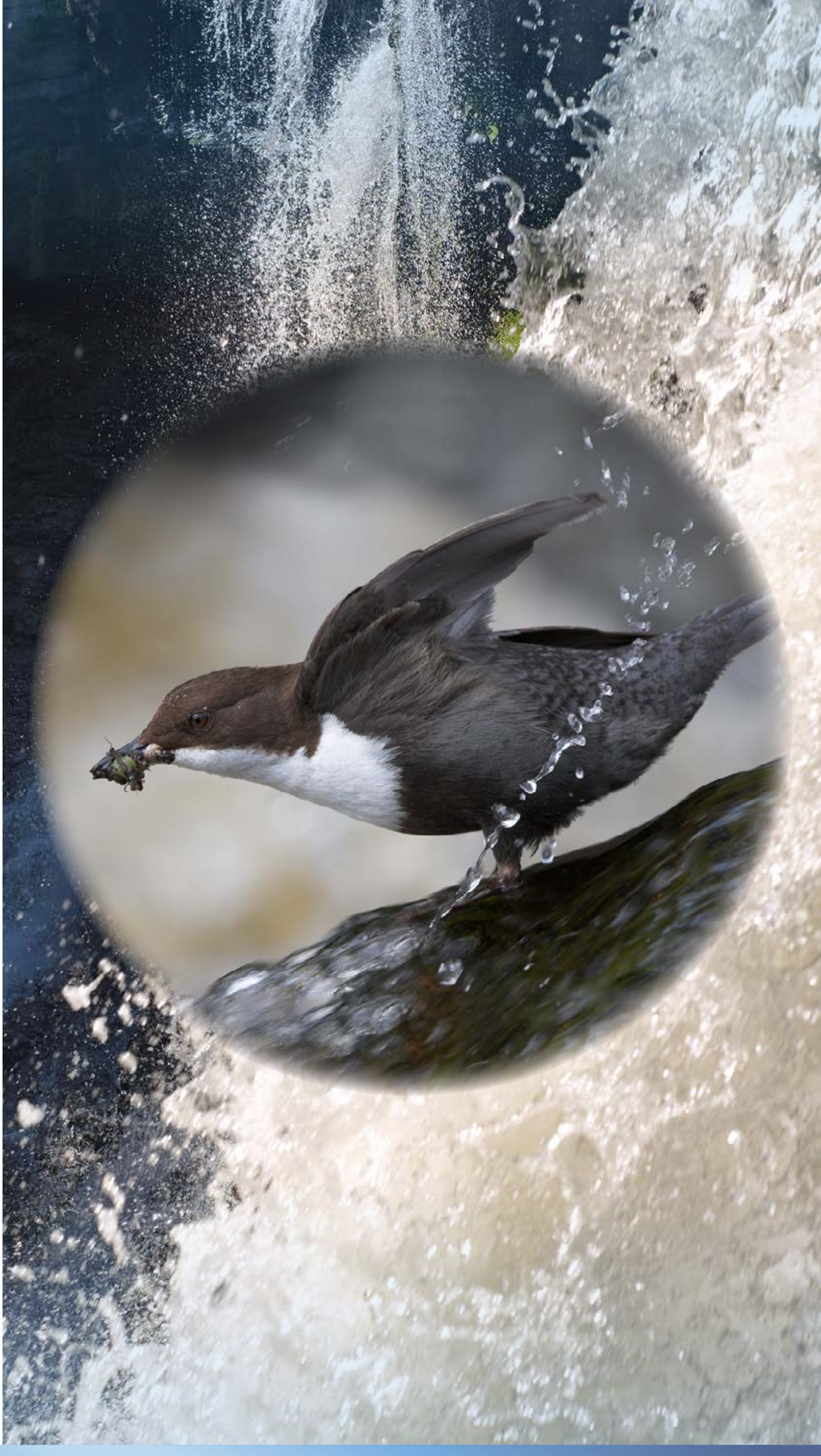
cbd
CENTRE FOR BIODIVERSITY DYNAMICS

Annual Report 2020



Norwegian
Centre of
Excellence

NTNU – Trondheim
Norwegian University of
Science and Technology

CBD IN SHORT

The aim of CBD is to produce research that will improve our ability to predict how changes in the environment, e.g. caused by human activities, affect the biological diversity at different organismal levels (gene, species and community). Our vision is to identify general principles and patterns which can be used to explain variation in biological diversity based on some basic properties of the systems. We will achieve this goal by a cross-disciplinary approach that integrates model development (focusing on stochastic effects), in-depth analyses of the dynamics of biological diversity in time and space in carefully selected study systems appropriate for examining model predictions and comparative analyses of extensive data sets.

CBD is organized into three research areas: (1) population ecology, (2) evolutionary biology, and (3) community dynamics. The overall approach is to implement stochastic models of single-species population dynamics into theories describing phenotypic evolution and community dynamics in fluctuating environments.

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COVER PHOTO:
White-throated dipper (*Cinclus cinclus*) eating a prey, in the river system of Lyngdalselva in southernmost Norway, where the population has been individually monitored the last few decades. Photo: Geir Rune Lovstad.

Background photo: © Shutterstock

COMMENTS FROM THE DIRECTOR:

Bernt-Erik Sæther
Director CBD

2020 became a very special year for CBD. On March 12 Norway closed down due to the Corona pandemic and strong restrictions on social contacts and all kinds of travels were imposed. This meant that almost all field activities planned during the spring had to be closed down. Fortunately, after a while CBD was allowed to continue field work in several of the ongoing long-term studies so that serious gaps in the time series were avoided.

Another implication of the pandemic was that social interactions among staff members were restricted to virtual platforms. In a cross-disciplinary research environment like CBD, in which frequent informal contacts among the members have been so important, this changed our way of doing science. Still, it is my feeling that the members of CBD adapted rapidly and to a large extent were able keep up with their original plans of progress. However, I think everyone at CBD found this lack of social contact challenging, making it much more difficult and laborious to maintain and develop interactions and networks with other colleagues both locally, nationally and internationally. For example, I am certain that the 4 PhD-students from CBD who graduated virtually in 2020 did not feel that the end of their academic education became the celebrative occasion they had hoped for and deserved.

The lockdown due to the pandemic also had other consequences for the activities at CBD. On April 16-19 CBD was supposed to host the 7th Annual Conference of the Evolutionary Society Demography, but this conference had to be cancelled. Instead, it was organized as a joint in-person and virtual conference at Røros during October 6-10. 33 people were able to participate in person at the conference, whereas 75 people followed the conference virtually. In spite of the logistical challenges, some of the virtual platforms generated more extensive interactions among the participants than are usually experienced at traditional in-person conferences. In my view, this way of virtual communication is something that should be developed and included in future meetings as well.

Several members of CBD have been heavily involved in the project *Evolvability: A New and Unifying Concept in Evolutionary Biology?* lead by professor Thomas F. Hansen, University of Oslo and professor Christophe Pelabon at NTNU as leaders. This project was organized as a Center of Advanced Study (CAS) at the Norwegian Academy of Science and Letters in Oslo for the academic year of 2019/2020. Although the travel restrictions due to the Corona pandemic reduced the number of international visitors that could be physically present in Oslo in the last period of the centre and also caused other logistical constraints in the daily operations, the extensive use of virtual platforms still made the organizers able to reach their scientific goals. In my view, some of the networks of researchers established during this year will without any doubt generate important advances that will influence the future development of this field of research.

Another important initiative at CBD initiated by Professor Jonathan Wright is a project entitled SQuID (Statistical Quantification of Individual Differences), which is an international collaboration of researchers and educators using customised data simulations to understand complex statistical mixed-effect models to investigate biological systems. The NFR-funded INTPART extension of SQuID, based at CBD, was started on December 1 2020 and involves 12 academic institutions in 10 countries (Norway, France, Germany, Hungary, USA, Canada, Australia, Brazil, Japan and UK) and combines world-class collaborative research with excellence in science education. This is a project of strategic importance for CBD because it provides a platform for integration of models and techniques developed at the centre into teaching and research in many fields within biology.

There were also in 2020 quite large changes in the staff. On August 1 Cameron Ghalambor started in his position as professor at the Department of Biology and became a member of CBD in Research Area 2. Ghalambor is an internationally leading evolutionary ecologist, working on many important questions such as the ecological and evolutionary implications of phenotypic plasticity, and factors generating and maintaining adaptive divergence within populations. Thus, professor Ghalambor has a research profile that fits well with several of the most central research questions at CBD and will therefore without any doubt soon become an important contributor to the research at the centre. Furthermore, professor Russell S. Lande increased his position as International Chair professor at NTNU to 100 % from December 1 and throughout the remaining period of CBD. Furthermore, 8 new PhD-students and 5 new postdocs became attached to CBD in 2020. Researcher Marlene Gamelon accepted from October 1 a position as permanent researcher at Centre national de la recherche scientifique (CNRS) in France, but fortunately agreed to keep 20 % of her position at CBD to the end of the center period. Postdoc Hannah Froy was in 2020 awarded a University Research Fellowship (URF) from The Royal Society of London for the project *Eco-evolutionary consequences of individual heterogeneity in density dependence*. This demonstrates that CBD members can compete successfully for attractive international research positions.

The research at CBD was originally divided into three research areas (RAs): population ecology, evolutionary biology and community dynamics. In later years it has become more evident that the potential significance of the research at CBD is highest on problems located in the intersections between the different RAs. As a consequence of this, it is nice to see from my perspective that it has become increasingly more difficult to categorize papers as output from a single RA. Good examples of this are papers published in 2020 by Tim Burton, Sigurd Einum and their collaborators on zooplankton, which link phenotypic variation to physiological (e.g. Burton et al., *Proceedings of the Royal Society London Ser. B*) or demographic (e.g. Issa et al., *Proceedings of the Royal Society London Ser. B*) characteristics with important implications for ecological and evolutionary processes (e.g. Burton et al., *American Naturalist*). Other examples of such papers dealing with research questions across RAs are the development of quantitative models including ecologically realistic assumptions (e.g. the paper by Engen et al. in *Evolution*) and the aims to relate patterns in strength of natural selection to variation in ecological conditions (e.g. Albertsen et al. in *Evolution*).

Another central research topic in the interface between RAs has been to include stochastic processes to improve our understanding of eco-evolutionary responses to changes in climate. For example, Holand et al. was able to demonstrate in a paper published in *Evolution* that spring warming induces in semi-domestic reindeer evolutionary changes in two traits, timing of birth and body mass of calves. Such selection on optimal timing of reproduction seems to be general in many species of birds and mammals (Villemereuil et al., *Proceedings of the National Academy of Sciences of the United States of America*). However, an extensive experiment on zebrafish by Morgan et al. published in the *Proceedings of the National Academy of Sciences of the United States of America* clearly revealed that the potential for evolutionary rescue from changes in climate may be more restricted than previously believed. One reason for this is perhaps that several fitness-related traits are simultaneously affected by such variation in the environment. This can generate correlated selection on several characters, which can have, as demonstrated by Layton-Matthews et al. (*Ecology Letters*) in the barnacle geese, unexpected consequences for the future growth of populations.

Within the research area in population ecology (RA1) at CBD an important focus has been to analyse and understand how consistent differences among individuals across years affect their contributions to the population growth rate. Such individual heterogeneity in demography causes challenges for predicting population responses to changes in the environment (e.g. caused by climate change) because it potentially introduces time lags in the population dynamics. Several researchers at CBD have been involved in a network of researchers to develop models and statistical methods to assess the effects of such individual heterogeneities in demography. As part of this, CBD contributed to a Lorentz workshop on *Individual heterogeneity in animals' life histories: more than meets the eye* in Leiden, the Netherlands, during February 3-7. This workshop was organized by Martijn van de Pol, Netherlands Institute for Ecology, the Netherlands, Stephanie Jenouvrier, Woods Hole Oceanographic Institution, USA , Sandra Hamel, Université Laval, Québec, Canada, and myself. This meeting provided an essential step ahead in developing a common statistical framework and identified several important problems that must be addressed before comparative analyses of individual heterogeneity in demography across species with different life histories can be done.

CBD has together with the Netherlands Institute for Ecology been heavily involved in building up the SPI-Birds database, which is a meta-database that includes a large number of population studies of especially hole nesting birds across Europe (see a more extensive description by Culina et al. in the *Journal of Animal Ecology*). This provides an excellent

Nearly all house sparrows in CBD's long-term study of an insular metapopulation off the coast of Helgeland in northern Norway are individually ringed and followed from they hatch until to they die. In 2020 data from this study was used to examine how differences between islands in for example population size affect the fitness consequences of inbreeding (Niskanen et al. PNAS). Photo: Hamish A. Burnett

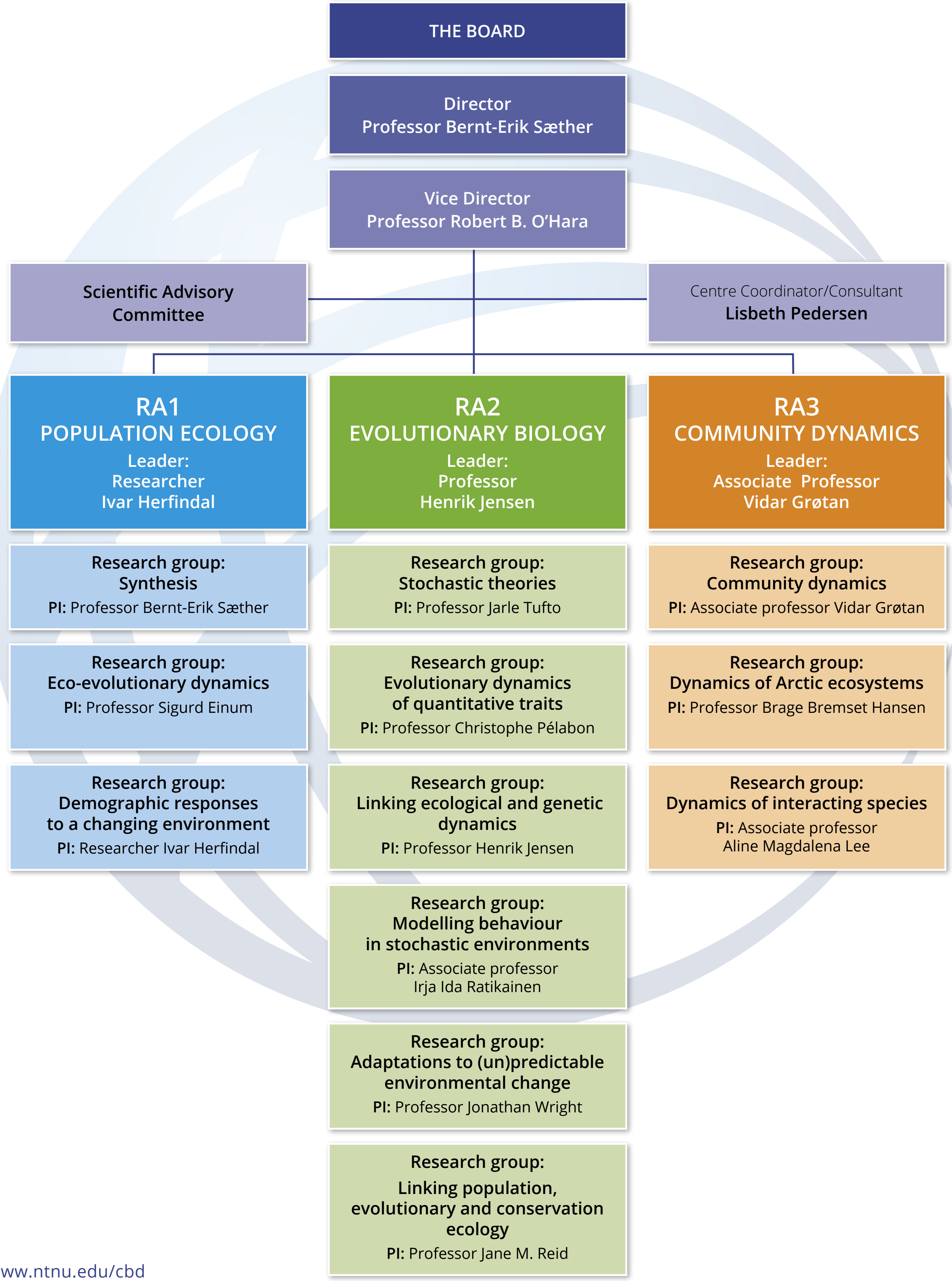
opportunity for analysing the effects of environmental changes on population processes and species interactions across large geographical areas.

The effects of geographical variation in the abundance of species have received a lot of focus in the research in the last period of CBD. In 2020 this materialized into the publication of several papers dealing with spatial processes. This includes on the population level how inter-island differences affect the fitness consequences of inbreeding in a house sparrow metapopulation (Niskanen et al., *Proceedings of the National Academy of Sciences of the United States of America*), how extreme climate events influence seasonal migration in the shag (Acker et al., *Journal of Animal Ecology*), and how covariation in weather affects the spatial scaling of temporal synchrony in body mass fluctuations of moose (Herfindal et al., *Journal of Animal Ecology*) and in shrub growth at Spitsbergen (Le Moullec et al., *Oikos*). An important contribution was also the perspective-rich review by Hansen et al. in Ecography on the Moran effect. For this paper, Hansen and Lee were elected as runner up for the E4 Award (Ecography award for Excellence in Ecology and Evolution), which is given to early career research scientists who send an exceptional review manuscript to *Ecography*.

In addition to these population-based approaches to studies of spatial dynamics, an increased focus in RA3: Community Dynamics is now on how dynamics of competing species and trophic interactions are affected by the spatial structure of the environment. Several papers appeared in 2020 on this topic (e.g. Lee et al. in *Ecology* and Jarillo et al. in *American Naturalist*). Furthermore, several of the research groups in this RA worked on the development of statistical methods to analyse spatial distributions of species diversity, especially focusing on combinations of different sources of data. A landmark in this work was the publication by Cambridge University Press of the book *Joint Species Distribution Modelling with Applications in R* by Otso Ovaskainen (20 % at CBD) and Nerea Abrego. I am sure that this book will provide a foundation for much of the future work on species distribution modelling.

A male house sparrow is enjoying the warmth from the autumn sun on one of the islands in CBD's long-term study of an insular house sparrow meta-population off the Helgeland coast in northern Norway. Photo: Hamish A. Burnett

ORGANIZATIONAL CHART 2020



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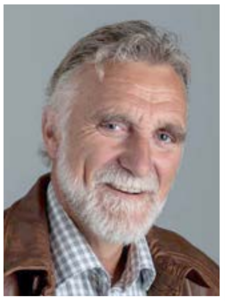

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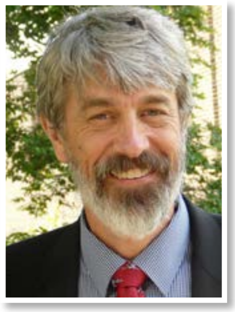

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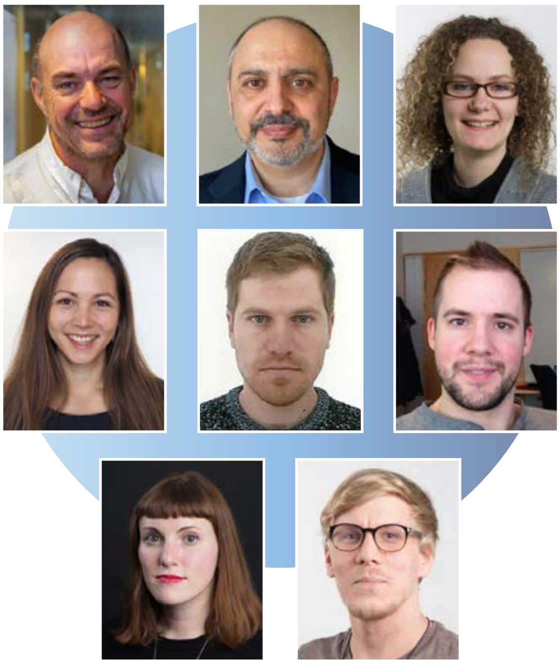
SCIENTIFIC ACTIVITY

RESEARCH GROUP: SYNTHESIS

Current group members:
PI: Professor Bernt-Erik Sæther
Professor Cameron Ghalambor
Researcher Marlène Gamelon
Postdoc Hannah Froy
Postdoc Rémi Fay
Postdoc Thomas Kvalnes
PhD candidate Lara Veylit
PhD candidate Stefan Vriend

Aim: *To apply stochastic models to understand processes affecting the dynamics of populations and phenotypes in fluctuating environments.*



Bernt-Erik Sæther, Cameron Ghalambor Marlène Gamelon, Hannah Froy, Rémi Fay, Thomas Kvalnes, Lara Veylit, Stefan Vriend

MAJOR SCIENTIFIC CONTRIBUTIONS

Two important events involved members of this RG in 2020. Researcher Marlene Gamelon was from October 1 appointed as permanent researcher at CNRS, France. However, she will still keep 20 % of her position at CBD until the end of the center period. In addition, postdoc Hannah Froy was awarded a University Research Fellowship (URF) from The Royal Society of London for the project *Eco-evolutionary consequences of individual heterogeneity in density dependence*.

The ecology and demography of wild boar

In November, Lara Veylit submitted her PhD thesis, entitled *Causes and consequences of body growth variation in hunted wild boar populations*, under the supervision of Bernt-Erik Sæther and Marlène Gamelon. She focused her research on "growth", a particularly interesting (and poorly studied) life-history trait linked to body size in adulthood, reproductive success, and longevity. Her main objective was to understand why body growth varies among populations and between individuals and the consequences of this variation. To reach this goal, she took advantage of data from individual long-term monitoring studies of wild boar *Sus scrofa* in France. This is an emblematic game species, living in different habitats, offering the opportunity to compare body growth patterns across contrasting environments in terms of habitat quality and hunting pressures. First, she estimated body growth early in life (until about 6 months of age) in different populations and assessed the effects of temperature, precipitations and density at birth on early-life growth (Figure 1).

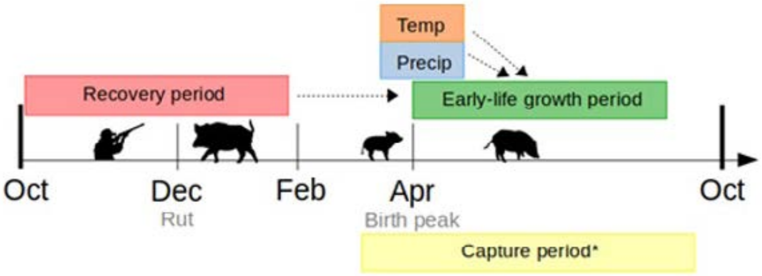


Figure 1. Wild boar life cycle. Data on the number of removed individuals are collected during the hunting season (October-February) coinciding with the rut and gestation periods. Weather variables (temperature and precipitation) that influence early-life growth rates were collected during the birth peak, in April, and the period of early-life growth coincides with the capture period (which may vary slightly between sites) (from Veylit et al. 2020a).

