Assessing changes in the phenology of bird migration: methodological and biological challenges

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”As the bird by wandering, as the swallow by flying, so the curse causeless shall not come”

Proverbs 26:2

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SUMMARY OF THESIS

Background

Man is a curious animal, and before curiosity there is a mystery. Some natural phenomena seem bound to have attracted the human mind from its early dawn and remain enigmatic until its dusk. But the spectacular beauty of bird migration and falling leaves did not only attract the minds of poets and philosophers; knowing seasonality and the movements of animal populations has been key to our survival. Understanding recent changes in seasonality and how they affect the distribution of organisms in space and time might be among the most important contemporary challenges for mankind [1]. It is often said that 'seeing is believing', and bird migration has clearly helped us see effects of climate change [2, 3]. Understanding them is, however, a more complicated matter [4], and a lack of understanding makes us reluctant to believe in what we see [5]. Broadly stated, the present piece of work