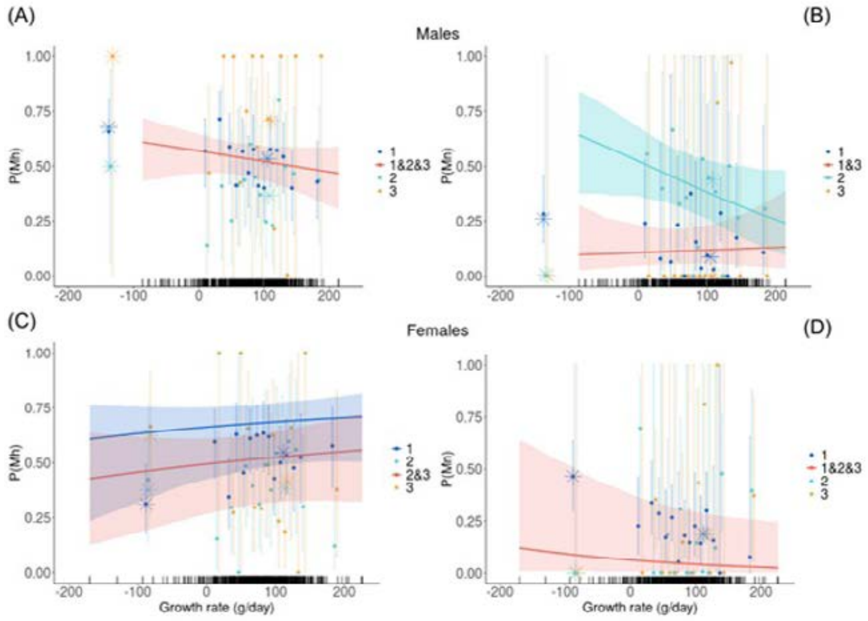


Figure 2. Age-specific hunting mortality (P(Mh) in A and C panels) and natural mortality (P(Mn) in B and D panels) as a function of early-life growth rate (in g/day) for male (A and B panels) and female (C and D panels) wild boar in Châteauvillain in France. The points depict the mortality estimates and 95% confidence intervals from a model for each class of early-life growth rates included as a categorical variable. The lines correspond to mortality estimates for each age class included in the selected models with early-life growth rate as a continuous variable and associated 95% confidence intervals. The rug plot shows the distributions of early-life growth rates for each sex. The stars depict age-specific mortality estimates from models with either negative to zero early-life growth rates or positive early-life growth rates. The estimates from the categorical models are plotted against the median value in the range of early-life growth rates for a given bin (from Veylit et al. 2020b).

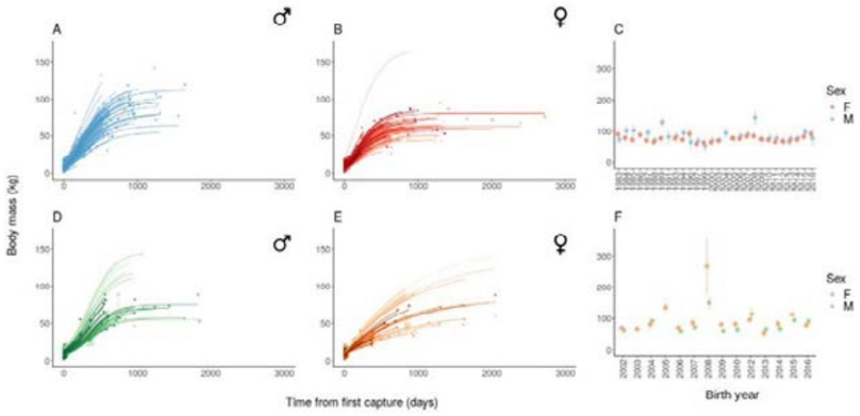


Figure 3. Body growth trajectories of wild boar in two localitets in France (Châteauvillain (first row) and Chizé (second row)), for males (panels A, D) and females (panels B, E). Points depict observations with matching colors of individual growth curves, from the selected models. Panels C and F show asymptotic body mass *A* according to birth year for both sexes (i.e. cohort effect on *A*).

Veylit found high variation in body growth rates across time, mainly driven by spring temperatures at birth with warmer spring favoring faster growth (Veylit et al. 2020a). Then, she empirically tested the well-known trade-off between growth and survival, by investigating whether fast early-life growth entailed a survival cost. She did not find evidence for this type of cost in the studied population (Figure 2) which is heavily hunted, the short lifespan of the individuals potentially masking long-term costs (Veylit et al. 2020b).

Then, Veylit broadened her focus to growth throughout the entire lifetime of an individual (i.e. not only early-life growth) to quantify growth trajectories across populations in contrasting environments using growth functions that encompass the expected range of growth shapes. She found context-dependent body growth (Figure 3); the shape of body growth varied between environments, sexes, and across individuals (Veylit et al. in revision).

Finally, Veylit assessed the role of acorns, an important food resource, on the probability for a female to move from a given body mass class to another within a year (i.e. growth transitions) and the consequences for the population dynamics. She found that acorn availability positively influences body growth, involving faster population growth rates in the studied populations (Gamelon et al. in press).

While having a focus on wild boar as a case study, Veylit's thesis improves our general knowledge on the causes and consequences of body growth variation in the wild.

Selection and adaptive evolution in fluctuating environments

Natural environments vary on multiple scales, which affects ecological and evolutionary processes of wild populations. Under long periods of evolutionary stasis, stabilizing selection is thought to be the most important mechanism that counteracts phenotypic changes by genetic drift and mutations. Few if any traits are free to evolve independently of other traits, instead selection may act on multiple traits that interact to create a combined phenotype. Correlational selection may then be an important process driving adaptive evolution, such that knowledge of the selective surface for combinations of genetically correlated traits become vital to predict how population mean phenotypes and fitness are affected when environments change. In semi-domestic reindeer in northern Finland, Holand et al. (2020) have shown that there is directional and stabilizing selection toward a combination of earlier birth date and heavier birth mass with an intermediate optimum along the major axis of the selection surface (Figure 4). In addition, there was found changes in the means towards earlier birth and heavier birth mass that were congruent with the direction of selection, and corresponding genetic changes in breeding values.

Most of the theory underlying predictions of responses to selection assumes a moving optimum phenotype, with predictions expressed in terms of the temporal variance and autocorrelation of this optimum. Phenological events, like timing of reproduction, are among the traits that are most sensitive to fluctuations and temporal changes in environmental conditions. In a meta-analysis, de Villemereuil et al. (2020) in collaboration with several people at CBD (Gamelon, Kvalnes and Tufto) investigated the extent of temporal variation in selection on breeding date in 39 populations of 21 species of birds and mammals. Breeding date can easily be compared across species and an optimum is likely because reproducing either too early or too late should limit reproductive success (including offspring survival). The study found support for a fitness function with a fluctuating optimum that caused temporal variation in the magnitude, but not the direction of selection. Birds and mammals displayed quite similar patterns, but mammals tended to display larger temporal variation in the optimum and selection. In addition, for several data sets there was clear evidence for phenotypic tracking of the optimum by plastic responses of individuals that reproduce in consecutive years. The signal of phenotypic tracking by plasticity was strongest in birds.

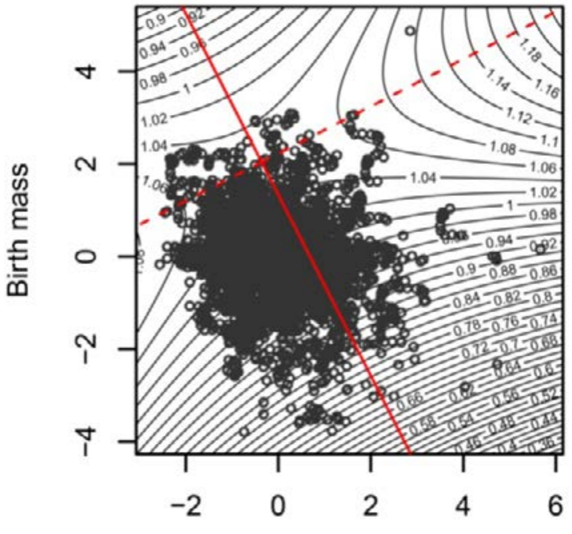


Figure 4. Estimated selection on birth date and birth mass of females in a semi-domestic reindeer population in northern Finland. Dashed line denotes the axis of the first eigenvector of the non-linear selection matrix. Solid line denotes the axis of the stabilizing correlational selection (second eigenvector of the non-linear selection matrix) between the two traits. Contours give the shape of the predicted individual selection landscape. Observed fitness values are given as open circles. One observation was excluded to improve clarity (at birth date = 9.238 and birth mass = −0.781).

RECOMMENDED READING:

de Villemereuil, P., Charmantier, A., Arlt, D., Bize, P., Brekke, P., Brouwer, L., Cockburn, A., Côté, S., Dobson, F.S., Evans, S.R., Festa-Bianchet, M., Gamelon, M., Hamel, S., Hegelbach, J., Jerstad, K., Kempenaers, B., Kruuk, L.E.B., Kumpula, J., Kvalnes, T., McAdam, A.G., McFarlane, S.E., Morrissey, M.B., Pärt, T., Pemberton, J.M., Qvarnström, A., Røstad, O.W., Schroeder, J., Senar, J.C., Sheldon, B.C., Van de Pol, M., Visser, M.E., Wheelwright, N.T., Tufto, J., Chevin, L.-M. 2020. Fluctuating optimum and temporally variable selection on breeding date in birds and mammals. Proceedings of the National Academy of Sciences of the United States of America, 117, 31969-31978. doi: 10.1073/pnas.2009003117

Gamelon, M., L. Touzot, É. Baubet, J. Cachelou, S. Focardi, B. Franzetti, E. Nivois, L. Veylit, and B.-E. Saether. in press. Effects of pulsed resources on the dynamics of seed consumer populations: A comparative demographic study in wild boar. Ecosphere.

Holand, H., Kvalnes, T., Røed, K.H., Holand, Ø., Sæther, B.-E., Kumpula, J. 2020. Stabilizing selection and adaptive evolution in a combination of two traits in an arctic ungulate. Evolution: 74, 103-115. doi:10.1111/evo.13894

Veylit, L., B.-E. Saether, J.-M. Gaillard, É. Baubet, and M. Gamelon. in revision. Evidence for context-, sex- and cohort-specific lifetime growth in a wild mammal.

Veylit, L., B.-E. Sæther, J.-M. Gaillard, E. Baubet, and M. Gamelon. 2020a. How do conditions at birth influence early-life growth rates in wild boar? Ecosphere 11:e03167.

Veylit, L., B.-E. Sæther, J.-M. Gaillard, É. Baubet, and M. Gamelon. 2020b. Grow fast at no cost: no evidence for a mortality cost for fast early-life growth in a hunted wild boar population. Oecologia:999–1012.

RESEARCH GROUP: ECO-EVOLUTIONARY DYNAMICS

Members in 2020:
PI: Professor Sigurd Einum
Researcher Tim Burton
PhD candidate Safa Chaabani
PhD candidate Semona Issa


Photo: Per-Harald Olsen

Tim Burton, Sigurd Einum, Safa Chaabani, Semona Issa

Aim: *To improve understanding of links between ecological and evolutionary responses to environmental change*

MAJOR SCIENTIFIC CONTRIBUTIONS

During 2020 we continued to contribute to the understanding of how environmental change influences aquatic ectotherms. When a change in the environment occurs, organisms can maintain an optimal phenotypic state via plastic, reversible changes to their phenotypes. While such phenotypic plasticity has been studied for more than half a century, global environmental change has stimulated renewed interest in quantifying variation in the rate and capacity with which this process occurs, particularly among ectothermic organisms. Yet, despite the likely ecological importance of acclimation capacity and rate, how these traits change throughout life among members of the same species is largely unstudied. Burton et al. (2020) investigated these relationships by measuring the acute heat tolerance of *Daphnia magna* of different size/age and acclimation status. The heat tolerance of individuals completely acclimated to relatively warm (28°C) or cool (17°C) temperatures diverged during development, indicating that older, larger individuals had a greater capacity to increase heat tolerance. However, when cool acclimated individuals were briefly exposed to the warm temperature (i.e. were 'heat-hardened'), it was younger, smaller animals with less capacity to acclimate that were able to do so more rapidly because they obtained or came closer to obtaining complete acclimation of heat tolerance. Our results illustrate that within a species, individuals can differ substantially in how rapidly and by how much they can respond to environmental change. These results were followed up by Burton and Einum (2020), where we used the thermal death time curve framework to investigate the relationship between temperature tolerance and size/age by measuring the change in heat tolerance of *Daphnia magna* across a range of temperature intensities (and hence exposures of varying duration) among individuals that differed up to 3-fold in size and thus varied in age also. Across the gradient of exposure temperatures, younger, smaller individuals were more tolerant than older, larger individuals. This suggests that the young and the small may be better equipped to withstand temperature challenges that are both intense/brief and more moderate/prolonged. Our study generalizes results obtained from more acute tolerance assays, providing physiological evidence consistent with the observed reductions in ectotherm body size as a response to warming in aquatic systems.

A second fundamental environmental factor that varies greatly in time and space is food abundance. Expression of phenotypic plasticity of life-history traits to such variation is crucial for individual fitness. Yet little is known about the neural signalling mechanisms underlying these reaction norms. Previous studies suggest a role for the dopamine system in regulating behavioural and morphological responses to food across a wide range of taxa. Issa et al. (2020) tested whether this neural signalling system also regulates life-history reaction norms by exposing *Daphnia magna* to both dopamine and the dopamine reuptake inhibitor bupropion, an antidepressant that enters aquatic environments via various pathways. We recorded a range of life-history traits across two food levels. Both treatments induced changes to the life-history reaction norm slopes. These were due to the effects of the treatments being more pronounced at restricted food ration, where controls had lower somatic growth rates, higher age and larger size at maturation. This translated into a higher population growth rate (r) of dopamine and bupropion treatments when food was restricted. Our findings show that the dopamine system is an important regulatory mechanism underlying life-history trait responses to food abundance and that bupropion can strongly influence life history.

RECOMMENDED READING:

Burton, T., Lakka, H.-K., Einum S. (2020) Acclimation capacity and rate change through life in the zooplankton *Daphnia*. Proceedings of the Royal Society B. 287: 20200189. doi.org/10.1098/rspb.2020.0189

Burton, T., Einum, S. (2020) The old and the large may suffer disproportionately during episodes of high temperature: evidence from a keystone zooplankton species. Conservation Physiology, 8: coaa038. doi.org/10.1093/conphys/coaa038

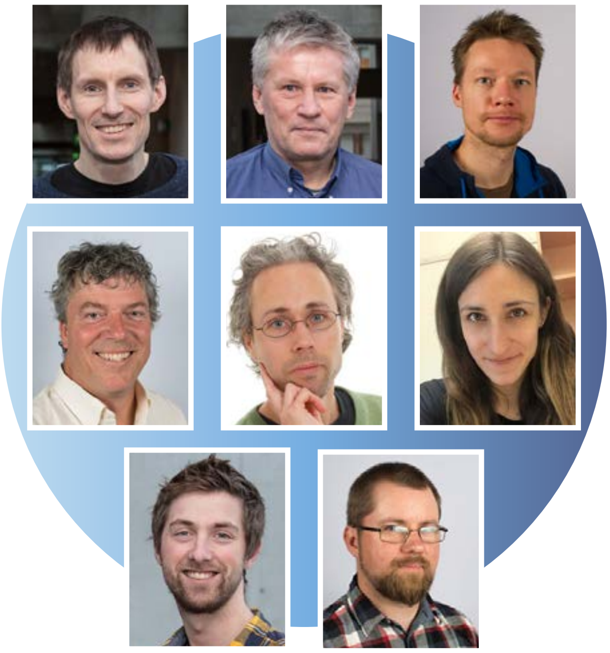
Issa, S., Gamelon, M., Maciej, T.C., Vike-Jonas, K., Asimakopoulos, A.G., Jaspers, V.L.B., Einum, S. (2020) Dopamine mediates life-history responses to food abundance in *Daphnia*. Proceedings of the Royal Society B. 287: 20201069. doi.org/10.1098/rspb.2020.1069

RESEARCH GROUP: DEMOGRAPHIC RESPONSES TO A CHANGING ENVIRONMENT

Current group members:
PI: Researcher Ivar Herfindal
Researcher Brett Sandercock (NINA)
Researcher Erlend Birkeland Nilsen (NINA)
Researcher Erling Johan Solberg (NINA)
Researcher Hanno Sandvik (NINA)
Postdoc Svenja Kroeger (NIBIO)
PhD candidate/Researcher Lars Rød-Eriksen (NINA)

Aim: *To understand causes and consequences of spatial and temporal variation in demography*

Our research group focuses on how individuals and populations respond to environmental variation and human activities. In 2020, much of the research focussed on consequences of environmental variation and human activities on spatial population dynamics and species interactions.



Ivar Herfindal, Erling Johan Solberg, Erlend Birkeland Nilsen, Brett Sandercock, Hanno Sandvik, Svenja Kroeger, Endre Grüner Ofstad and Lars Rød-Eriksen.

MAJOR SCIENTIFIC CONTRIBUTIONS

Environmental variation is often correlated in space, and this affects the spatial correlation in the dynamics of different populations, also known as spatial population synchrony. Herfindal et al. 2020 explored how the environment synchronised populations by using data on juvenile body mass in moose and semi-domestic reindeer. As expected, weather conditions that had the strongest impact on juvenile body mass, and in a similar manner among all populations, had the strongest synchronising effect. However, even if precipitation had a strong effect on body mass in both species, it did not synchronise body mass. This was due to a high spatial heterogeneity in precipitation. Temperature, on the other hand, was correlated over great distances.

The level of interspecific interactions varies spatially and can also explain why populations are not synchronous. Previous models of interspecific competition assumed similar effects across populations, and that all individuals are influenced similarly. Gamelon et al. (2020) explored to what extent this holds true in a study of two chamois populations in Switzerland, both of them co-existing with red deer. Vital rates of chamois were not influenced by red deer abundance in the population with low spatial overlap between the two species. In contrast, in the population where chamois had a high spatial overlap with red deer vital rates were negatively affected by red deer abundance, but only among young and senescent individuals. Such habitat-dependent consequences on demography were also found in a study of marmots by Kroeger et al. 2020. Here, daughters born to older mothers had greater annual and greater lifetime reproductive success than daughters born to younger mothers. However, at lower elevation, daughters born to older mothers also had greater age-specific decreases in annual reproductive success, whereas in the higher elevation environment, daughters born to older mothers tended to die before reaching ages at which senescent decreases could be observed.

The level of interspecific interactions is often affected by human activities, and often through indirect mechanisms. One important consequence of our activity is invasion of species into novel habitats, and this was the topic of Lars Rød Eriksen's PhD thesis which he successfully defended in spring 2020. In one of his papers (Rød-Eriksen et al. 2020), he shows how the large amount of human waste along alpine highways attracts scavenging species such as corvids and red fox. This increased both the nest predation along the road and the competition between the boreal species red fox and the alpine species arctic fox. Because the red fox is the stronger competitor arctic fox avoided areas nearby highways where abundance of human waste was high (Figure 1). This shows how human infrastructure may have unexpected consequences on local fauna.

In anthropogenically altered ecosystems where human activities often affect the individual vital rates, a detailed understanding of seasonal and demographic variation in these rates is often needed for sustainable management. Israelsen et al. 2020 used detailed data from an ongoing field study of willow ptarmigan to decompose the annual mortality risks for different age- and sex classes. As expected, harvest represented a main source of mortality in the fall, whereas other natural causes dominated in other seasons (Figure 2). The highest risk of mortality was in the fall and in the spring during the breeding season. These analyses provide unique insight into demographic and seasonal patterns in willow ptarmigan mortality risks in a harvested population and revealed a complex interplay across seasons, risk factors, and demographic classes. Such insight is valuable when designing sustainable management plans in a world undergoing massive environmental perturbations.

Another important human impact on ecosystems is introduction of alien species, and their ecological impact is a function of the area colonised. Impact assessments of alien species are thus incomplete unless they take the spatial component of invasion processes into account. Sandvik (2020) and Sandvik et al. (2020) developed a measure, termed expansion speed, that quantifies the speed with which a species increases its spatial presence in an assessment area. The method utilises time series of spatio-temporal observation data, and takes into account that the detection probability of new occurrences is often far from 100% and may vary through time. The method has been applied during the impact assessments of 1519 alien species in Norway, organised by the Norwegian Biodiversity Information Centre.

RECOMMENDED READING:

Gamelon, M., Filli, F., Sæther, B.-E., & Herfindal, I. (2020). Multi-event capture-recapture analysis in two Alpine chamois populations reveals population-specific responses to interspecific competition. Journal of Animal Ecology, 89, 2279-2289.

Herfindal, I., Tveraa, T., Stien, A., Solberg, E.J., & Grøtan, V. (2020). When does weather synchronise life history traits? Spatiotemporal patterns in juvenile body mass of two ungulates. Journal of Animal Ecology, 89, 1419-1432.

Israelsen, M.F., Eriksen, L.F., Moa, P.F., Hagen, B.R., and Nilsen, E.B. 2020. Survival and cause-specific mortality of harvested willow ptarmigan (*Lagopus lagopus*) in central Norway. Ecology and Evolution, 10, 11144-11154.

Kroeger, S.B., Blumstein, D.T., Armitage, K.B., Reid, J.M. and Martin, J.G.A. 2020. Older mothers produce more successful daughters. Proceedings of the National Academy of Sciences of the United States of America 117, 4809-4814.

Rød-Eriksen, L., Skrutvold, J., Herfindal, I., Jensen, H., & Eide, N. E. (2020). Highways associated with expansion of boreal scavengers into the alpine tundra of Fennoscandia. Journal of Applied Ecology 57, 1861-1870.

Sandvik, H. (2020) Expansion speed as a generic measure of spread for alien species. Acta Biotheoretica 68, 227–252.

Sandvik, H., O. Hilmo, S. Henriksen et al. (2020) Alien species in Norway: results from quantitative ecological impact assessments. Ecological Solutions and Evidence, 1, e12006.

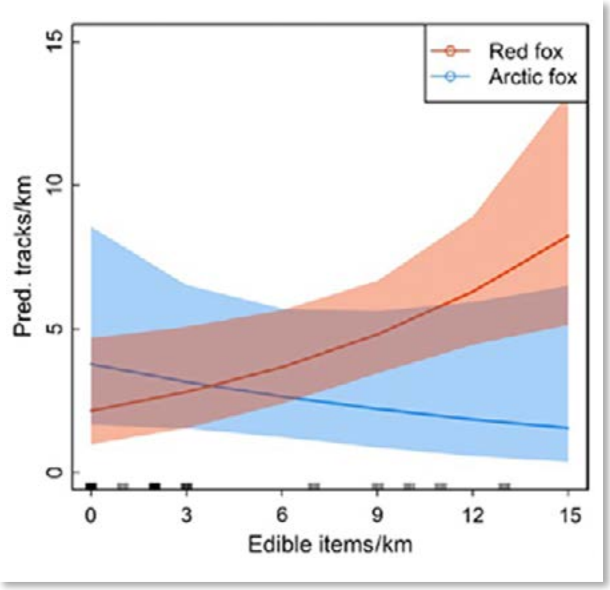


Figure 1. Predicted number of tracks of red (red line) and arctic (blue line) fox per km in relation to the number of edible items of anthropogenic origin per km found along road verges. From Rød-Eriksen et al. 2020.

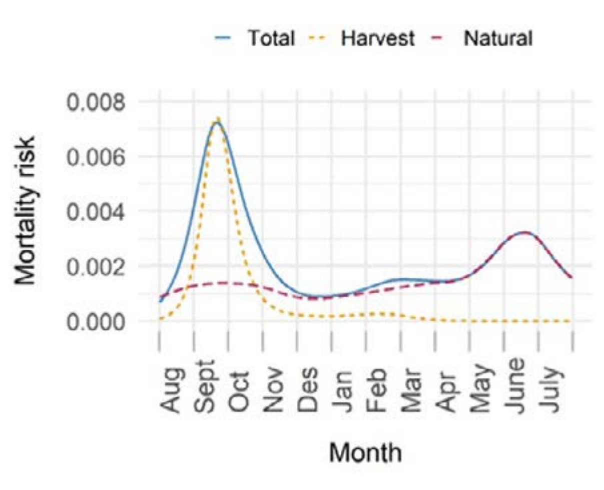
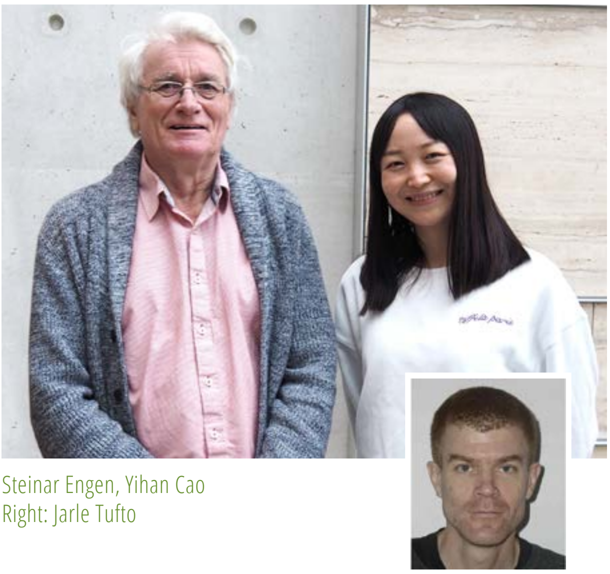


Figure 2. Willow ptarmigan seasonal mortality risks, decomposed to harvest mortality vs other mortality

RESEARCH GROUP: STOCHASTIC THEORIES

Current group members:
PI: Professor Jarle Tufto
Professor Steinar Engen
PhD candidate Yihan Cao

Aim: *To develop theories for the dynamics of populations, phenotypes and communities in fluctuating environments.*



Steinar Engen, Yihan Cao
Right: Jarle Tufto

The group aims to develop stochastic theoretical models and statistical methods for estimating parameters of such models to understand ecological and evolutionary processes involving different forms of environmental and demographic stochasticity.

MAJOR SCIENTIFIC CONTRIBUTIONS

Many species show synchronous fluctuations in population size over large geographical areas, which are likely to increase their regional extinction risk. In Jarillo et. al. (2020) the degree of spatial synchrony in population dynamics affected by trophic interactions using a two-species predator-prey model with spatially correlated environmental noise is examined. It is shown that the predator has a larger spatial scale of population synchrony than the prey if the population fluctuations of both species are mainly determined by the direct effect of stochastic environmental variation in the prey. This result implies that in ecosystems regulated from the bottom up, the spatial scale of synchrony of the predator population increases beyond the scale of the spatial autocorrelation in the environmental noise and in the prey fluctuations. Harvesting the prey increases the spatial scale of population synchrony of the predator, while harvesting the predator reduces the spatial scale of the population fluctuations of its prey. Hence, the development of sustainable harvesting strategies should also consider the impact on unharvested species at other trophic levels as well as human perturbations of ecosystems, whether the result of exploitation or an effect on dispersal processes, as they can affect food web structures and trophic interactions over large geographical areas.

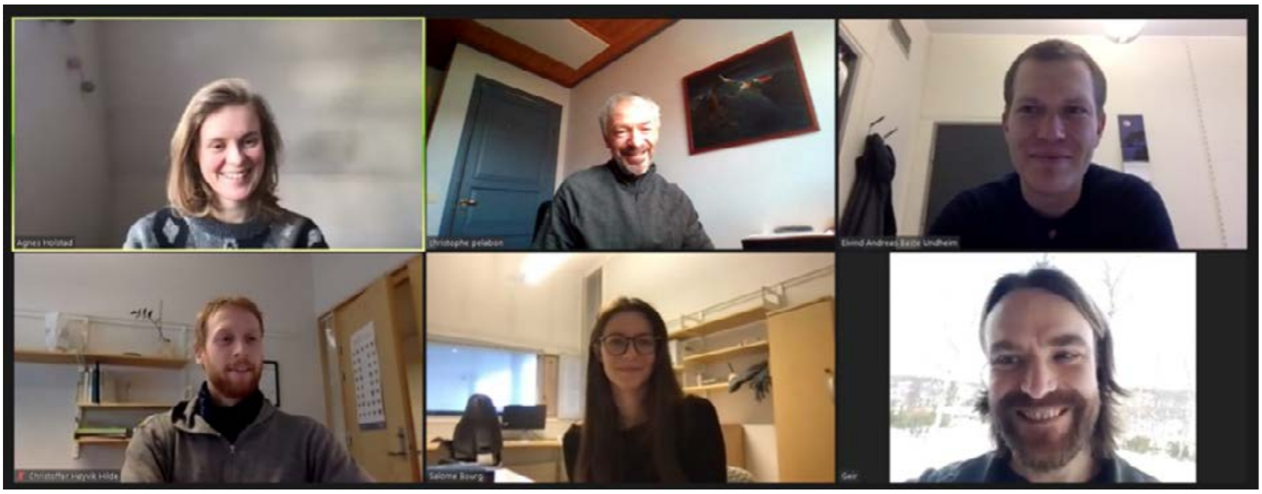
Many ecological and evolutionary processes strongly depend on the way natural selection varies over time. However, a gap remains when trying to connect theoretical predictions to empirical work on this question: Most theory assumes that adaptation involves tracking a moving optimum phenotype through time, but this is seldom estimated empirically. Several CBD members including Tufto, Gamelon and Kvalnes participated in an international team, assembling a large database of wild bird and mammal populations, to estimate patterns of fluctuations in the optimum breeding date and its influence on the variability of natural selection (Villemereuil et. al. 2020). They find that fluctuations in phenotypic optima are prevalent. However, their influence on temporal variance in natural selection is partly buffered by tracking of the optimum phenotype through individual phenotypic plasticity (see also the RG: Synthesis).

RECOMMENDED READING:

J. Jarillo, B.-E. Sæther, S. Engen, F. J. Cao-Carcía (2020) Spatial Scales of Population Synchrony in Predator-Prey Systems. American Naturalist 195: 216-230

P. de Villemereuil, A. Charmantier, D. Arlt, P. Bize, P. Brekke, L. Brouwer, A. Cockburn, S. D. Côté, F S. Dobson, S. R. Evans, M. Festa-Bianchet, M. Gamelon, S. Hamel, J. Hegelbach, K. Jerstad, B. Kempenaers, L. E. B. Kruuk, J. Kumpula, T. Kvalnes, A. G McAdam, S. E. McFarlane, M. B. Morrissey, T. Pärt, J. M. Pemberton, A. Qvarnström, O. W. Røstad, J. Schroeder, J. C. Senar, B. C. Sheldon, M. van de Pol, M. E. Visser, N. T. Wheelwright, J. Tufto, L.-M. l Chevin (2020) Fluctuating optimum and temporally variable selection on breeding date in birds and mammals. Proceedings of the National Academy of Sciences 117: 31969-31978.

Research Group: Evolutionary dynamics of quantitative traits



Agnes Holstad, Christophe Pélabon, Eivind Undheim, Christoffer H Hilde, Salomé Bourg, Geir H Bolstad

Current group members:
PI: Professor Christophe Pélabon
Researcher Geir H. Bolstad (NINA)
Postdoc Eivind Undheim
Postdoc Salomé Bourg
PhD candidate Agnes Holstad
PhD candidate Christoffer H Hilde

Aim: *Understand the evolutionary dynamics of complex traits.*

The group is testing predictive models for the evolutionary dynamics of multivariate quantitative traits, focusing particularly on the evolutionary constraints generated by the genetic architecture of the traits. Using both experimental and comparative approaches, the group aims at operationalizing measures of the evolutionary potential or evolvability. In collaboration with R. Morgan and F. Jutfelt from the physiology group at the institute of Biology (NTNU), the group has published a paper on the subject in 2020 in PNAS. Together with Prof. T. Hansen from the university of Oslo, C. Pélabon has co-organized a one-year workshop on Evolvability at the Centre of Advance Studies (CAS) in Oslo that ended in June 2020.

MAJOR SCIENTIFIC CONTRIBUTIONS

The evolutionary potential of thermal tolerance

The rapid change in the global temperature generates great concern about the ability of organisms to adapt to warmer environments. During heat waves, upper thermal tolerance is often critical for survival, but it remains unknown whether and how rapidly tolerance can evolve. The paper published in the Proceedings of the National Academy of Science with Rachael Morgan as lead author reports the results of an artificial selection experiment on upper thermal tolerance in a tropical fish. After six episodes of selection, upper thermal tolerance evolved but at a slower rate toward higher than lower temperatures. Furthermore, acclimation capacity decreased in the lines selected for higher thermal tolerance. These results suggest the existence of a hard limit in upper thermal tolerance that generates directional epistasis, that is, changes in interaction among loci when allele substitutions at different loci systematically reinforce (positive epistasis) or weaken (negative epistasis) allelic effects. In the case of upper thermal tolerance, allele substitutions that increase the mean systematically decrease the effect of other allele substitutions (negative epistasis). Such directional epistasis provokes changes in additive variance with changes in the mean upper thermal tolerance at short (ecological) time scale (see figure 1).

The project on Evolvability at the Centre for Advanced study CAS – Oslo 2019-2020

The project on Evolvability at the Centre for Advanced Study (CAS) in Oslo ended in June 2020. This project aimed at unifying the theory of evolvability and promoting this concept as one of the major concepts in the evolutionary theory. Two main axes of activity have been followed during this year. The first one in theory of Science (leader Laura Nuño de la Rosa), consisted of interviewing scientists that have been central in developing the concept of evolvability during the last 30 years. The idea of this project is to present both a conceptual and historical view of evolvability as seen by the people that developed this concept. The group has completed 19 interviews of many of the key actors in the different disciplines, including some prominent figures such as Richard Dawkins, Massimo Pigliucci, and Günter Wagner. The second part of the project was to synthesise the research in evolvability in order to identify commonality and differences in the use of the concept in different fields of evolutionary biology. This part of the project will be the main subject of a book on Evolvability to be published by MIT press in the Vienna Series in Theoretical Biology edited by G. Muller during the fall 2021.

RECOMMENDED READING:

Morgan, R., M.H. Finnøen, H. Jensen, C. Pélabon, & F. Jutfelt. 2020 Low potential for evolutionary rescue from climate change in a tropical fish. *PNAS* 117: 33365–33372. https://doi.org/10.1073/pnas.2011419117

Hilde, C. H., Gamelon, M., Sæther, B. E., Gaillard, J. M., Yoccoz, N. G., & Pélabon, C. (2020). The demographic buffering hypothesis: evidence and challenges. *Trends in Ecology & Evolution*. https://doi.org/10.1016/j.tree.2020.02.004

Pélabon, C., Hilde, C.H., Einum, S., & Gamelon, M. (2020). On the use of the coefficient of variation to quantify and compare trait variation. *Evolution Letters*. https://doi.org/10.1002/evl3.171

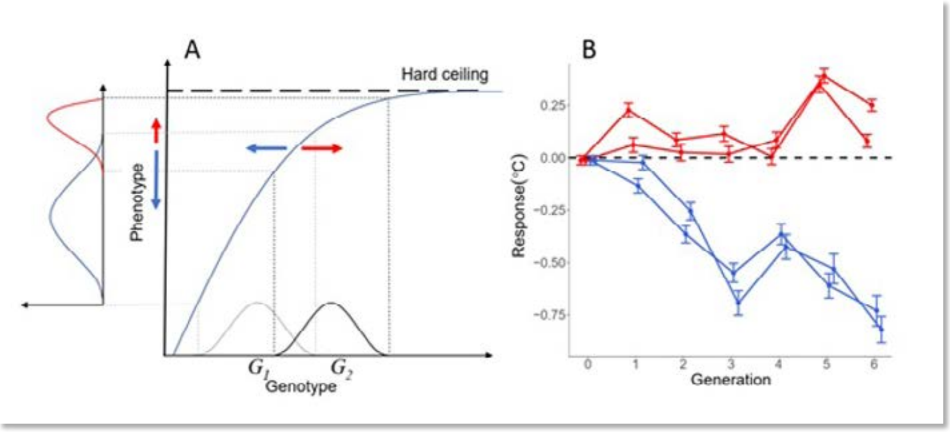


Figure 1: Non-linear GP map with a ceiling (A), that result from physiological constraints such as protein denaturation with temperature. The concave shape generates negative directional epistasis as the trait is increasing. Therefore, the same distribution of molecular genetic effects at different positions on the x-axis will generate different trait distributions and hence different evolvabilities at different positions on the y-axis. The consequence is an asymmetric response to selection (B), which is decelerating in the up lines and accelerating in the down lines (redrawn from Morgan et al. 2020).

RESEARCH GROUP: LINKING ECOLOGICAL AND GENETIC DYNAMICS

Current group members:
PI: Professor Henrik Jensen
Professor Ingelin Steinsland
Professor Stig W. Omholt
Associate Professor Arild Husby
Associate Professor Michael D. Martin
Associate Professor Stefanie Muff
Associate Professor Thor Harald Ringsby
Researcher Ingerid J. Hagen (NINA)
Researcher Peter S. Ranke
Postdoc Laurène Lecaudey
PhD candidate Dilan Saatoglu
PhD candidate Fabian Kellner
PhD candidate Gabriel David (Uppsala University)
PhD candidate Hamish A. Burnett
PhD candidate Isabelle Russell
PhD candidate Janne C. Hetle Aspheim
PhD candidate John McAuley (University of Edinburgh)
PhD candidate Maria L. Selle
PhD candidate Michael Le Pepke
PhD candidate Sarah Lundregan
PhD candidate Sindre L. Sommerli
PhD candidate Vanessa Bieker
PhD candidate Ådne M. Nafstad
Engineer Henrik Pärn
Engineer Oskar Speilberg

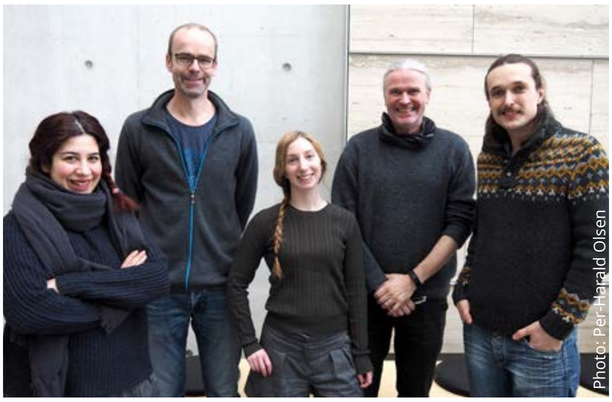


Photo: Per-Harald Olsen

Dilan Saatoglu, Henrik Jensen, Sarah Lundregan, Thor Harald Ringsby, Michael P. Pedersen

Aim: *To improve our understanding of interactions between ecological and genetic dynamics.*

Our research group produces knowledge targeting key questions at the interface between RA1 and RA2. In particular, our goals are to examine how spatiotemporal variation in population dynamics (including the effects of density dependence, environmental stochasticity and dispersal) interact with phenotypic variation and evolutionary dynamics, and the role of genetic variation in these interactions. Furthermore, our group seeks to understand the genetic basis of the evolution of diversity within and across species, which may be very rapid on geological time-scales. To achieve our goals we combine state-of-the-art genomic tools with development and application of novel statistical methods. Using such interdisciplinary approaches, we analyze individual-based data on fitness-related phenotypic traits, life history traits, and fitness components, as well as genome-level genetic variation across populations and species. Our main study systems are several intensively studied natural vertebrate metapopulations, including house sparrows, water voles, arctic foxes and Atlantic salmon, as well as various groups of plants such as Daisy trees and ragweed. We also provide molecular genetic resources and assistance needed by other research groups in all three RAs at CBD. Furthermore, the empirical individual-based data on phenotypic traits, fitness, and genetic variation we produce are, along with results from our studies not only needed to parameterize and test models developed by other RGs at CBD, but also particularly attractive for scientists who wish to use our unique data in international and national collaborative projects that test hypotheses and answer questions in various fields in biology.

MAJOR SCIENTIFIC CONTRIBUTIONS

Fitness-effects of inbreeding in natural populations

Inbreeding may increase the extinction risk of small populations by causing inbreeding depression, a reduction in individual fitness. Natural populations often experience different environmental conditions and differ in demographic history and genetic composition, characteristics that can affect the severity of inbreeding depression. Studying these mechanisms in wild vertebrates has been prevented by the difficulty of collecting long-term data on multiple populations. Furthermore, studies using modern genomic tools to investigate inbreeding depression in nature have been limited to single populations, and little is known about the dynamics of inbreeding depression in fragmented populations over time. We utilized extensive long-term data on more than 3,100 individuals from eight islands in an insular house sparrow metapopulation to examine the generality of inbreeding effects. Using genomic estimates of realized inbreeding, we discovered that inbred individuals had lower survival probabilities and produced fewer recruiting offspring than non-inbred individuals. Inbreeding depression, measured as the decline in fitness-related traits per unit inbreeding, did however not vary appreciably among populations or with time. As a consequence, populations with higher average levels of inbreeding (due to their demographic history) paid a higher total fitness cost, evidenced by a larger variance in fitness explained by inbreeding within these populations. Our results highlight the importance of considering inbreeding in conservation and management of populations with a wide range of characteristics.

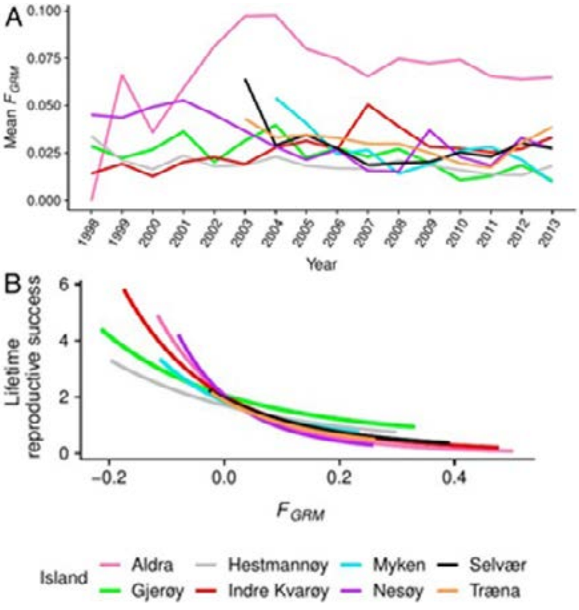


Figure 1. Mean inbreeding coefficient (FGRM) of adult individuals on eight islands in a metapopulation of house sparrows at the coast of Helgeland, Norway (A). Island-specific effects of inbreeding on lifetime reproductive success on the same eight islands (B).

The genetic architecture and adaptive potential of response to parasite challenge

Host–parasite relationships are likely to change in response to climate change and increased anthropogenic stressors. Understanding the genetic architecture of parasite resistance will aid prediction of species' responses to intensified parasite challenge. The gapeworm *"Syngamus trachea"* is prevalent in natural bird populations and causes symptomatic infections ranging from mild to severe. The parasite may affect ecological processes by curtailing bird populations and is important due to its propensity to spread to commercially farmed birds. Because our large-scale data set on an insular house sparrow metapopulation in northern Norway includes information on gapeworm prevalence and infection intensity, we could assess the genetics of parasite resistance in a natural system. To determine whether parasite resistance has a heritable genetic component, we performed variance component analyses using suitable statistical models, so-called animal models. Resistance to gapeworm had substantial additive genetic and dominance variance, and genome-wide association studies to identify single nucleotide polymorphisms associated with gapeworm resistance yielded multiple loci linked to immune function. Together with genome partitioning results, this indicates that resistance to gapeworm is under polygenic control in the house sparrow, and probably in other bird species. Hence, our results provide the foundation needed to study any eco-evolutionary processes related to gapeworm infection, and show that it is necessary to use methods suitable for polygenic and nonadditive genetic effects on the phenotype.

Spatial modelling improves genetic evaluation in breeding programs

When performing genetic evaluation, breeders and geneticists use statistical models to separate genetic and environmental effects on phenotype. A common way to separate these effects is to model a descriptor of an environment, a contemporary group or herd, and account for genetic relationship between animals across environments. However, separating the genetic and environmental effects in smallholder systems is challenging due to small herd sizes and weak genetic connectedness across herds. We performed simulations and real dairy cattle data analysis to evaluate the potential of spatial modelling to improve genetic evaluation in dairy cattle smallholder systems, and compared models using pedigree or genomic data. Our results showed that in smallholder systems spatial modelling increases the accuracy of genetic evaluation for phenotyped and non-phenotyped animals, and that spatial modelling

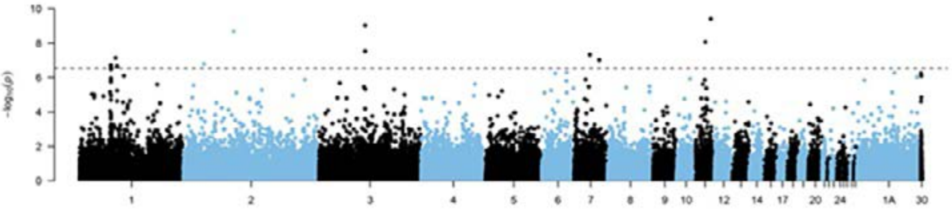
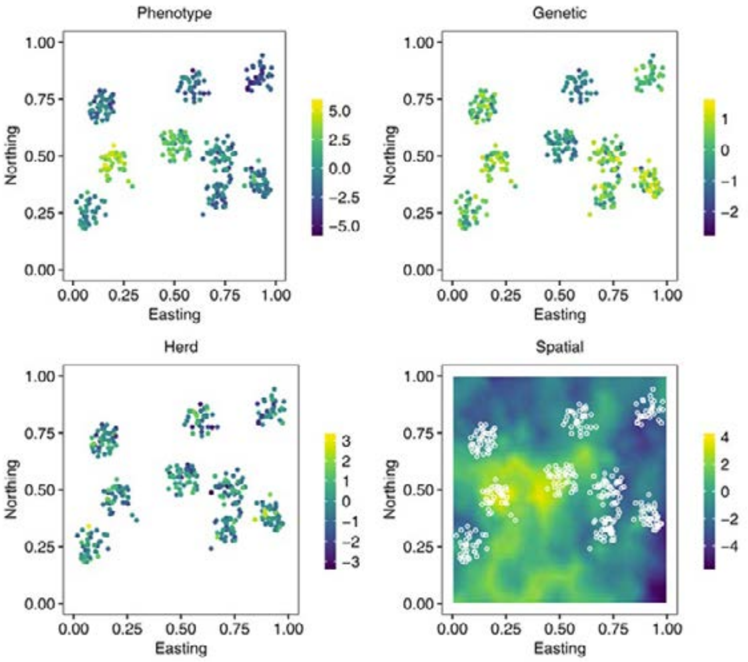


Figure 2. Results from genome-wide association studies on S. trachea resistance (faecal egg count) in an insular house sparrow metapopulation at the coast of Helgeland, Norway, using nonadditive association tests. The plot shows the negative logarithm of the p-value for markers against the chromosomal position in the house sparrow genome, and the horizontal dashed line indicate an FWER of 0.05. 18 SNPs were significant at this threshold.

Figure 3. A conceptual illustration of the simulation used to evaluate the potential of spatial modelling to improve genetic evaluation (Selle et al. 2020). The simulated data resembled the smallholder systems commonly observed in East Africa with small herds clustered in villages and a varying level of genetic connectedness. Each point denotes an animal, their location in a country and colour of the point denotes value of phenotype (top left panel) and underlying genetic (top right panel), herd (bottom left panel) and spatial (bottom right panel) effects. Note the most bottom-right village (cluster) with high genetic merit animals, but intermediate phenotypes due to negative spatial effects.



was beneficial when using either pedigree or genomic data. This improvement was driven by establishing environmental connectedness between herds, which enhances separation of genetic and environmental effects. This may be important not only in animal breeding, and we suggest that spatial modelling could also have a major impact in studies of human and wild populations.

RECOMMENDED READING:

Lundregan, S.L., Niskanen, A.K., Muff, S., Holand, H., Kvalnes, T., Ringsby, T.-H., Husby, A., and Jensen, H. 2020. Resistance to gapeworm parasite has both additive and dominant genetic components in house sparrows, with evolutionary consequences for ability to respond to parasite challenge. Molecular Ecology, 29, 3812–3829.

Niskanen, A.K., Billing, A.M., Holand, H., Hagen, I.J., Araya-Ajoy, Y.G., Husby, A., Rønning, B., Myhre, A.M., Ranke, P.S., Kvalnes, T., Pärn, H., Ringsby, T.H., Lien, S., Sæther, B.-E., Muff, S., and Jensen, H. 2020. Consistent scaling of inbreeding depression in space and time in a house sparrow metapopulation. Proceedings of the National Academy of Sciences of the United States of America, 117, 14584-14592.

Selle, M.L., Steinsland, I., Powell, O., Hickey, J.M., and Gorjanc, G. 2020. Spatial modelling improves genetic evaluation in smallholder breeding programs. Genetics Selection Evolution, 52, 69.

RESEARCH GROUP: MODELLING BEHAVIOUR IN STOCHASTIC ENVIRONMENTS

Current group members:
PI: Associate professor Irja Ida Ratikainen
Guest researcher Martin I. Lind

Aim: *To increase understanding of behavioural and life history strategies in stochastic environments*


Photo: Per-Harald Olsen

Martin Lind, Irja Ida Ratikainen

MAJOR SCIENTIFIC CONTRIBUTIONS

Generalists versus specialists in fluctuating environments: a bet-hedging perspective

Graduated PhD candidate Thomas Haaland has led the modelling of how specialists and generalists do in environments that fluctuate in different ways. In this work we have shown that environmental variability affects optimal amounts of phenotypic variation within and among individuals to maximize genotype fitness, and we disentangle the effects of individual-level optimization and genotype-level bet-hedging by comparing long-term arithmetic versus geometric mean fitness. The results depend on the type of trait. Some traits, such as foraging-related traits, have additive fitness effects within lifetimes, and for these traits it is equally good for a genotype to be a generalist as a diversified, bet-hedging, specialist. For traits that have multiplicative fitness effects within lifetimes, such as traits affecting sequential survival probabilities, generalist individuals are always favored. In this case, the long-term benefits of within-individual phenotypic variation are so beneficial to a genotype that it will cause individuals to be more generalist than required to simply maximize their own expected fitness.

In contrast to previous results in the bet-hedging literature, this generalist strategy is always favored over diversifying bet-hedging where individuals will produce different specialist offspring. Our results link the evolution of behavioral and ecological specialization with earlier models of bet-hedging and can aid our understanding of a range of natural phenomena from habitat choice to host specificity in parasites.

Experimental evolution of anticipatory parental effects

Parents can help their offspring by adjusting offspring's phenotype to match their environment. Such anticipatory parental effects would be beneficial, but only if parents can accurately predict the environment in which their offspring will develop and live. The plausibility of such anticipatory parental effects is hotly debated. The theory is clear that the predictability of the environment should play a defining role. We used an "experimental evolution" approach in a fast reproducing nematode worm *Caenorhabditis remanei* to tackle this question and follow the evolution of parental effects in different environments in real time. We found that populations evolving in a novel but predictable environment indeed had anticipatory parental effects that increased fitness of their offspring in that environment. In contrast, when evolving in an unpredictable environment where such parental effects would be disadvantageous, the parental effect was rapidly lost in evolution. Our novel experimental environments were constructed by exposing worms to increased temperature. Anticipatory parental effects play an important role in adaptation to novel environments and will affect the viability of populations under climate heating.

RECOMMENDED READING:

Haaland, T.R., Wright, J. and Ratikainen, I.I. 2020. Generalists versus specialists in fluctuating environments: a bet-hedging perspective. Oikos 129 (6) 879-890. doi: 10.1111/oik.07109

Lind MI, Zwoinska MK, Andersson J, Carlsson H, Krieg T, Larva T and AA Maklakov (2020). Environmental variation mediates the evolution of anticipatory parental effects. *Evolution Letters* 4: 371-381

RESEARCH GROUP: ADAPTATIONS TO (UN)PREDICTABLE ENVIRONMENTAL CHANGE

Current group members:
PI: Professor Jonathan Wright
Postdoc Yimen Araya-Ajoy
PhD candidate Mette Helene Finnøen
PhD candidate Myranda O'Shea

Aim: *To explore adaptive evolution in fluctuating environments.*

Jonathan Wright, Mette Helene Finnøen,
Yimen Araya-Ajoy
Right: Myranda O'Shea

This research group contributes to the research program of CBD primarily in Research Area 2. A variety of approaches is applied: from the development of mathematical models and wider conceptual frameworks to detailed life history and behavioural studies on vertebrates in the field and laboratory. Environmental variation is becoming more frequent and unpredictable as a consequence of anthropogenic change, yet we currently lack the tools to evaluate the extent to which organisms can adapt to this phenomenon. Adaptations to predictable short-term environmental variation should favour reversible or irreversible (developmental) plasticity, whilst unpredictable long-term environmental variation will favour bet-hedging and adaptive tracking. A fundamental challenge here is in defining such adaptive phenomena for phenotypes that vary hierarchically among species, populations, genotypes and individuals, and also within individuals for repeatedly expressed labile phenotypic traits (behaviour, physiology and morphology). To address this challenge, we combine approaches from behavioural ecology and quantitative genetics, using statistical models and the concept of the reaction norm to explore phenotypic variation among individuals alongside within-individual plasticity in labile and social phenotypes. Working at the interface between theoretical and empirical research, we are involved in a wide range of activities from the development of mathematical models and wider conceptual frameworks to detailed life history and behavioural studies on vertebrates in the field and laboratory.

MAJOR SCIENTIFIC CONTRIBUTIONS

1 Density-dependent selection at different life stages creates a second 'pace-of-life' axis

There has been much recent research interest in the existence of a major axis of life history variation along a fast-slow pace-of-life continuum within almost all major taxonomic groups. Eco-evolutionary models of density-dependent selection provide a general explanation for such observations of interspecific variation in the pace-of-life. One issue, however, is that some large-bodied long-lived 'slow' species (e.g. trees and large fish) often show an explosive 'fast' type of reproduction with many small offspring, and species with 'fast' adult life stages can have comparatively 'slow' offspring life stages (e.g. mayflies). We attempt to explain such life history evolution using the same eco-evolutionary modelling approach but with two life stages, separating adult reproductive strategies from offspring survival strategies (Fig.1).

When the population dynamics in the two life stages are closely linked and affect each other, density-dependent selection occurs in parallel on both reproduction and survival, producing the usual one-dimensional fast-slow continuum (Fig.2A). However, strong density dependence at either the adult reproduction or offspring survival life stage creates quasi-independent population dynamics, allowing fast-type reproduction alongside slow-type survival (e.g. trees and large fish), or the perhaps rarer slow-type reproduction alongside fast-type survival (e.g. mayflies - short-lived adults producing few long-lived offspring) – Fig.2B. Therefore, most types of species life histories in nature can potentially be explained via the eco-evolutionary consequences of density-dependent selection given the possible separation of demographic effects at different life stages.

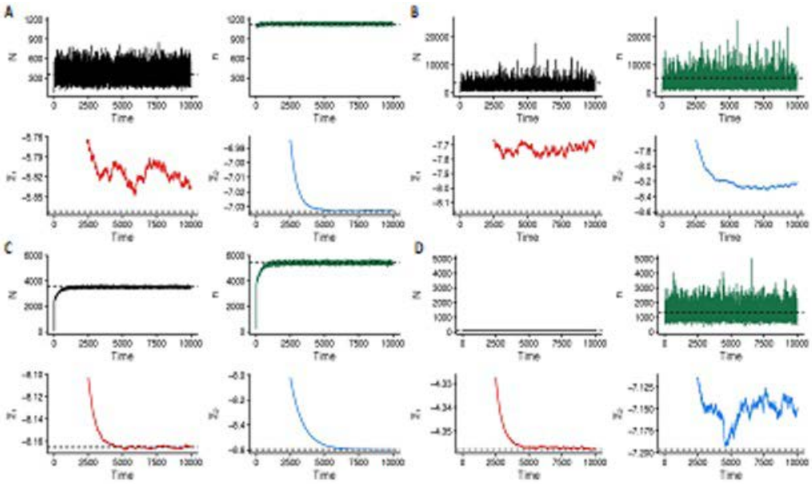


Figure 1. Model simulation results representing four extreme types of life history: **A** 'mayflies' with fast-selected adult reproduction and slow-selected offspring survival; **B** 'houseflies' with fast-selected reproduction and survival; **C** 'blue whales' with slow-selected reproduction and survival; and **D** 'oak trees' with slow-selected reproduction and fast-selected survival. Changes over time (generations) are shown as lines for populations sizes of adults (*N*, black) and offspring (*n*, green), and for values of the reproduction ($\bar{z}_1$, red) and survival ($\bar{z}_2$, blue) traits, with deterministic values for simulations with no environmental stochasticity (black dashed horizontal lines) for comparison.

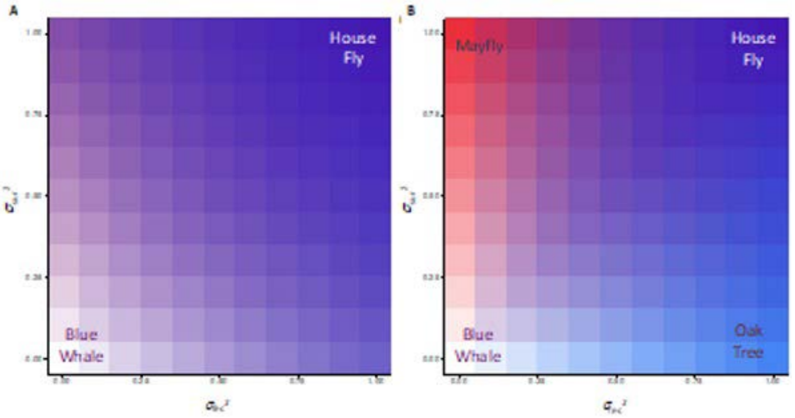


Figure 2. Model simulation results for adult reproduction trait $\bar{z}_1$ (red) and offspring survival trait $\bar{z}_2$ (blue). White contours indicate 0.3 intervals in mean trait values ($\bar{z}_1$ solid, $\bar{z}_2$ dashed). Results are shown for increasing levels of environmental stochasticity in offspring survival populations (σ^2_{sur}) and in adult reproductive populations (σ^2_{fec}). In **A** limited density dependence produces the traditional one-dimensional fast-slow life history continuum. However, in **B** strong density dependence allows quasi-independent population dynamics in the two life stages, orthogonal changes in the contours, and all four colours and alternative types of life history ('housefly', 'blue whale', 'oak tree' and 'mayfly' – model values as in Fig.1).

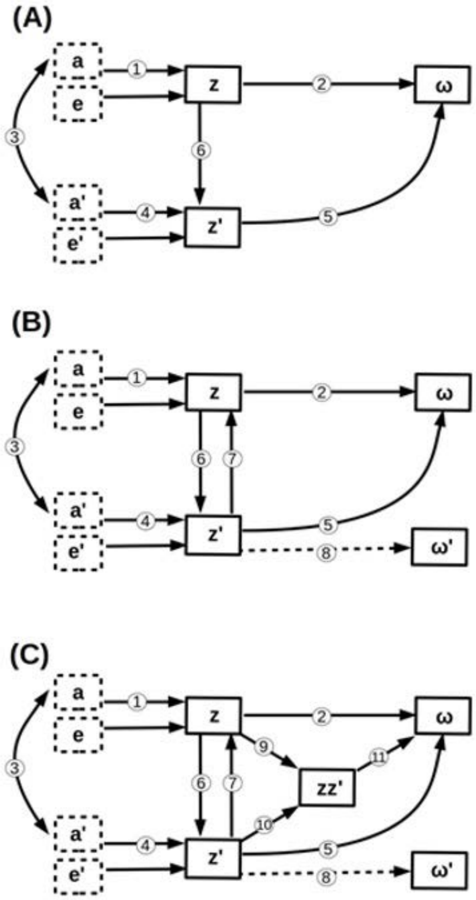


Figure 3. Path diagrams of social evolution. Symbols in solid line boxes are measured variables, symbols in dashed line boxes represent unmeasured (statistically inferred) variables. Numbers in circles are paths (ρ) representing the relationships between variables. **(A) Indirect routes to fitness**. ρ_1 reflects the genetic underpinning of the focal individual's trait, represented as the effect of breeding values a on trait z with e representing unmeasured environmental effects. ρ_2 is the relationship between the trait of the focal individual z and its relative fitness ω (β_n). ρ_3 represents the genetic relatedness (r) or covariance between interacting individuals. ρ_4 reflects the genetic underpinning of the trait z' of social partner(s), represented as the effect of genes a' on trait z' with e' again representing unmeasured environmental effects. ρ_5 is the relationship between the trait of the social partner z' and the focal individual's fitness ω, which can be interpreted as the social selection gradient (β_S). ρ_6 is the social impact ($\Psi_{zz'}$) of the phenotype of individual z on the phenotype z' of the social partner(s).
(B) Social responsiveness and the evolution of the social environment. ρ_7 represents the social responsiveness ($\Psi_{z'z}$) of the phenotype of the focal individual to the phenotype of its social partner. ρ_8 represents the direct selective pressesures (β'_N) on the social partner(s) phenotype and ω' the fitness of the social partner(s).
(C) Interacting fitness effects. ρ_9 and ρ_{10} represent the influences of the focal and social partner(s) traits on the aggregate character zz'. ρ_{11} represents interactive fitness effects (β_I) mediated by the aggregate character (zz').

2 Pathways to social evolution and their evolutionary feedbacks

In the context of social evolution, the ecological drivers of selection are the phenotypes of other individuals. The social environment can thus evolve, potentially changing the adaptive value for different social strategies. Different branches of evolutionary biology have traditionally focused on different aspects of these feedbacks. We synthesize behavioural ecology theory concerning evolutionarily stable strategies when fitness is frequency dependent with quantitative genetic models providing statistical descriptions of evolutionary responses to social selection. Using path analyses, we review how social interactions influence the strength of selection and how social responsiveness, social impact, and non-random social assortment affect responses to social selection. We then detail how the frequency-dependent nature of social interactions fits into this framework and how it imposes selection on traits mediating social responsiveness, social impact, and social assortment, further affecting evolutionary dynamics. Throughout, we discuss the parameters in quantitative genetics models of social evolution from a behavioural ecology perspective and identify their statistical counterparts in empirical studies. This integration of behavioural ecology and quantitative genetic perspectives should lead to greater clarity in the generation of hypotheses and more focused empirical research regarding evolutionary pathways and feedbacks inherent in specific social interactions.

RECOMMENDED READING:

Wright, J., Solbu, E.B. & Engen, S. (2020) Contrasting patterns of density-dependent selection at different life stages can create more than one axis of life-history variation. *Ecol. & Evol*. 10, 3068-3078.

Engen, S., Wright, J., Araya-Ajoy, Y. & Sæther, B.-E. (2020) Phenotypic evolution in stochastic environments: the contribution of frequency- and density-dependent selection. *Evolution* 74, 1923–1941.

Araya-Ajoy, Y.G., Westneat, D.F. & Wright, J. (2020) Pathways to social evolution and their eco-evolutionary feedbacks. *Evolution* 74, 1894–1907

Research group:
Linking population, evolutionary and conservation ecology

Current group members:
PI: Professor Jane Margaret Reid
Posdoc Paul Acker
PhD candidate Lisa Dickel
PhD candidate Sarah Fenn
PhD candidate Vicki Dale

Aim: *To understand how population dynamics and evolutionary dynamics can affect each other, and to apply such understanding to help conserve wild animal populations.*

Jane M. Reid, Paul Acker,
Lisa Dickel

Major scientific contributions

In pure science, our research group focused on understanding how different forms of movement, namely dispersal and reversible seasonal migration, can shape population and evolutionary dynamics.

First, we used long-term data from free-living song sparrows (*Melospiza melodia*) to examine how incoming immigrants into a focal population alter patterns of genetic variation and the progress of evolution (Figure 1). We showed that immigrants import genes that increase the degree of reproductive mate fidelity, and hence decrease the degree to which a female's offspring are sired by multiple males. Immigration thereby alters the reproductive system, and alters the form of genetic constraints acting across interacting females and males (Reid & Arcese 2020). This also provided important evidence that immigrants can import genes that decrease local survival, and hence constrain the course of adaptive evolution (Reid et al. 2020). The PhD student, Lisa Dickel, is now extending this project to full quantify effects of immigrants on individual and population fitness.

Second, we used multi-year data from European shags (*Phalacrocorax aristotelis*) to quantify patterns of phenotypic variation in, and natural selection on, the expression of seasonal migration versus year-round residence. This project is run in close collaboration with Dr Francis Daunt and colleagues at the UK Centre for Ecology & Hydrology. We showed that there is considerable among-individual variation in expression of seasonal migration versus residence, with associations with reproductive success that also differed between two focal years (Reid et al. 2020). We also showed that, across nine years, episodes of strong selection against year-round residence occurred, and were closely associated with extreme climatic events manifested as severe winter storms (Figure 2, Acker et al. 2020). Together these results demonstrate substantial phenotypic variation in a key movement trait that directly shapes spatio-seasonal population dynamics and distributions, and demonstrates that such variation can be subject to strong and highly variable selection.

We also advanced projects on joint population and evolutionary dynamics involving mating systems and inbreeding (with PhD students Max Tschol and Anders Paulsen, and collaborator Dr Greta Bocedi at University of Aberdeen), and on ecological and life-history predictors of changing migration phenology (with PhD student Vicki Dale at University of Aberdeen).

In applied science, I led the science base for ongoing conservation management for a protected bird, the red-billed chough (*Pyrrhocorax pyrrhocorax*), in Scotland. PhD student

Figure 1. An immigrant song sparrow, whose genes could reduce local survival and alter the reproductive system.

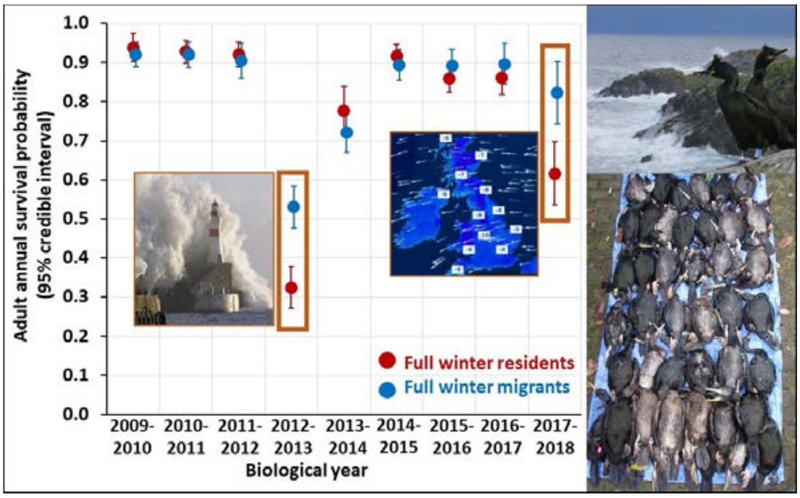


Figure 2. Estimated annual survival probabilities of full-winter resident and full-winter migrant European shags. Two years of strong selection against residents are highlighted.

Sarah Fenn (University of Aberdeen) and our colleagues showed that a programme of supplementary feeding which had been designed to target sub-adults had unplanned collateral benefits by also increasing adult survival and hence population growth rate (Fenn et al. 2020, *Journal of Applied Ecology*). These results, alongside existing understanding of ecological and genetic constraints on population persistence, were incorporated into a major commissioned report for NatureScot, which is now informing plans for future conservation actions (Trask et al. 2020).

RECOMMENDED READING:

Acker, P, Daunt, F, Wanless, S, Burthe, SJ, Newell, M, Harris, MPH, Grist, H, Sturgeon, J, Gunn, C, Payo-Payo, A, Reid, JM (2020) Strong survival selection on seasonal migration versus residence induced by extreme climatic events. Journal of Animal Ecology online. https://doi.org/10.1111/1365-2656.13410

Fenn, SR, Bignal, EM, Trask, AE, McCracken, DI, Monaghan, P, Reid, JM (2020) Collateral benefits of targeted supplementary feeding on demography and growth rate of a threatened population. Journal of Applied Ecology 57, 2212-2221. https://doi.org/10.1111/1365-2664.13721

Reid, JM, Arcese, P (2020) Recent immigrants alter the quantitative genetic architecture of paternity in song sparrows. Evolution Letters 4, 124-136. https://doi.org/10.1002/evl3.162

Reid, JM, Arcese, P, Nietlisbach, P, Wolak, ME, Muff, S, Dickel, L, Keller, LF (2020) Immigration counter-acts local micro-evolution of a major fitness component: migration-selection balance in free-living song sparrows. Evolution Letters online. https://doi.org/10.1002/evl3.214

Reid, JM, Souter, M, Fenn, SR, Acker, P, Payo-Payo, A, Burthe, SJ, Wanless, S, Daunt, F (2020) Among-individual and within-individual variation in seasonal migration covaries with subsequent reproductive success in a partially-migratory bird. Proceedings of the Royal Society B 287, 20200928. https://doi.org/10.1098/rspb.2020.0928

Trask, AE, Bignal, E, Bignal, S, McCracken, DI, Fenn, SR, Monaghan, P, Reid, JM (2020) Conservation strategy for red-billed choughs in Scotland: Assessment of the impact of supplementary feeding and evaluation of future management strategies. Commissioned Research Report for NatureScot. https://www.nature.scot/sites/default/files/2020-07/Publication%202020%20-%20SNH%20Research%20Report%201152%20-%20Conservation%20strategy%20for%20red-billed%20choughs%20in%20Scotland.pdf

RESEARCH GROUP: COMMUNITY DYNAMICS

Current group members:
PI: Associate professor Vidar Grøtan
Professor Anders Gravbrøt Finstad
Professor Bob O'Hara
Professor Otso Ovaskainen
Senior researcher Ola Diserud
Researcher Knut Anders Hovstad
(Norwegian Biodiversity Information Centre)
Postdoc Christophe Coste
Postdoc Emily Grace Simmonds
PhD candidate Bert van der Veen (NIBIO)
PhD candidate Caitlin Mandeville
PhD candidate Ellen Claire Martin
PhD candidate Kwaku Adjei
PhD candidate Lisa Sandal
PhD candidate Sam Perrin
PhD candidate Tanja Petersen
PhD candidate Wouter Koch
(Norwegian Biodiversity Information Centre)

Tanja Petersen, Lisa Sandal, Anders Gravbrøt Finstad, Bob O'Hara, Emily Grace Simmonds, Vidar Grøtan
Right: Sam Perrin, Christophe Coste

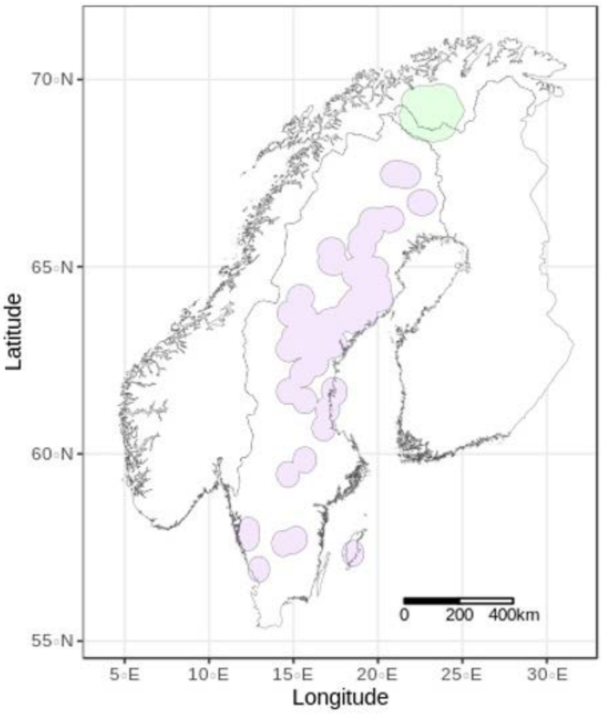
Aim: *To examine how community dynamics in time and space of different taxa along ecological gradients are affected by environmental stochasticity.*

MAJOR SCIENTIFIC CONTRIBUTIONS

The PhD thesis of Sam Perrin was submitted in October 2020 and successfully defended January 2021 (Perrin 2021). The thesis focuses around constructing the basis of a modelling framework that will forecast likely establishments of non-native species in freshwater ecosystems and their impacts on freshwater fish communities. In order to achieve this, questions regarding the potential effects that the combined anthropogenic factors of climate change and non-native species will have on freshwater ecosystems were explored.

In the paper "Integrating dispersal along freshwater ecosystems into species distribution models" (Perrin et al. 2020) from the thesis, the ability of species distribution models to account for dispersal is investigated. Accounting for such dispersal in SDMs has usually been accomplished through the integration of population connectivity. However for this to be effective, connectivity parameters need to have a sufficiently tangible link to the relevant species' dispersal capacity. For example, the linear distance "as the crow flies" is unlikely to be a good indicator of dispersal for freshwater fish species. Freshwater fish depend upon dendritic waterways where dispersal possibilities upstream are determined by terrain topography. To investigate the effect of different connectivity measures, recolonization of fish into lakes previously treated with the piscicide rotenone was used as a historical experiment to determine dispersal capacity. Further, a Joint Species Distribution Model (JSDM) was used to account for environmental and connectivity variables while simultaneously estimating biotic associations between species using a detailed dataset on fish presence / absence in the Kautokeino watershed in northern Norway. Inclusion of connectivity parameters improved our JSDM, suggesting that carefully considered connectivity metrics can improve the ability to model species, future distributions. This is likely to be of particular importance when assessing effects of land use impacts or restoration efforts, such as dam construction or removal, on the spread of invasive freshwater species or on the ability of native species to track thermal habitat alterations caused by climate change. Changing climate is also likely to modify interactions in waters where species currently coexist, potentially allowing one species to outcompete or increase predation pressure on

Figure Location of sites used in research article Integrating dispersal along freshwater ecosystems into species distribution models, which makes up chapter two of this thesis. Locations are freshwater lakes which have been treated with rotenone in Sweden (purple) and surveyed lakes within the Kautokeino watershed in northern Norway (green).



Arctic charr (*Salvelinus alpinus*). Photo: Anders G. Finstad

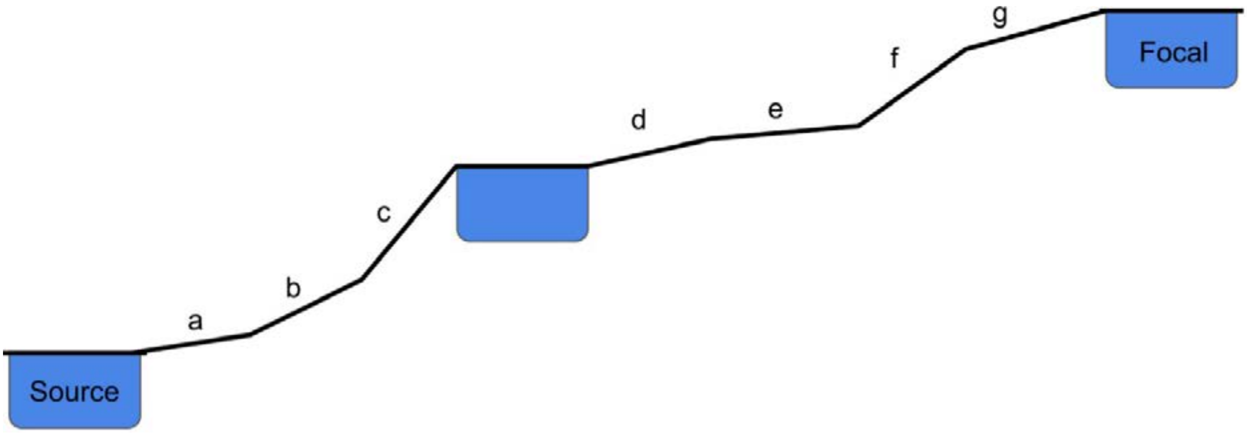


Figure Visual representation of different slope measurements of the pathway between a downstream (source) lake and an upstream (focal) lake. In this case, the slope is broken up into 7 "pixels" across two stream "sections," with the sections separated in this case by an intermediary lake. The slope of each pixel is represented by the letters a-g. Slope characteristics of the full pathway are calculated by aggregating characteristics of the sections by mean weighted by section length (for slope mean, third quartile and maximum) or by the maximum of the sections (for absolute maximum). For example, third quartile of the slope is calculated using the average third quartile of both sections, weighted by stream length (in this case (f × 4 + b × 3)/7). Absolute maximum slope is calculated by taking the maximum of the two stream sections' maximum slopes (in this case c)

the other. With regard to scandinavian freshwaters, we may in the future expect increased negative associations between cold-tolerant species like arctic charr and species tolerant of warmer waters, particularly perch, roach and pike. Accordingly, species distribution models also need to incorporate species associations and how these change with a changing climate.

RECOMMENDED READING:

Perrin, SW, Englund, G, Blumentrath, S, Brian O'Hara, R, Amundsen, P-A, Gravbrøt Finstad, A. Integrating dispersal along freshwater ecosystems into species distribution models. Divers Distrib. 2020; 26: 1598– 1611. https://doi.org/10.1111/ddi.13112

Perrin, S. W., & Norges teknisk-naturvitenskapelige universitet Institutt for biologi. (2021). Freshwater fish community responses to climate change and invasive species (Vol. 2021:27). Norwegian University of Science and Technology, Faculty of Natural Science, Department of Biology.

RESEARCH GROUP: DYNAMICS OF ARCTIC ECOSYSTEMS

Current group members:
PI: Professor Brage Bremset Hansen
Senior researcher Vebjørn Veiberg (NINA)
Postdoc Bart Peeters
Postdoc Mathilde Le Moullec
PhD candidate Kate Layton-Matthews
PhD candidate Laura Bartra Cabré


Photo: Per-Harald Olsen

Bart Peeters, Mathilde Le Moullec, Brage Bremset Hansen
Laura Bartra Cabré, Kate Layton-Matthews

Aim: *Our research applies demographic modelling and multi-species stochastic approaches to understand how environmental change and trophic interactions influence population and community dynamics, as well as eco-evolutionary dynamics, in time and space*

MAJOR SCIENTIFIC CONTRIBUTIONS

The project INSYNC (Research Council Norway, 2018-2022) uses novel field-experimental approaches and demographic time-series analyses to explore how climate drivers of key ecosystem components shape spatiotemporal dynamics of the tundra community in Svalbard. Collaborators include Univ. Aberdeen (UK), Univ. Groningen (NL), Univ. Iceland, CNRS Montpellier (FR), Norwegian Meteorological Institute, and the Univ. Centre in Svalbard.

Interactions between harvest and climate change

We are particularly interested in understanding and predicting how impacts of climate change may interact with other natural or anthropogenic drivers of ecological and evolutionary dynamics. In Peeters et al. 2020, we demonstrated important consequences of overharvesting (causing regional extirpations), human-made reintroduction programs and sea-ice loss for the current population genetics of Svalbard reindeer (Figure 1). These anthropogenic drivers appear to interact, such that the effects of past regional extirpations due to overharvest are modified by recent lack of sea-ice (an important dispersal corridor), thereby restricting recolonization, delaying large-scale population recovery, and limiting gene flow. Such links between spatiotemporal population dynamics and eco-evolutionary dynamics are key to predict future consequences of climate change and, therefore, a focal topic in our research plan.

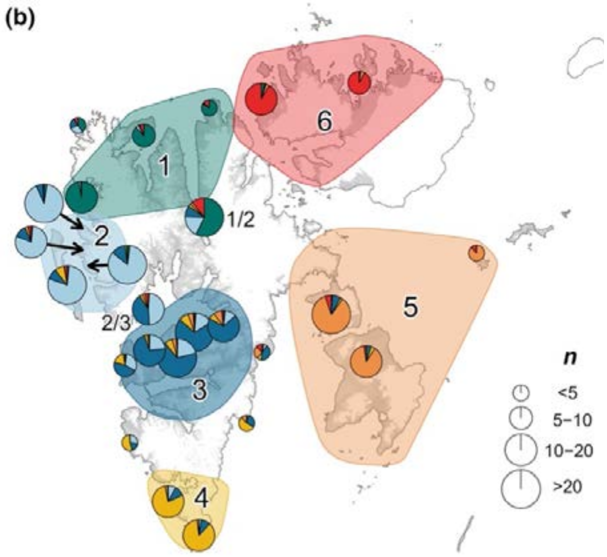


Figure 1 (Peeters et al. 2020): Bayesian clustering analyses of Svalbard reindeer spatial population genetics revealed six clusters (K = 6). This figure maps the genetic structure at 25 sampling sites (pie charts increasing in size relative to number of sampled individuals n), indicating strong interactive effects of past overharvest (local extirpations), reintroduction programs and recent climate change (loss of sea-ice as dispersal corridor).

Spatial population synchrony

We have recently been focusing on how weather events and climate change impact larger-scale patterns of population dynamics, notably the level and scaling of spatial population synchrony. In a paper by Le Moullec et al. 2020, we used dendrochronology to investigate how weather and climate impact shrub growth across Svalbard (Figure 2). Fluctuations in summer temperature largely explained annual shrub growth across the archipelago and, thereby, contributed significantly to spatially synchronous growth over large distances. On the contrary, negative impacts of occasional large-scale rain-on-snow events on shrub growth were only evident in some coastal regions, acting as a potentially de-synchronizing agent on large spatial scales. In such a bottom-up regulated trophic system, the level and scaling of spatial co-fluctuations in plant growth may have implications for spatiotemporal community-level dynamics. However, we have shown that the annual population fluctuations of the main herbivore, the Svalbard reindeer, are mainly driven by density-dependent effects of winter harshness (rain-on-snow events and ice-locked pastures), while bottom-up effects of e.g. warmer summers and increased plant growth can be more delayed, operating through the long-term carrying capacity K. Annual variation in rain-on-snow events thus contribute to spatially synchronous reindeer population size fluctuations from year to year, whereas gradual 'Arctic greening' and longer snow-free seasons cause similar long-term trends in abundance among populations (Hansen et al. 2020).

Considering the general importance of the Moran effect (i.e. the impact of large-scale weather fluctuations and climate on spatial population co-fluctuations) and the fact that spatial population synchrony patterns are crucial for long-term extinction risks, surprisingly few studies have investigated how climate change may influence population synchrony. In a paper receiving the runner-up prize in the E4 Awards (Ecography Excellence in Ecology and Evolution), we reviewed the existing literature and outlined, through simple population modelling and simulations, different potential pathways through which global warming may significantly alter patterns of spatial synchrony (Hansen et al. 2020). A key result was that changes in both the mean, variability and spatial autocorrelation of weather can impact population synchrony over time (Figure 3). This is particularly likely under a 'generalized Moran effect', i.e. when relaxing Moran's strict assumption of identical log-linear density-dependence, which is highly unrealistic in the wild.

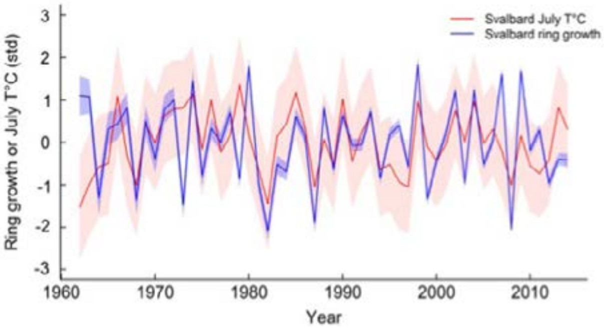


Figure 2 (Le Moullec et al. 2020): Fluctuations in July temperature largely explain annual ring growth in the dwarf shrub *Salix polaris* across the Svalbard archipelago, and thereby contribute significantly to a large-scale spatial synchrony in primary production, with potential implications for the whole tundra community.

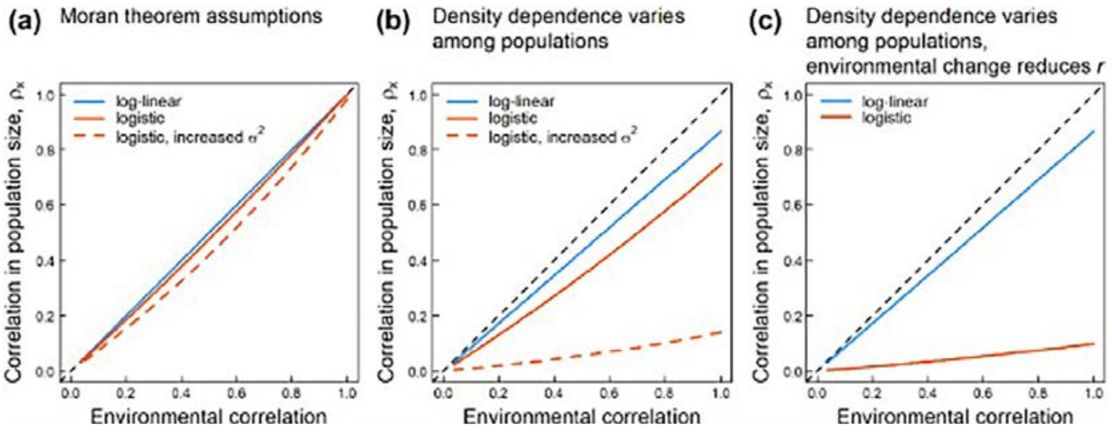


Figure 3 (Hansen et al. 2020, *Ecography*): From our theoretical population model we see, in accordance with Moran's theorem, that given equal log-linear density dependence among populations, the correlation in abundances (i.e. population synchrony) will be equal to the correlation in the environment (panel a). Importantly, for nonlinear dynamics, the correlation in abundances is always less than that of the environment (panels a, b, c). With variation in density dependence among populations in the nonlinear logistic model, the magnitude of this reduction will depend on β_1, β_2, $\sigma 2$ and environmental correlation ρe (panel b).

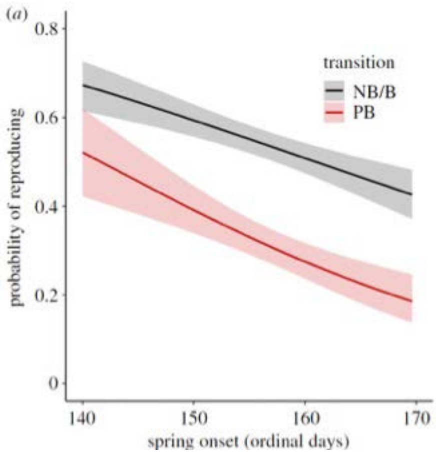


Figure 4 (Fjelldal et al. 2020): The later the spring onset, the less likely that barnacle geese in Ny-Ålesund, Svalbard, breed. This effect is particularly strong in 'pre-breeders' (PB; individuals that never bred before), resulting in a long-term temporal trend in age of first reproduction as the advancement of the timing of spring onset proceeds under climate warming.

Furthermore, climate change can influence spatial population synchrony indirectly, through its effects on dispersal and species interactions. Because changes in population synchrony may cascade through food-webs, we argue that the (generalized) Moran effect is key to understanding and predicting impacts of global warming on large-scale ecological dynamics, with implications for extinctions, conservation and management. Spatial population synchrony under changing environments is therefore one of our current focal areas of research.

Eco-evolutionary dynamics in barnacle geese

Kate Layton-Matthews' PhD project has contributed to great progress in our understanding of eco-evolutionary implications of climate change and trophic interactions in Arctic geese. For instance, a rapidly advancing timing of spring onset has overall positive effects on reproduction in barnacle geese (Layton-Matthews et al. 2020), and even causes earlier age of first reproduction (Fjelldal et al. 2020) with potential evolutionary consequences. However, this effect on egg laying is offset by increased predation of fledglings by Arctic foxes (Layton-Matthews et al. 2020). As part of Laura Bartra Cabré's current PhD project we are now using a combination of empirical and theoretical work to investigate whether such strong trophic links may lead to cascading effects of climate change across whole communities.

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RECOMMENDED READING:

Fjelldal MA, Layton-Matthews K, Lee AM, Grøtan V, Loonen MJJE & Hansen BB (2020). High-Arctic family planning: earlier spring onset advances age at first reproduction in barnacle geese. Biology Letters 16:20200075.

Hansen BB, Pedersen ÅØ, Peeters B, Le Moullec M, Albon SD, Grøtan V, Herfindal I, Sæther B-E & Aanes R (2020). Spatial heterogeneity in climate change effects decouples the long-term dynamics of wild reindeer populations in the high Arctic. Global Change Biology 25:3656-3668.

Hansen BB, Grøtan V, Herfindal I & Lee AM (2020). The Moran effect revisited: spatial population synchrony under global warming. Ecography 43: 1591-1602.

Layton-Matthews K, Hansen BB, Grøtan V, Fuglei E & Loonen MJJE (2020). Contrasting consequences of climate change for migratory geese: Predation, density dependence and carryover effects offset benefits of high-arctic warming. Global Change Biology 26:642-657.

Le Moullec M, Sandal L, Grøtan V, Buchwal A & Hansen BB (2020). Climate synchronises shrub growth across a high-warctic archipelago: contrasting implications of summer and winter warming. Oikos 129:1012-1027.

Peeters, B, Le Moullec M, Raeymaekers JAM, Marquez JF, Røed KH, Pedersen ÅØ, Veiberg V, Loe LE & Hansen BB (2020). Sea ice loss increases genetic isolation in a high Arctic ungulate metapopulation. Global Change Biology 26:2028-2041.

Research group: Dynamics of interacting species

Current group members:
PI: Associate Professor Aline Magdalena Lee
Researcher Elena Albertsen (NIBIO)
Postdoc Marie Vestergaard Henriksen (NIBIO)
PhD candidate Jonatan Fredricson Marquez
PhD candidate Ragnhild Bjørkås

Aline Magdalena Lee, Elena Albertsen,
Marie Vestergaard Henriksen, Jonatan Fredricson Marquez,
Ragnhild Bjørkås

Aim: *To understand stochastic population dynamics in the presence of species interactions, using a combination of theoretical modeling and data analysis.*

We work in the gap between classical single-species population ecology and community ecology, studying the dynamics of interacting species in fluctuating environments. We are interested in how interacting species covary in space and time, and how their dynamics are driven by combinations of factors, such as life history, spatial movement, characteristics of their interactions, and different types of environmental stochasticity. Our work involves a combination of theoretical modeling and empirical data analysis.

Major scientific contributions

This year we have been joined by new PhD candidate Ragnhild Bjørkås who is studying the role of interspecific interactions in determining spatio-temporal population dynamics under shared environmental variation. Focusing on the avian community of the Serengeti, she aims to increase our understanding of the processes and mechanisms behind this interspecific population synchrony.

Species interactions influence global warming effects

Shared environmental conditions and fluctuations are known to synchronize population dynamics in what is commonly called the Moran effect. When populations are synchronized over large areas, the overall (meta-)population becomes more sensitive to unexpected environmental events and extinction. In Hansen et al. (2020) we explore how global warming might change population synchrony. Species interactions provide several pathways for such changes (Figure 1). For example, global warming is causing changes in community composition through species extinctions and range shifts. Because predation and competition both influence the population synchrony of the interacting species, such changes are likely to alter the population synchrony of many species within affected communities. This paper was selected as 1st Runner-Up for the Ecography E4 award for Excellence in Ecology and Evolution.

Age-dependent patterns of spatial synchrony in three marine fish species

Species can exhibit distinct patterns of spatial synchrony in their abundance dynamics due to differences in processes such as dispersal rates, environmental sensitivity and trophic interactions. These processes can also vary greatly between the age classes of a population, which led to the question, does spatial synchrony vary between the age classes of a population? Using data from three marine fish species cohabiting in the Barents Sea we found that spatial autocorrelation could vary between age classes in some species, however, the variation with age was not consistent among species. We found that spatial synchrony increased with age in cod, decreased with age in beaked redfish and stayed constant between the age classes of haddock (Figure 2). In addition, we found that in the cases of haddock and cod

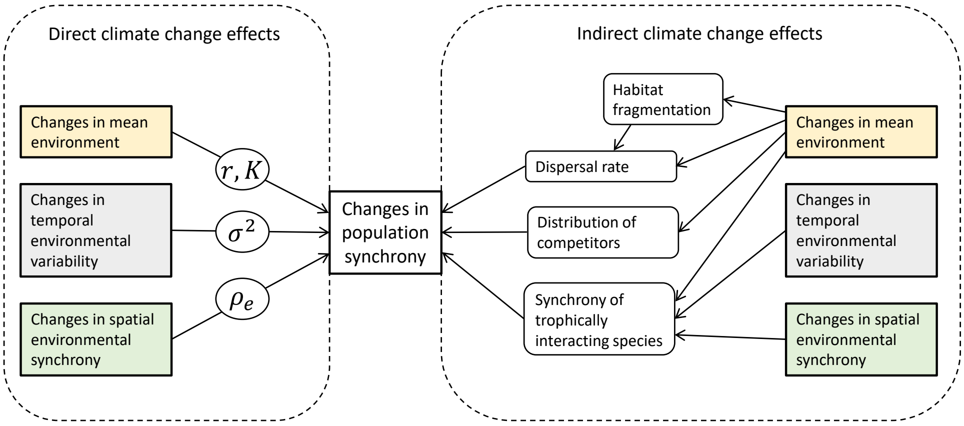


Figure 1. Direct and indirect pathways through which climate change might affect population synchrony. In addition to direct effects through changes in the intrinsic population growth rate r, carrying capacity K, environmental variance σ2 and correlation in environmental noise ρe, there are many possible indirect effects, and species interactions play a central role in several of these.

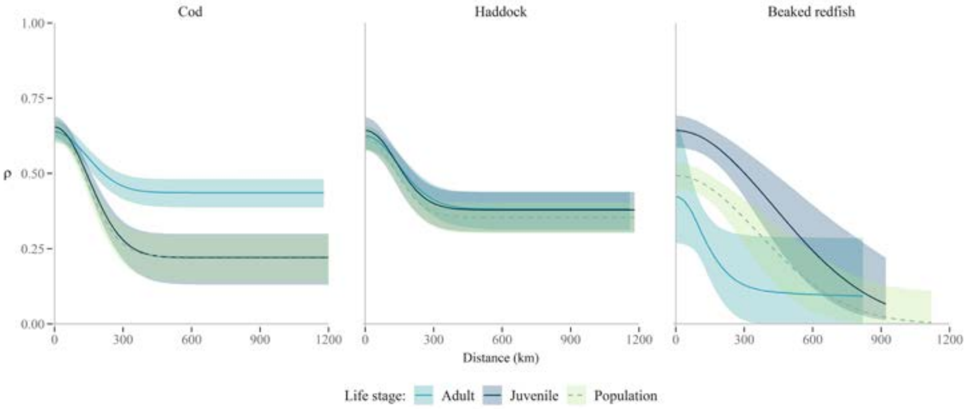


Figure 2. Decay of autocorrelation in density, ρ, with increased distance for three species of marine fish. The green dashed lines represent the spatial autocorrelation of the population density, while the solid dark and light blue lines represent the autocorrelation of the density of juveniles and adults, respectively. Smoothers represent the 95% intervals obtained from parametric bootstrap analyses.

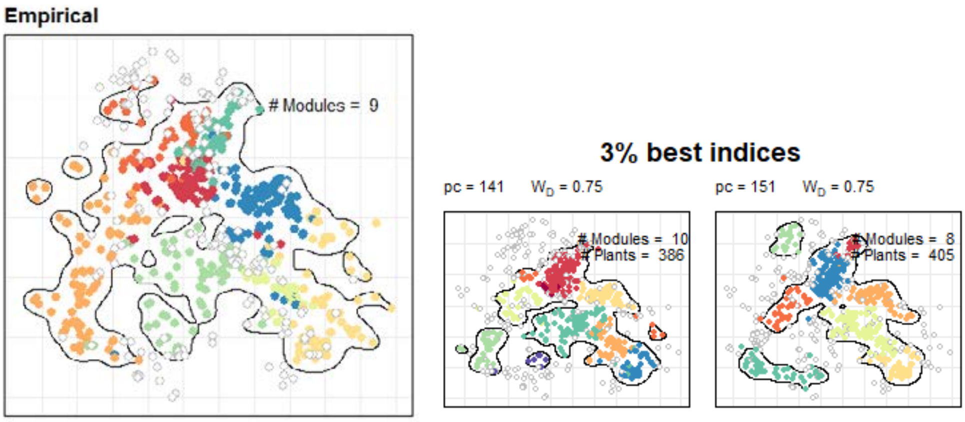


Figure 3. Spatial distribution of plants (circles) within the patch coloured according to sub-group (i.e. module in the network). In the best fit models (3% best indices), bumblebee foraging choice was highly dependent on the distance to nearby plants. This resulted in spatially distinct sub-groups of plants that were visited by the same bumblebee individuals and aligned with the spatial grouping of plants in the empirical data.

the spatial autocorrelation patterns of older age classes were partly explained by the density distribution of the cohort during the previous year. Our results indicate that differences in life history strategies between species play an important role in the spatial autocorrelation pattern of individual age classes. In addition, since different age classes can have different spatial autocorrelation, changes in age structure could indirectly alter the spatial synchrony pattern of the entire population. These differences among species in the patterns and underlying mechanisms of population synchrony could play a major role in how communities respond to environmental change.

Plant-pollinator interactions: do plant characteristics influence bumblebee movement?

Plant-pollinator interactions are crucial elements of many natural communities and gaining a better understanding of these interactions is essential for sustainable management. In Chudzinska et al. (2020), we investigated the movement patters of a pollinator to determine what influences their choices when moving from flower to flower within a patch of resources. We used a combination of agent-based modelling and network statistics to evaluate how small-scale, within-patch movement decisions of the bumblebee Bombus pascuorum are related to plant characteristics and the spatial distribution of resources. A key advantage of combining ABM and network statistics is the ability to capture emergent properties of animal movement using relatively simple and transparent sets of rules governing individual behaviours. Thus, we used network statistics to compare emergent patterns from the model with those derived from empirical data. Our results showed that local movement patterns of bumblebees can be modelled using simple foraging rules based on the spatial arrangement of flowers. Thus, distance to nearby plant was by far the most important factor in determining flower choice. Preference for neighbouring plants resulted in spatially distinct sub-areas within the patch that were repeatedly visited by the same set of bumblebee individuals (Figure 3).

RECOMMENDED READING:

Lee, A.M., Sæther, B.-E. and Engen, S. 2020. Spatial covariation of competing species in a fluctuating environment. Ecology 101, e02901.

Hansen, B.B., Grøtan, V., Herfindal, I. and Lee, A.M. (2020), The Moran effect revisited: spatial population synchrony under global warming. Ecography, 43: 1591-1602

Chudzinska, M., Dupont, Y.L., Nabe-Nielsen, J., Maia, K.P., Henriksen, M.V., Rasmussen, C., Kissling, W.D., Hagen, M., Trøjelsgaard, K. 2020. Combining the strengths of agent-based modelling and network statistics to understand animal movement and interactions with resources: example from within-patch foraging decisions of bumblebees. Ecological Modelling, 430, 109119, https://doi.org/10.1016/j.ecolmodel.2020.109119.

NEW IN TRONDHEIM

Cameron Ghalambor, August 2020

From Colorado to Trondheim

I joined CBD in August 2020 after spending the last 17 years at Colorado State University. I consider myself to be an integrative evolutionary ecologist – which means I'm interested in how organisms behaviorally and physiologically respond to the environment and how these responses influence subsequent ecological and evolutionary change. My research interests are fairly broad, and I'm most excited by questions at the intersection of evolution, ecology, physiology, and behavior. I have current projects on microgeographic adaptation in morphology and physiology in birds, the role of phenotypic plasticity in rapid evolution of fish, trade-offs between physiological tolerance and biotic interactions with competitors, predators, and parasites in insects and fish, and the physiological correlates of vulnerability to global change in ectotherms.

I was drawn to CBD and Biology at NTNU because so many researchers are interested in similar questions, making the transition a very exciting and natural one.

However, moving from the United States to Norway during a global pandemic was certainly challenging and it wasn't obvious my family and I would be able to travel until a month before our departure. Fortunately, my wonderful new colleagues in CBD made the transition an easy one once we arrived. While there is a lot for me to learn, I'm looking forward to the new opportunities ahead.

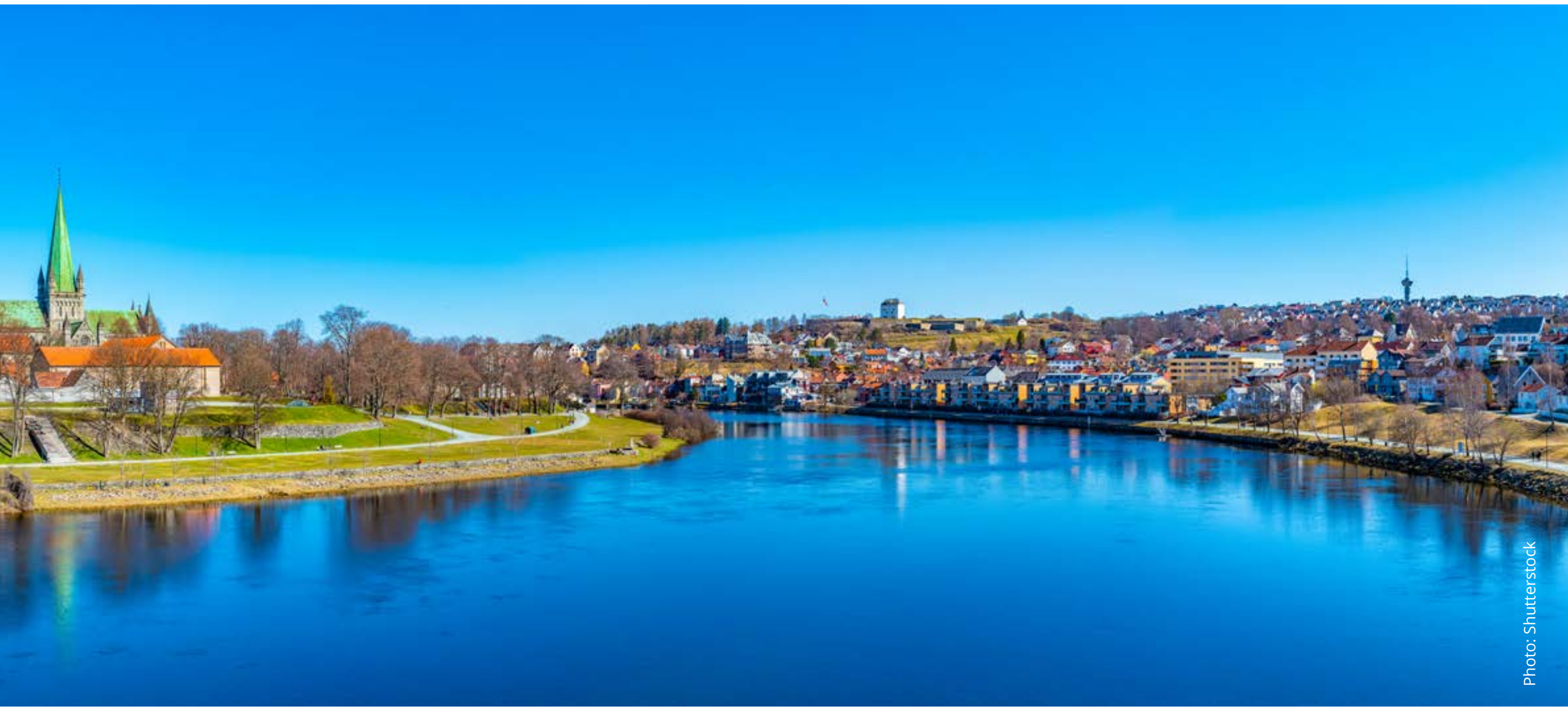
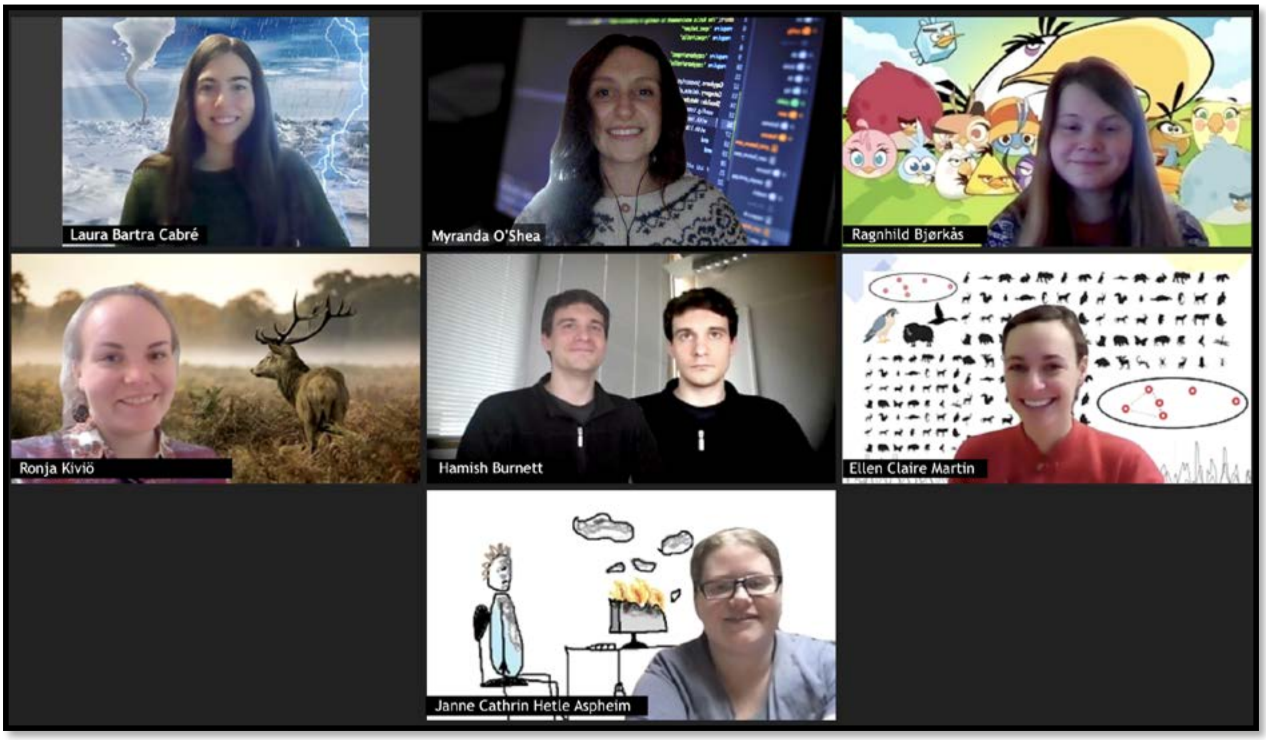


Photo: Shutterstock

Laura, Myranda, Ragnhild, Ronja, Hamish, Ellen and Janne

New PhDs



2020 will forever be burned in our collective memories as the year we started our PhDs during a pandemic. This year was challenging for people around the world, undoubtedly, but we also must take the opportunity for some self-pity to be starting this daunting chapter of our lives digitally (note: four years from now when we are all asking for extensions, give us some sympathy…). As a group of new PhD students in CBD, we mostly know one another through Zoom calls and some strained digital "coffee breaks". We used this annual report as an opportunity to get to know one another through one-on-one interviews. Below you will find brief highlights of the digital hollowed out husks of new humans at CBD:

Laura Bartra Cabré

Amidst the chaos of 2020, Laura focuses on the good things that came about in her life this year. For one thing, she's here. On the day of her master's defense, just as she was celebrating one milestone, she found out she would be starting a new and exciting journey with CBD. Within a month she was up in Svalbard assisting with field work and scouting for polar bears. Laura is no stranger to all that Norway has to offer – she first came to Norway on Erasmus in Telemark wanting to escape the summer heat and the tourists back home in Barcelona. Motivated by research opportunities and the landscape, she came back for a master's degree at NMBU. Laura arrived in Trondheim in late summer, and like many of us, experienced the empty corridors of D1 with only the sound of her footsteps for company… But it didn't take her long to find other PhD candidates lurking about and adapt to connecting with other colleagues over Zoom. Setting into her life in Trondheim, Laura describes her year as a logistic function (with a bit of pandemic noise) and looks forward to what lies ahead and continuing her research on the community-wide effects of extreme climatic events. In her spare time, you can find her doing yoga and pilates to decompress.

- *Myranda O'Shea*

Hamish Burnett

Technically, Hamish is no stranger to CBD, and the heading `New at CBD' doesn't quite give justice to the great work Hamish has accomplished in the few years he has already been here. Hamish moved to Trondheim from Perth, Australia (pronounced Paaaaaaath) to study reindeer for his Master's degree in 2018. He has remained in Trondheim ever since. Although `Biologist' is a far cry from his childhood dream of being a pilot (didn`t work out, a little too colorblind), Hamish is doing his best to make this new career path as interesting as possible, from field visits in Svalbard, to spotting teeny tiny bands on legs of teeny tiny birds on islands in Helgeland. During COVID, Hamish has really learned to appreciate the small things, and in particular, those small things that Norway has to offer that were never taken from us during the pandemic. His favorite memories from the past year happened when chasing the Northern Lights in Bymarka. In fact, if you look closely on his Zoom background, you can see a picture he took of the lights dancing over Trondheim silhouetting him during the many, many, many Zoom calls which now dominate our lives. All in all, Hamish remains optimistic and shockingly positive for someone who comes to an empty office to think about the great mysteries of the sparrows every day. Welcome Hamish, we are glad to have your institutional knowledge and positivity to help the rest of us out along the way!

- *Ellen Martin*

Janne Cathrin Hetle Aspheim

Janne is an infiltrated computer expert that joined the CBD family of biologists at the end of last summer. Despite not having a biological background, Janne is enjoying more and more working with quantitative genetics, so hopefully she'll stay in the right path, helping us understanding nature. Surprisingly, she did not find a great difference between her life in the tiny (and boring) Ås and the city of Trondheim, but she does appreciate that now it is way easier for her to get a haircut. She actually managed to go through corona times as if not much had changed, as she continues sitting in front of her computer, looking at her numbers, and, from time to time, eating some ice-cream while she cries a little. However, 2020 combined with Trondheim gave her the opportunity to live a simple life in a caravan, a few meters from her beloved retired 24-year-old horse that keeps her company and sane. Not bad! She describes her past year as y = 0 function: not much going on, but consistent and comfortable. We are so glad you joined CBD and showed everyone how important it is to always keep a sense of humour!

- *Laura Bartra Cabré*

Myranda O'Shea

Myranda comes from a small town in Ontario, Canada. After taking a bachelor's degree in biology, she moved to Toronto and took a hiatus from science. At some point she started taking classes in statistics and big data but wished there were more biology-related examples. She and her partner decided to continue with their education but were also growing tired of life in the city, so they Googled "nice places to study" and ended up applying to master's programs at NTNU. They agreed that if they both got accepted, they should go for it. After they both simultaneously got their acceptance letters, they reacted with: "Oh snap, we're moving to Norway!". During her master's in natural resource management at NTNU, the final stages of her thesis felt more like the beginning rather than an end, so she was thrilled when a related PhD position opened up at the CBD focusing on social interactions, demographic covariance in fitness and evolutionary rescue. Doing a PhD is never just fun and games, and she feels that the supervisors and the people around her are the key to keeping the motivation up. Myranda likes to spend her free time skiing, hiking and enjoying the company of her German Shepard mix, Lady. She loves to have nature right outside her front door. When asked to sum up the past year by using a mathematical function, she describes it as a sine-function. Lots of peaks and valleys.

- *Janne Cathrin Hetle Aspheim*

Ellen Claire Martin

Coming from Alaska via Switzerland, where she worked for the IUCN Greenlist program, Ellen moved to Trondheim to start her PhD at CBD in 2020. She applied for the position for the chance to expand her research from shorebirds to bigger systems and was attracted by the research going on here at CBD. It happened to be a lucky coincidence that Norway also reminds her of home in Alaska in many ways – particularly the smell of the forests and bogs which she finds especially comforting with the travel restrictions preventing her from visiting home. That said, she claims the northern lights are better in Alaska (where they actually have clear skies more than a handful of days each year!), and laments the difficulty in finding a good coffee shop that hasn't shut down permanently due to COVID here in Trondheim. Despite the difficulties of moving to a new country during a pandemic, Ellen has appreciated the fact it encouraged her to take holidays around Norway instead of abroad, so she's had the opportunity to see much more of this beautiful country than she would have otherwise! Welcome Ellen, and hopefully someone can point you to a good coffee shop!

- *Hamish Burnett*

Ragnhild Bjørkås

Ragnhild grew up in a small place in Northern Norway called Sørreisa, but lived in Tromsø for the past 8 years. She has a master's degree in terrestrial ecology from UiT Arctic University of Norway. After graduation she worked as a research technician for a couple of years. In her PhD, she is studying interspecific population synchrony and how this is affected by species interactions. She is using data on the very diverse bird community of Serengeti, which is super exciting! CBD has turned out to be a nice place to be surrounded with nice people. Even though she started in the middle of corona in April 2020 and the only possible way to meet colleagues was on Zoom, she felt very welcome. However, she looks forward to be able to spend more time at the office in the future. When not at the (home) office, Ragnhild enjoys hiking, knitting and meeting friends. The first one turned out to be a quite corona friendly hobby, the second hobby she started because it was corona friendly, while the last one has been slightly more challenging during corona... Even though she would prefer life without corona (who wouldn't?), it turns out that there are still many things that we can do. She has, for instance, learned to bake bread. Corona has also made us all appreciate "normal" life even more!

- Ronja Kiviö

Ronja Kiviö

Ronja grew up in the southern coast of Finland in Turku but did her studies in the University of Jyväskylä majoring in ecology and evolutionary biology. After graduation she started looking for job opportunities and ended up here in Trondheim in November 2020. She's doing her PhD on exploring the potential of using genetic information in cervid monitoring and management as a collaboration between NINA and CBD. Ronja hadn't visited Trondheim before moving here and was delighted to find out that it has the big city feeling wrapped up in a compact package. This means she gets to have all the perks of living in a big city but the nature is present in everyday life. Even though COVID has hindered the formation of social bonds, Ronja has been positively surprised by how many new people she has got to know in her brief time here and has enjoyed the welcoming environment both in NINA and CBD. In her free time, she likes to hike, play her accordion or saxophone (sadly the accordion still remains behind in Finland), reading a good book or doing arts and crafts.

- Ragnhild Bjørkås

Chloe Rebecca Nater, April 2020

Drifting fog – or “moving home and work in 2020”

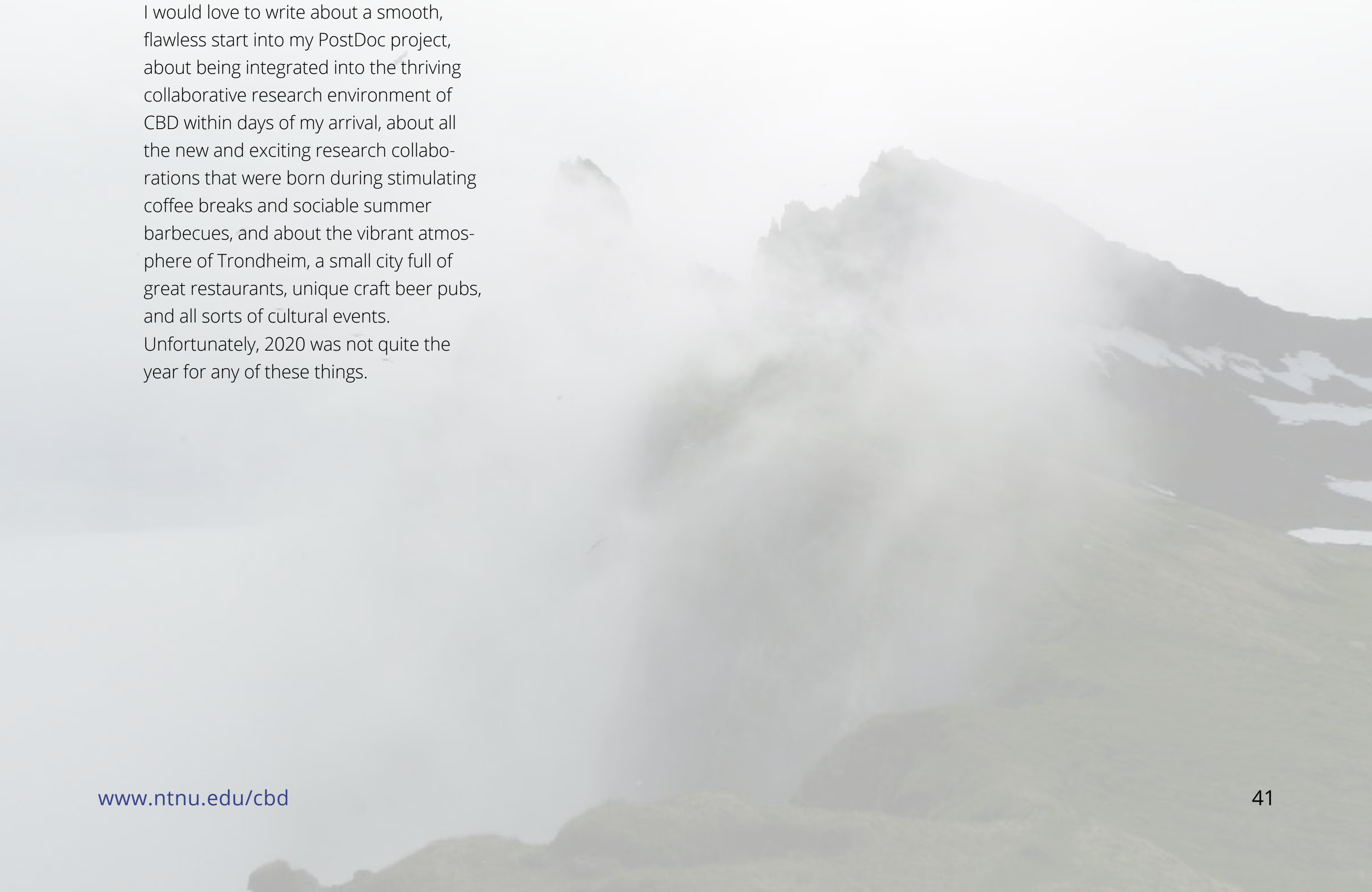
I started my PostDoc at CBD on 1. April. No joke, even though it did – at times – feel a bit like one since it wasn't just any 1. April. It was 1. April 2020.

When I arrived in Trondheim at the end of March, Norway had been in the first corona-lockdown for a bit over a fortnight. The first piece of furniture I got for my new place was an adjustable home office desk, from which I started making plans for my new projects and had countless online meetings with “local” colleagues that I would not meet for two, three, four or even more months to come. On some days, the rapidly changing Trondheim April weather was the only thing reminding me that time had not come to a halt entirely.

I would love to write about a smooth, flawless start into my PostDoc project, about being integrated into the thriving collaborative research environment of CBD within days of my arrival, about all the new and exciting research collaborations that were born during stimulating coffee breaks and sociable summer barbecues, and about the vibrant atmosphere of Trondheim, a small city full of great restaurants, unique craft beer pubs, and all sorts of cultural events. Unfortunately, 2020 was not quite the year for any of these things.

My 2020 as a new PostDoc in a new work environment and a new city reminded me a lot of the place that made me decide to become an ecologist in the first place: the Icelandic Westfjords, where sunlight and thick fog trade places in a matter of minutes. When the fog thickens you slow down, lay low, and plan for once it clears. You keep going, because those sunlit moments in between totally make it worth your while, time and time again. Among my sunlit moments in 2020 were many actual walks and kayak trips in the sun, but also a bike trip with CBD that finally allowed me to meet some of my colleagues, summer picnics in the park, occasional in-person presentations and (scientific) discussions, and the EvoDemoS conference in Røros just before the next lockdown.

After a year of drifting fog, I still feel kind of “new at CBD” and “new in Trondheim”, but this also means I get to hold on to this feeling of excitement about what the next sunny day will bring.



Paul Acker, September 2020

MIGRATING FURTHER NORTH

In mid-September 2020, I joined CBD for a 4-year postdoc, after having spent two years in Scotland where I started studying the eco-evolutionary dynamics underlying migration. Before moving to Scotland, I spent a year in Paris. And before that, I was living in Toulouse, where I did my PhD on habitat selection and dispersal movements. I often get asked if my own research explains everyone's prediction that my next stopover is Tromsø and I will end up finding residence in Svalbard!

I arrived in Trondheim just on time to enjoy some authorised professional and social interactions for a couple of months, before covid-19 eventually stroke back and predominance of home office was enforced again. But no doubts that we've been very lucky here so far; meanwhile, it has been almost a year that my former colleagues in Aberdeen have not had the opportunity to go in their office...

CBD members warmly welcomed me, and soon after my arrival we left for Røros to attend the stimulating conference of the evolutionary demography society. I quickly got to meet all my new colleagues, dive in a wide breadth of relevant topics, connect with the international community, and get a hint of Norwegian culture. And when restrictions came back, CBD members have been able to maintain common work life through seminars, regular meetings, and other initiatives online.

So, avoiding negative consequences of the virus down south was certainly not the only benefit of migrating further north that I could foresee before starting my job at NTNU. CBD is one of these institutes which can claim title of "the place to be" for a scientist in my field. Overall, I am very much enjoying working here, and still excited by my professional and personal times ahead in Norway!

Agnes Holstad and Salomé Bourg

FROM SUSHI TO ENTHUSIASTIC DISCUSSIONS

We used the winter to migrate from Oslo to darker and colder regions: Trondheim. One of us (Agnes) is Norwegian and already particularly suited to this habitat since she studied at NTNU for many years. Temperature, day light and Norwegian behaviours are ordinary habits that naturally run through her veins. The second (Salomé), which is expanding the French mafia that already has invaded the CBD, is still trying to adapt to Norwegian habits. At the present time, she still refuses to eat like them, insisting that tube food is not a meal and struggles to master the art of braking in cross-country skiing.

We worked together in Oslo for a year at the Centre for Advanced Study (CAS) on the Evolvability project, where we got the terrible habit of eating sushi for every lunch. We had the chance to meet, on a daily basis, distinguished researchers (such as David Houle, Michael Morissey, James Cheverud, Laura Nuño de la Rosa among others) working on quantitative genetics and evolutionary biology. Our intensive training around questions related to evolvability was co-supervised by Christophe Pélabon and Thomas F. Hansen with whom we are lucky to collaborate today.

After these 12 months surrounded by geniuses (of an average advanced ages) and sometimes endless philosophical discussions, we are delighted to integrate the CBD, its teams full of PhD students and post-docs and its lunchtime filled with enthusiastic discussions. Due to the current situation, we have not yet had the chance to make the most of the CBD dynamism. Nevertheless, we have heard rumours of its greatness and look forward to better times to continue our integration into this department which already sounds like a new scientific family for us.

Oh oops.. We are also here to work. So, Agnes started her PhD by computing a meta-analysis on evolvability and divergence. Over the next few years, she will continue to explore patterns of short-term evolvability on quantitative traits. Salomé continues her post-doc as a modeller and is currently working on the role of complexity and architectural genetic constraints on evolvability.

6 TIPS TO SURVIVE CORONA

1. Good heating in your house (and preferably a puppy to sit on your feet under the desk).
2. Coffee machine at home (or a good coffee shop nearby).
3. Accept that the world is a dark and gloomy place so that we can all evolve into the disillusioned shadows of ourselves that we are destined to become. And wine.
4. Avoid in-person teaching if you don’t want to get repeatedly quarantined and the only open coffee shop on campus if you do not want to get repeatedly corona tested.
5. Use a fun Zoom background. Other people will ask about it and the “small talk” before each video meeting doesn’t get that awkward.
6. Keep in touch with other people as much as you can, even if it was only through zoom etc.

WORKSHOPS AND CONFERENCES 2020

NORDIC SOCIETY OIKOS CONFERENCE IN REYKJAVIK

The 4th biannual conference of the Nordic Society Oikos, hosted by the Icelandic Ecological Society, was held in Reykjavik, Iceland, from the 2nd to the 5th of March. Before the main conference started, the Oikos journal hosted the Per Brinck symposium, which revolved around the topic of ecological networks. Themed “Ecology in the Anthropocene”, this year’s Oikos conference had a major focus on human impacts on ecology and evolution. The Centre for Biodiversity Dynamics, which was involved in the organization of the previous conference in Trondheim, took the opportunity to share its latest research with other researchers from across all Nordic countries. The conference was attended by around 350 participants, and 150 talks and 130 posters were presented. CBD was well represented among the participants; over a dozen of our researchers and students contributed with talks and posters.

During the conference, excursions were organized to visit some of the local gems, such as the natural history museum in Perlan, a prominent landmark overlooking Reykjavik, and the “smoking” Reykjanes peninsula, southwest of the capital. Iceland truly represented a completely new and unique landscape for many of us! CBD would like to congratulate the organizers of this conference for their amazing job.

INDIVIDUAL HETEROGENEITY IN ANIMALS' LIFE HISTORIES – MORE THAN MEETS THE EYE

Stéphanie Jenouvrier and Bernt-Erik Sæther organized the first workshop, entitled *"Prediction of climate change effects on the dynamics of species with complex life histories",* in Trondheim in December 2019. It brought together population ecologists (both theoreticians and empiricists) from Europe and North America. The main goals of the workshop were to construct population models to assess the dynamical consequences of individual heterogeneity in demography for a large range of species along the slow-fast continuum of life history variation. The second edition was held in the Netherlands, at the Lorentz Center in Leiden, February 3-7 2020.

Lorentz center
Workshop @Snellius

Individual Heterogeneity in Animal's Life Histories

3 February - 7 February 2020, Leiden, the Netherlands

Scientific Organizers

- Martijn van de Pol, Netherlands Institute of Ecology
- Stephanie Jenouvrier, Woods Hole Oceanographic Institution
- Sandra Hamel, Laval University
- Bernt-Erik Sæther, Norwegian University of Science and Technology

Topics

- Quantify Unobserved Individual Heterogeneity in Life-History Traits
- Compare Intraspecific Patterns of Heterogeneity across Species
- Implications of Intraspecific Heterogeneity for Life-History Evolution and Population Ecology

The objectives of the workshop were to:

- Quantify individual heterogeneity in vital rates along the slow-fast continuum of life histories and across environmental conditions;
- Study the relative importance of individual heterogeneity and individual stochasticity in the variance of life history outcomes;
- Understand the impact of individual heterogeneity on population dynamics.

In addition to Stéphanie Jenouvrier and Bernt-Erik Sæther, Matthieu Authier, Emmanuelle Cam, Sandra Hamel, and Martijn van de Pol played a key role in organizing this second workshop.

Nearly 20 researchers were present with access to some of the most extensive datasets of individual-based demography that exist for any species.

This workshop was very fruitful. It resulted in several advances, including:

1. A simulation study quantifying individual heterogeneity in vital rates for contrasting life histories;
2. A multi-species comparison including some of the longest datasets of individual-based data in vertebrates;
3. A study investing temporal variation and covariation in vital rates along the slow-fast continuum of life history variation.

This workshop was also the starting point of Rémi Fay's postdoc at CBD, who now successfully leads these studies!

Photo: Brage Bremset Hansen

EvoDemo7

The 7th Annual Meeting of the Evolutionary Demography Society, EvoDemo7, was hosted in UNESCO's World Heritage site of Røros, Norway, between the 6th and 11th of October. The EvoDemo7 meeting was organized by Bernt-Erik Sæther, Lisbeth Pedersen, Stefan Vriend and Jonatan Marquez (CBD) with the financial support from The Norwegian Environmental Agency and the Norwegian Research Council.

The Evolutionary Demography Society organizes the annual meeting to give researchers from various fields, such as ecology, evolutionary biology, genetics, demography and epidemiology, an opportunity to present their research, share ideas and develop new collaborations. This year's meeting had a particular focus on Evolutionary Demography under Global Change. Due to this year's special circumstances, this annual meeting was the first that combined physical and virtual attendance.

Even though the organizing team was posed with a few new and unexpected challenges, the attendance of EvoDemo7 exceeded all expectations, welcoming 108 participants, of which 75 attended virtually, and hosting a total of 70 talks, including 13 keynote addresses from world leading scientists. All talks were live-streamed and questions to presenters and communication between attendants happened on an online platform. Participants connected to the live stream from at least 17 countries and represented more than 53 organizations. Despite the distance between participants, the discussions and interactions on the online platform came very close to the familiarity of physical conferences.

In addition to the talks, two workshops were held: Eco-evolutionary consequences of harvesting in a changing environment, organized by Bart Peeters, Lara Veylit and Marlène Gamelon, and Quantifying plastic and genetic responses to (multivariate) traits changes in communities, organized by Lynn Govaert and Christophe Coste. The introductions by the organizers spurred some interesting discussions and most likely sparked new research ideas and collaborations.

The lucky participants that had the opportunity of attending physically had the chance to explore some of the secrets of the UNESCO's World Heritage site of Røros through guided tours of the town, the old Olav's Mine and local art galleries. The more adventurous had the chance to go on a dog sledding tour through the local landscape.

The recordings from all presentations have been stored online, so that participants can revisit them at any time. More information about EvoDemo7 can be found at https://evodemo7.weebly.com.

Bernt-Erik Sæther opening EvoDemo7

The Auditorium

Excusion to Røros Museum –
Olav's Mine

NATIONAL AND INTERNATIONAL COLLABORATION

Collaboration between researchers at CBD with colleagues in Norway as well as abroad is essential for the fulfilment of many of the research goals of CBD, emphasizing the integration of models with empirical data. In 2020 such collaboration in person became almost impossible because of travel restrictions imposed due to the Corona-pandemic. Although the use of different virtual platforms has been extensive, it is now obvious that they could not fully replace the advantages of contacts in person. Still, most of the networks of research interactions involving CBD-members were maintained during this difficult period.

A Lorentz Center workshop was organized by Sandra Hamel, Stephanie Jenouvrier, Martijn van de Pol and Bernt-Erik Sæther on the topic Individual Heterogeneity in Animal's Life Histories – More than Meets the Eye in Leiden, the Netherlands during February 3-7 2020. The main goal was to assemble a community of researchers, following up the previous workshop in Trondheim in December 2019, to perform the first large-scale analysis of unobserved individual differences in vital rates using standardized statistical approaches. A central aim of these analyses was to provide a comprehensive overview of the relative importance of both observed and unobserved heterogeneity for life-history strategies within species, for a group of species that are situated along the slow-fast continuum. Such individual heterogeneity in demography causes a huge challenge when predicting population responses to changes in the environment (e.g. caused by climate change) because it potentially introduces time lags in the population dynamics. This makes it difficult to distinguish the dynamical consequences of environmental variation from those caused by individual heterogeneity in demography. The program was a productive mixture of plenary lectures, discussion session and hands-on sessions to analyze the long-term dataset that people brought from their study system. This successful workshop resulted in that several working groups were established, dealing with different key topics identified during the discussions at the meeting.

Under the leadership of professor Thomas F. Hansen, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, and professor Christophe Pelabon, CBD, a Center of Advanced Study (CAS) at the Norwegian Academy of Science and Letters in Oslo for the academic year of 2019/2020 was organized for the project Evolvability: A New and Unifying Concept in Evolutionary Biology? This CAS, involving several researchers located both in Oslo and at CBD, brought in a large number of international visitors before the close-down due to the Corona pandemic. However, by an extensive use of virtual platforms the organizers enabled to reach their scientific goals of the project. Several of the networks of researchers established during this CAS-year are still very active with weekly virtual meetings, involving large numbers of scientists from almost all parts of the world.

CBD continued also in 2020 its large involvement in the SPI-Birds Network and Database, which is a community-driven initiative that is successfully connecting researchers working on Studies of Populations of Individual birds located at the Netherlands Institute of Ecology (NIOO) in Wageningen, the Netherlands. Two members of CBD (Chloe Rebecca Nater and Stephan G.J. Vriend) have been heavily involved in creating tailored pipelines to convert each unique data set into a standard format, and to provide a platform to find and access these datasets. For further description of this working model for data standardisation, exchange, and integration, facilitating international collaboration among researchers, see the paper from 2020 by Antica Culina et al. in the Journal of Animal Ecology.

Members of CBD have been heavily involved in many national collaborative actions with researchers from many Norwegian universities and applied research institutions. Many of those interactions were established through the large integrated project SUSTAIN, e.g. involving analyses of ecosystem processes in the Arctic, harvest strategies of interacting marine fish species in the Barents Sea and dynamics of biological diversity in a changing environment.

Popular Science

Several of the results obtained at CBD have relevance for the management of biodiversity in Norway.

In 2020, CBD-members have therefore presented their results on several occasions to management agencies at different levels. For example, a lecture on principles for the design of national monitoring programmes for biodiversity was given on a workshop organized by the Norwegian Environmental Agency. Input on how to implement predictive models in practical management of biodiversity has also been provided. Furthermore, researchers at CBD are members of several board and committees appointed by different management agencies. For example, the director is member of the Scientific Council for the National Monitoring Programme of Carnivores in Norway, Sigurd Einum is a member of the Norwegian Scientific Advisory Committee for Atlantic Salmon and Jane Reid acts as a scientific adviser to NatureScot, through the Scottish Chough Forum. In addition, Anders G. Finstad is member of the Scientific Committee in the Global Biodiversity Information Facility, GBIF.

Members of the CBD attracted attention in the public media. For example, the director was involved in a newspaper chronicle arguing for the necessity to increase the public funding for monitoring of biodiversity, and in another chronicle arguing for the importance of easing access to universities, especially for younger researchers, during the lock-down due to the Corona-pandemic. Research at CBD was also presented in a prime-time television show in NRK. Research from the Arctic ecosystem at Svalbard and the house sparrow studies at Helgeland, as well as the study on impact of highways on local and invasive fauna, received particular attention in national and international media, including forskning.no, Science Daily, ScienceMag, Nature World News, EOS (Science News by American Geophysical Union), Phys.org, as well as a number of Norwegian newspapers. Irja Ida Ratikainen and Aline Magdalena Lee are strongly involved in communicating science to the public through being responsible and authoring topics within ecology and ethology in the Norwegian online encyclopaedia “Store Norske Leksikon”, snl.no.

Red fox *(Vulpes vulpes)*

Photo: NINA / Lars Rød-Eriksen

PHD-DISSERTATIONS

Five PhD candidates defended their thesis at CBD in 2020:

February 28th	**Rachael Morgan** *"Physiological plasticity and evolution of thermal performance in zebrafish"*
Opponents:	Professor Suzanne Currie, Acadia University, Canada Associate Professor Felix Mark, Alfred Wegener Institute for Polar and Marine Research, Germany
April 3rd	**Yihan Cao** *"Statistical methods for estimating fluctuating selection"*
Opponents:	Professor Jarrod Hadfield, University of Edinburgh, UK Professor Hans J. Skaug, University of Bergen, Norway
May 22nd	**Kate Layton-Matthews** *"Demographic consequences of rapid climate change and density dependence in migratory Arctic geese"*
Opponents:	Professor Rolf Anker Ims, University of Tromsø, Norway Stephanie Jenouvrier, Woods Hole Oceanographic Institution, USA
June 12th	**Lars Rød-Eriksen** *"Drivers of change in meso-carnivore distributions in a northern ecosystem"*
Opponents:	Professor Emeritus Jon Swenson, NMBU, Norway Associate Professor Laura Prugh, University of Washington, USA
July 23th	**Maria Lie Selle** *«Novel statistical variance and dependency models in quantitative genetics: Enabled by recent inference methods»*
Opponents:	Professor Robert J. Tempelman, Department of Animal Science and Department of Statistics and Probability, Michigan State University, Michigan, USA Professor Janine Illian, School of Mathematics & Statistics, University of Glasgow, Glasgow, UK

KEY FIGURES 2020

GENDER EQUALITY

At CBD there is predomination of females in the earlier stages of a scientific career, which was strengthened by that 7 of 8 new graduate students hired in 2020 were females. In order to ease the transition from postdoc to faculty CBD, in collaboration with the Department of Biology offered female researchers the possibility to allocate a proportion of their time to undergraduate teaching. Hopefully, the success of younger females at CBD in competing internationally for attractive positions in research or for permanent faculty positions at Norwegian universities will also motivate young women for a career in science.

The Department of Biology has an Equal Opportunities Committee which includes two members from CBD.

KEY FIGURES

Key numbers in CBD	2020	
	F	M
Professors/Associate professors	5	22
Researchers	2	13
Postdocs	8	8
PhD candidates	25	16
Technical staff		3
Administration	3	
All staff at CBD	43	62
Total	105	
Scientific Advisory Board	1	5

Costs and funding	KNOK
Cost	
Salary and indir. cost	27 311
Other operating cost	3 031
Sum cost	30 342
Funding	
NFR	11 339
Other funding	500
NTNU	18 503
Sum funding	30 342

Funding associated projects	14 544

CBD MEMBERS

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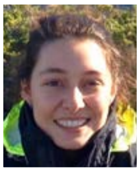

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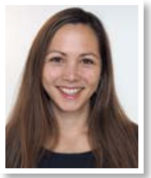

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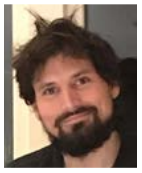

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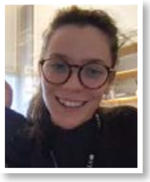

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cbd
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PUBLICATION LIST

Acker, P., Daunt, F., Wanless, S., Burthe, S.J., Newell, M.A., Harris, M.P., Grist, H., Sturgeon, J., Swann, R.L., Gunn, C., Payo-Payo, A., and Reid, J.M. 2020. Strong survival selection on seasonal migration versus residence induced by extreme climatic events. Journal of Animal Ecology, in press.

Albertsen, E., Opedal, Ø.H., Bolstad, G.H., Pérez-Barrales, R., Hansen, T.F., Pélabon, C., and Armbruster, W.S. 2020. Using ecological context to interpret spatiotemporal variation in natural selection. Evolution, 75, 294-309.

Araya-Ajoy, Y.G., Westneat, D.F., and Wright, J. 2020. Pathways to social evolution and their evolutionary feedbacks. Evolution, In press.

Ashwood, L.M., Norton, R.S., Undheim, E.A.B., Hurwood, D.A., and Prentis, P.J. 2020. Characterising functional venom profiles of anthozoans and medusozoans within their ecological context. Marine Drugs, 18, 202.

Bellier, E., Sæther, B.-E., and Engen, S. 2020. Sustainable strategies for harvesting predators and prey in a fluctuating environment. Ecological Modelling, in press.

Bowler, D.E., Kvasnes, M.A.J., Pedersen, H.C., Sandercock, B.K., and Nilsen, E.B. 2020. Impacts of predator-mediated interactions along a climatic gradient on the population dynamics of an alpine bird. Proceedings of the Royal Society B: Biological Sciences, 287, 20202653.

Broder, E.D., Ghalambor, C.K., Handelsman, C.A., Ruell, E.W., Reznick, D.N., and Angeloni, L.M. 2020. Rapid evolution and plasticity of genitalia. Journal of Evolutionary Biology, 33, 1361-1370.

Burgazzi, G., Laini, A., Ovaskainen, O., Saccò, M., Stubbington, R., and Viaroli, P. 2020. Communities in high definition: Spatial and environmental factors shape the micro-distribution of aquatic invertebrates. Freshwater Biology, In press.

Burton, T., and Einum, S. 2020. The old and the large may suffer disproportionately during episodes of high temperature: Evidence from a keystone zooplankton species. Conservation Physiology, 8, coaa038.

Burton, T., Lakka, H.-K., and Einum, S. 2020. Measuring phenotypes in fluctuating environments. Functional Ecology, 34, 606-615.

Burton, T., Lakka, H.-K., and Einum, S. 2020. Acclimation capacity and rate change through life in the zooplankton Daphnia. Proceedings. Biological Sciences, 287, 20200189.

Burton, T., Rollinson, N., McKelvey, S., Stewart, D.C., Armstrong, J.D., and Metcalfe, N.B. 2020. Adaptive maternal investment in the wild? Links between maternal growth trajectory and offspring size, growth, and survival in contrasting environments. American Naturalist, 195, 678-690.

Carlson, C.J., Chipperfield, J.D., Benito, B.M., Telford, R.J., and O'Hara, R.B. 2020. Species distribution models are inappropriate for COVID-19. Nature Ecology & Evolution 4, 770-771.

Chaverri, G., Araya-Ajoy, Y.G., and Sagot, M. 2020. Contact calling in context: intra- and intergroup variation in vocalization rates depend on a call's function. Behavioral Ecology and Sociobiology, 74, 57.

Chow, C.Y., Chin, Y.K.Y., Ma, L., Undheim, E.A.B., Herzig, V., and King, G.F. 2020. A selective NaV1.1 activator with potential for treatment of Dravet syndrome epilepsy. Biochemical Pharmacology, 181, 113991.

Coste, C.F.D., and Pavard, S. 2020. Analysis of a multitrait population projection matrix reveals the evolutionary and demographic effects of a life history trade-off. Ecological Modelling, 418, 108915.

Culina, A., Adriaensen, F., ..., Nater, C.R., ..., Sæther, B.-E., Vriend, S.J.G., ..., Erikstad, K.E., ..., and Visser, M.E. 2020. Connecting the data landscape of long-term ecological studies: The SPI-Birds data hub. Journal of Animal Ecology, In press.

Dallas, T.A., Antão, L.H., Pöyry, J., Leinonen, R., and Ovaskainen, O. 2020. Spatial synchrony is related to environmental change in Finnish moth communities. Proceedings of the Royal Society B: Biological Sciences, 287, 20200684.

Dawson, S.K., Berglund, H., Ovaskainen, O., Snäll, T., Jonsson, B.G., and Jönsson, M. 2020. Convergence of fungal traits over time in natural and forestry-fragmented patches. Biological Conservation, 251, 108789.

De Villemereuil, P., ..., Gamelon, M., ..., Kvalnes, T., ..., Tufto, J., and Chevin, L.-M. 2020. Fluctuating optimum and temporally variable selection on breeding date in birds and mammals. Proceedings of the National Academy of Sciences of the United States of America, 117, 31969–31978.

Dehnhard, N., Skei, J., Christensen-Dalsgaard, S., May, R., Halley, D., Ringsby, T.H., and Lorentsen, S.-H. 2020. Boat disturbance effects on moulting common eiders *Somateria mollissima*. Marine Biology, 167, 12.

Del Mar Delgado, M., ..., and Ovaskainen, O. 2020. Differences in spatial versus temporal reaction norms for spring and autumn phenological events. Proceedings of the National Academy of Sciences of the United States of America, 117, 31249–31258.

Dingemanse, N.J., Moiron, M., Araya-Ajoy, Y.G., Mouchet, A., and Abbey-Lee, R.N. 2020. Individual variation in age-dependent reproduction: Fast explorers live fast but senesce young? Journal of Animal Ecology, 89, 601-613.

Dingemanse, N.J., and Wright, J. 2020. Criteria for acceptable studies of animal personality and behavioural syndromes. Ethology, 126, 865–869.

Engen, S., Wright, J., Araya-Ajoy, Y.G., and Sæther, B.-E. 2020. Phenotypic evolution in stochastic environments: The contribution of frequency- and density-dependent selection. Evolution, 74, 1923–1941.

Englund, G., Öhlund, G., Olajos, F., Finstad, A.G., Bellard, C., and Hugueny, B. 2020. Holocene extinctions of a top predator-Effects of time, habitat area and habitat subdivision. Journal of Animal Ecology, 89, 1202-1215.

Fenn, S.R., Bignal, E.M., Trask, A.E., McCracken, D.I., Monaghan, P., and Reid, J.M. 2020. Collateral benefits of targeted supplementary feeding on demography and growth rate of a threatened population. Journal of Applied Ecology, 57, 2212-2221.

Fjelldal, M.A., Layton-Matthews, K., Lee, A.M., Grøtan, V., Loonen, M.J.J.E., and Hansen, B.B. 2020. High-Arctic family planning: Earlier spring onset advances age at first reproduction in barnacle geese. Biology Letters, 16, 20200075.

Fort, T., Pauvert, C., Zanne, A.E., Ovaskainen, O., Caignard, T., Barret, M., Compant, S., Hampe, A., Delzon, S., and Vacher, C. 2020. Maternal effects shape the seed mycobiome in Quercus petraea. New Phytologist, In press.

Freckleton, R.P., Ellison, A., Liow, L.H., and O'Hara, R.B. 2020. Ten years of Methods in Ecology and Evolution. Methods in Ecology and Evolution, 11, 4–5.

Froy, H., and Gamelon, M. 2020. Late-life costs of raising sons in bighorn sheep. Proceedings of the National Academy of Sciences of the United States of America, 117, 5556-5558.

Gamelon, M., Filli, F., Sæther, B.-E., and Herfindal, I. 2020. Multi-event capture-recapture analysis in Alpine chamois reveals contrasting responses to interspecific competition, within and between populations. Journal of Animal Ecology, 89, 2279-2289.

Gamelon, M., and Froy, H. 2020. Biodemography: Unifying concepts from biology, demography, and mathematics. Trends in Ecology & Evoluton, 35, 475-476.

Gomo, G., Rød-Eriksen, L., Andreassen, H.P., Mattisson, J., Odden, M., Devineau, O., and Eide, N.E. 2020. Scavenger community structure along an environmental gradient from boreal forest to alpine tundra in Scandinavia. Ecology and Evolution, 10, 12860-12869.

Hagen, I.J., Lien, S., Billing, A.M., Elgvin, T.O., Trier, C., Niskanen, A.K., Tarka, M., Slate, J., Sætre, G.-P., and Jensen, H. 2020. A genome-wide linkage map for the house sparrow (Passer domesticus) provides insights into the evolutionary history of the avian genome. Molecular Ecology Resources, 20, 544-559.

Hamilton, B.R., Marshall, D.L., Casewell, N.R., Harrison, R.A., Blanksby, S.J., and Undheim, E.A.B. 2020. Mapping enzyme activity on tissue by functional-mass spectrometry imaging. Angewandte Chemie International Edition, 59, 3855-3858.

Hansen, B.B., Grøtan, V., Herfindal, I., and Lee, A.M. 2020. The Moran effect revisited: spatial population synchrony under global warming. Ecography, 43, 1591-1602.

Helsen, K., Acharya, K.P., Graae, B.J., Kort, H. de, Brunet, J., Chabrerie, O., Cousins, S.A.O., Frenne, P. de, Hermy, M., Verheyen, K., and Pélabon, C. 2020. Earlier onset of flowering and increased reproductive allocation of an annual invasive plant in the north of its novel range. Annals of Botany, 126, 1005–1016.

Hemphill, E.J.K., Flagstad, Ø., Jensen, H., Norén, K., Wallén, J.F., Landa, A., Angerbjörn, A., and Eide, N.E. 2020. Genetic consequences of conservation action: Restoring the arctic fox (Vulpes lagopus) population in Scandinavia. Biological Conservation, 248, 108534.

Herfindal, I., Tveraa, T., Stien, A., Solberg, E.J., and Grøtan, V. 2020. When does weather synchronise life history traits? Spatiotemporal patterns in juvenile body mass of two ungulates. Journal of Animal Ecology, 89, 1419-1432.

Hilde, C.H., Gamelon, M., Sæther, B.-E., Gaillard, J.-M., Yoccoz, N.G., and Pélabon, C. 2020. The demographic buffering hypothesis: evidence and challenges. Trends in Ecology & Evoluton, 35, 523-538.

Holand, H., Kvalnes, T., Røed, K.H., Holand, Ø., Sæther, B.-E., and Kumpula, J. 2020. Stabilizing selection and adaptive evolution in a combination of two traits in an arctic ungulate. Evolution, 74, 103-115.

Haaland, T.R., Wright, J., and Ratikainen, I.I. 2020. Generalists versus specialists in fluctuating environments: a bet-hedging perspective. Oikos, 129, 879-890.

Israelsen, M.F., Eriksen, L.F., Moa, P.F., Hagen, B.R., and Nilsen, E.B. 2020. Survival and cause-specific mortality of harvested willow ptarmigan (Lagopus lagopus) in central Norway. Ecology and Evolution, 10, 11144-11154.

Issa, S., Ciesielski, T.M., Mikkelsen, Ø., Einum, S., and Jaspers, V.L.B. 2020. Biofilms grown in aquatic microcosms affect mercury and selenium accumulation in Daphnia. Ecotoxicology, 29, 485–492.

Issa, S., Gamelon, M., Ciesielski, T.M., Vike-Jonas, K., Asimakopoulos, A.G., Jaspers, V.L.B., and Einum, S. 2020. Dopamine mediates life-history responses to food abundance in Daphnia. Proceedings of the Royal Society B: Biological Sciences, 287, 20201069.

Isaac, N.J.B., Jarzyna, M.A., Keil, P., Dambly, L.I., Boersch-Supan, P.H., Browning, E., Freeman, S.N., Golding, N., Guillera-Arroita, G., Henry, P.A., Jarvis, S., Lahoz-Monfort, J., Pagel, J., Pescott, O.L., Schmucki, R., Simmonds, E.G., and O'Hara, R.B. 2020. Data integration for large-scale models of species distribution. Trends in Ecology & Evoluton, 35, 56-67.

Jarillo, J., Sæther, B.-E., Engen, S., and Cao-García, F.J. 2020. Spatial scales of population synchrony in predator-prey systems. American Naturalist, 195, 216-230.

Juárez, R., Araya-Ajoy, Y.G., Barrantes, G., and Sandoval, L. 2020. House Wrens Troglodytes aedon reduce repertoire size and change song element frequencies in response to anthropogenic noise. Ibis, in press.

Järnegren, J., Brooke, S., and Jensen, H. 2020. Effects and recovery of larvae of the cold-water coral Lophelia pertusa (Desmophyllum pertusum) exposed to suspended bentonite, barite and drill cuttings. Marine Environmental Research, 158, 104996.

Kroeger, S.B., Blumstein, D.T., Armitage, K.B., Reid, J.M., and Martin, J.G.A. 2020. Older mothers produce more successful daughters. Proceedings of the National Academy of Sciences of the United States of America, 117, 4809-4814.

Layton-Matthews, K., Grøtan, V., Hansen, B.B., Loonen, M.J.J.E., Fuglei, E., and Childs, D.Z. 2020. Environmental change reduces body condition, but not population growth, in a high-arctic herbivore. Ecology Letters, in press.

Le Moullec, M., Sandal, L., Grøtan, V., Buchwal, A., and Hansen, B.B. 2020. Climate synchronises shrub growth across a high-arctic archipelago: contrasting implications of summer and winter warming. Oikos, 129, 1012-1027.

Le Pepke, M., and Eisenberg, D.T. 2020. Accounting for phylogenetic relatedness in cross-species analyses of telomere shortening rates. Experimental Results, 1, E11.

Lee, A.M., Myhre, A.M., Markussen, S.S., Engen, S., Solberg, E.J., Haanes, H., Røed, K.H., Herfindal, I., Heim, M., and Sæther, B.-E. 2020. Decomposing demographic contributions to the effective population size with moose as a case study. Molecular Ecology, 29, 56-70.

Lee, A.M., Sæther, B.-E., and Engen, S. 2020. Spatial covariation of competing species in a fluctuating environment. Ecology, 101, e02901.

Lind, M.I., Zwoinska, M.K., Andersson, J., Carlsson, H., Krieg, T., Larva, T., and Maklakov, A.A. 2020. Environmental variation mediates the evolution of anticipatory parental effects. Evolution Letters, 4, 371-381.

Loe, L.E., Liston, G.E., Pigeon, G., Barker, K., Horvitz, N., Stien, A., Forchhammer, M., Getz, W.M., Irvine, R.J., Lee, A.M., Movik, L.K., Mysterud, A., Pedersen, Å.Ø., Reinking, A.K., Ropstad, E., Trondrud, L.M., Tveraa, T., Veiberg, V., Hansen, B.B., and Albon, S.D. 2020. The neglected season: Warmer autumns counteract harsher winters and promote population growth in Arctic reindeer. Global Change Biology, in press.

Lundregan, S.L., Niskanen, A.K., Muff, S., Holand, H., Kvalnes, T., Ringsby, T.H., Husby, A., and Jensen, H. 2020. Resistance to gapeworm parasite has both additive and dominant genetic components in house sparrows, with evolutionary consequences for ability to respond to parasite challenge. Molecular Ecology, 29, 3812–3829.

Mauro, A.A., and Ghalambor, C.K. 2020. Trade-offs, pleiotropy, and shared molecular pathways: A unified view of constraints on adaptation. Integrative and Comparative Biology, 60, 332–347.

Merkel, B., Descamps, S., Yoccoz, N.G., Grémillet, D., Daunt, F., Erikstad, K.E., Ezhov, A.V., Harris, M.P., Gavrilo, M., Lorentsen, S.-H., Reiertsen, T.K., Steen, H., Systad, G.H., Þórarinsson, Þ.L., Wanless, S., and Strøm, H. 2020. Individual migration strategy fidelity but no habitat specialization in two congeneric seabirds. Journal of Biogeography, In press. https://doi.org/10.1111/jbi.13883

Moiron, M., Araya-Ajoy, Y.G., Teplitsky, C., Bouwhuis, S., and Charmantier, A. 2020. Understanding the social dynamics of breeding phenology: Indirect genetic effects and assortative mating in a long-distance migrant. American Naturalist, 196, 556-576.

Morgan, R., Finnøen, M.H., Jensen, H., Pélabon, C., and Jutfelt, F. 2020. Low potential for evolutionary rescue from climate change in a tropical fish. Proceedings of the National Academy of Sciences of the United States of America, 117, 33365-33372.

Mutanen, M., Ovaskainen, O., Várkonyi, G., Itämies, J., Prosser, S.W.J., Hebert, P.D.N., and Hanski, I. 2020. Dynamics of a host-parasitoid interaction clarified by modelling and DNA sequencing. Ecology Letters, 23, 851-859.

Møller, A.P., Søraker, J.S., and Soler, J.J. 2020. Extra-pair paternity and antiparasitic defence. Avian Research, 11, 37.

Nahid, M.I., Fossøy, F., Stokke, B.G., Begum, S., Røskaft, E., and Ranke, P.S. 2020. How does human disturbance affect brood parasitism and nest predation in hosts inhabiting a highly fragmented landscape? Global Ecology and Conservation, 24, e01295.

Naves, R.P., Grøtan, V., Prado, P.I., Vidal, E., and Batista, J.L.F. 2020. Tropical forest management altered abundances of individual tree species but not diversity. Forest Ecology and Management, 475, 118399.

Nilsson, A.L.K., Reitan, T., Skaugen, T., L'Abée-Lund, J.H., Gamelon, M., Jerstad, K., Røstad, O.W., Slagsvold, T., Stenseth, N.C., Vøllestad, L.A., and Walseng, B. 2020. Location is everything, but climate gets a share: Analyzing small-scale environmental influences on breeding success in the white-throated dipper. Frontiers in Ecology and Evolution, 8, 542846.

Nilsson, A.L.K., Skaugen, T., Reitan, T., L'Abée-Lund, J.H., Gamelon, M., Jerstad, K., Røstad, O.W., Slagsvold, T., Stenseth, N.C., Vøllestad, L.A., and Walseng, B. 2020. Hydrology influences breeding time in the white-throated dipper. BMC Ecology, 20, 70.

Niskanen, A.K., Billing, A.M., Holand, H., Hagen, I.J., Araya-Ajoy, Y.G., Husby, A., Rønning, B., Myhre, A.M., Ranke, P.S., Kvalnes, T., Pärn, H., Ringsby, T.H., Lien, S., Sæther, B.-E., Muff, S., and Jensen, H. 2020. Consistent scaling of inbreeding depression in space and time in a house sparrow metapopulation. Proceedings of the National Academy of Sciences of the United States of America, 117, 14584-14592.

Nordén, J., Abrego, N., Boddy, L., Bässler, C., Dahlberg, A., Halme, P., Hällfors, M., Maurice, S., Menkis, A., Miettinen, O., Mäkipää, R., Ovaskainen, O., Penttilä, R., Saine, S., Snäll, T., and Junninen, K. 2020. Ten principles for conservation translocations of threatened wood-inhabiting fungi. Fungal Ecology, 44, 100919.

Murray, D., & Sandercock, B.K. (Eds.) 2020. Population ecology in practice. Wiley-Blackwell.

Nuijten, R.J., Vriend, S.J.G., Wood, K.A., Haitjema, T., Rees, E.C., Jongejans, E., and Nolet, B.A. 2020. Apparent breeding success drives long-term population dynamics of a migratory swan. Journal of Avian Biology, 51, e02574.

Ofstad, E.G., Markussen, S.S., Sæther, B.-E., Solberg, E.J., Heim, M., Haanes, H., Røed, K.H., and Herfindal, I. 2020. Opposing fitness consequences of habitat use in a harvested moose population. Journal of Animal Ecology, 89, 1701-1710.

Opedal, Ø.H., Ovaskainen, O., Saastamoinen, M., Laine, A.-L., and van Nouhuys, S. 2020. Host-plant availability drives the spatiotemporal dynamics of interacting metapopulations across a fragmented landscape. Ecology, 101, e03186.

Ovaskainen, O., and Abrego, N. (2020). Joint species distribution modelling: With applications in R. Ecology, biodiversity and conservation. Cambridge University Press.

Ovaskainen, O., ..., and Kurhinen, J. 2020. Chronicles of nature calendar, a long-term and large-scale multitaxon database on phenology. Scientific Data, 7, 47.

Ovaskainen, O., Somervuo, P., and Finkelshtein, D. 2020. Mathematical and simulation methods for deriving extinction thresholds in spatial and stochastic models of interacting agents. Methods in Ecology and Evolution, In press. https://doi.org/10.1111/2041-210X.13498

Ovaskainen, O., Somervuo, P., and Finkelshtein, D. 2020. A general mathematical method for predicting spatio-temporal correlations emerging from agent-based models. Journal of the Royal Society, Interface, 17, 20200655.

Pavard, S., and Coste, C.F.D. 2020. Goodman, Keyfitz & Pullum (1974) and the population frequencies of kinship relationships. Theoretical Population Biology, 133, 15–16.

Peeters, B., Le Moullec, M., Raeymaekers, J.A.M., Marquez, J.F., Røed, K.H., Pedersen, Å.Ø., Veiberg, V., Loe, L.E., and Hansen, B.B. 2020. Sea ice loss increases genetic isolation in a high Arctic ungulate metapopulation. Global Change Biology, 26, 2028-2041.

Pélabon, C., Hilde, C.H., Einum, S., and Gamelon, M. 2020. On the use of the coefficient of variation to quantify and compare trait variation. Evolution Letters, 4, 180-188.

Petersen, T.K., Speed, J.D.M., Grøtan, V., and Austrheim, G. 2020. Urban aliens and threatened near-naturals: Land-cover affects the species richness of alien- and threatened species in an urban-rural setting. Scientific Reports, 10, 8513.

Pineda, S.S., Chin, Y.K.Y., Undheim, E.A.B., Senff, S., Mobli, M., Dauly, C., Escoubas, P., Nicholson, G.M., Kaas, Q., Guo, S., Herzig, V., Mattick, J.S., and King, G.F. 2020. Structural venomics reveals evolution of a complex venom by duplication and diversification of an ancient peptide-encoding gene. Proceedings of the National Academy of Sciences of the United States of America, 117, 11399–11408.

Ranke, P.S., Skjelseth, S., Hagen, I.J., Billing, A.M., Pedersen, Å.A.B., Pärn, H., Ringsby, T.H., Sæther, B.-E., and Jensen, H. 2020. Multi-generational genetic consequences of reinforcement in a bird metapopulation. Conservation Genetics, 21, 603-612.

Reid, J.M., and Arcese, P. 2020. Recent immigrants alter the quantitative genetic architecture of paternity in song sparrows. Evolution Letters, 4, 124-136.

Reid, J.M., Souter, M., Fenn, S.R., Acker, P., Payo-Payo, A., Burthe, S.J., Wanless, S., and Daunt, F. 2020. Among-individual and within-individual variation in seasonal migration covaries with subsequent reproductive success in a partially migratory bird. Proceedings. Biological Sciences, 287, 20200928.

Rybicki, J., Abrego, N., and Ovaskainen, O. 2020. Habitat fragmentation and species diversity in competitive communities. Ecology Letters, 23, 506–517.

Rød-Eriksen, L., Skrutvold, J., Herfindal, I., Jensen, H., and Eide, N.E. 2020. Highways associated with expansion of boreal scavengers into the alpine tundra of Fennoscandia. Journal of Applied Ecology, 57, 1861-1870.

Sandvik, H. 2020. Expansion speed as a generic measure of spread for alien species. Acta Biotheoretica, 68, 227-252.

Sandvik, H., ..., and Gederaas, L. 2020. Alien species in Norway: Results from quantitative ecological impact assessments. Ecological Solutions and Evidence, 1, e12006.

Schielzeth, H., Dingemanse, N.J., Nakagawa, S., Westneat, D.F., Allegue, H., Teplitsky, C., Réale, D., Dochtermann, N.A., Garamszegi, L.Z., and Araya-Ajoy, Y.G. 2020. Robustness of linear mixed-effects models to violations of distributional assumptions. Methods in Ecology and Evolution, 11, 1141–1152.

Shah, A.A., Bacmeister, E.M.S., Rubalcaba, J.G., and Ghalambor, C.K. 2020. Divergence and constraint in the thermal sensitivity of aquatic insect swimming performance. Current Zoology, 66, 555–564.

Shah, A.A., Woods, H.A., Havird, J.C., Encalada, A.C., Flecker, A.S., Funk, W.C., Guayasamin, J.M., Kondratieff, B.C., Poff, N.L., Thomas, S.A., Zamudio, K.R., and Ghalambor, C.K. 2020. Temperature-dependence of metabolic rate in tropical and temperate aquatic insects: Support for the Climate Variability Hypothesis in mayflies but not stoneflies. Global Change Biology, in press.

Simmonds, E.G., Cole, E.F., Sheldon, B.C., and Coulson, T. 2020. Testing the effect of quantitative genetic inheritance in structured models on projections of population dynamics. Oikos, 129, 559-571.

Simmonds, E.G., Cole, E.F., Sheldon, B.C., and Coulson, T. 2020. Phenological asynchrony: A ticking time-bomb for seemingly stable populations? Ecology Letters, 23, 1766–1775.

Sæther, B.-E., Engen, S., Gustafsson, L., Grøtan, V., and Vriend, S.J.G. 2020. Density-dependent adaptive topography in a small passerine bird, the collared flycatcher. The American Naturalist, in press.

Tidière, M., Gaillard, J.-M., Garel, M., Lemaître, J.-F., Toïgo, C., and Pélabon, C. 2020. Variation in the ontogenetic allometry of horn length in bovids along a body mass continuum. Ecology and Evolution, 10, 4104-4114.

Tikhonov, G., Duan, L., Abrego, N., Newell, G., White, M., Dunson, D., and Ovaskainen, O. 2020. Computationally efficient joint species distribution modeling of big spatial data. Ecology, e02929.

Touzot, L., Schermer, É., Venner, S., Delzon, S., Rousset, C., Baubet, E., Gaillard, J.-M., and Gamelon, M. 2020. How does increasing mast seeding frequency affect population dynamics of seed consumers? Wild boar as a case study. Ecological Applications, e02134.

Tsuboi, M., Kopperud, B.T., Syrowatka, C., Grabowski, M., Voje, K.L., Pélabon, C., and Hansen, T.F. 2020. Measuring complex morphological traits with 3D photogrammetry: A case study with seer antlers. Evolutionary Biology, 47, 175-186.

Van Lieshout, S.H.J., Froy, H., Schroeder, J., Burke, T., Simons, M.J.P., and Dugdale, H.L. 2020. Slicing: A sustainable approach to structuring samples for analysis in long-term studies. Methods in Ecology and Evolution, 11, 418–430.

Van Moorter, B., Engen, S., Fryxell, J.M., Panzacchi, M., Nilsen, E.B., and Mysterud, A. 2020. Consequences of barriers and changing seasonality on population dynamics and harvest of migratory ungulates. Theoretical Ecology, 13, 595–605.

Veylit, L., Sæther, B.-E., Gaillard, J.-M., Baubet, E., and Gamelon, M. 2020. Grow fast at no cost: no evidence for a mortality cost for fast early-life growth in a hunted wild boar population. Oecologia, 192, 999-1012.

Veylit, L., Sæther, B.-E., Gaillard, J.-M., Baubet, E., and Gamelon, M. 2020. How do conditions at birth influence early-life growth rates in wild boar? Ecosphere, 11, e03167.

Walker, A.A., Robinson, S.D., Hamilton, B.F., Undheim, E.A.B., and King, G.F. 2020. Deadly proteomes: A practical guide to proteotranscriptomics of animal venoms. Proteomics, 20, e1900324.

Westneat, D.F., Araya-Ajoy, Y.G., Allegue, H., Class, B., Dingemanse, N.J., Dochtermann, N.A., Garamszegi, L.Z., Martin, J.G.A., Nakagawa, S., Réale, D., and Schielzeth, H. 2020. Collision between biological process and statistical analysis revealed by mean centring. Journal of Animal Ecology, 89, 2813-2824.

Wetzel, D.P., Mutzel, A., Wright, J., and Dingemanse, N.J. 2020. Novel sources of (co)variation in nestling begging behavior and hunger at different biological levels of analysis. Behavioral Ecology, 31, 960–970.

Wright, J., Solbu, E.B., and Engen, S. 2020. Contrasting patterns of density-dependent selection at different life stages can create more than one fast–slow axis of life-history variation. Ecology and Evolution, 10, 3068-3078.

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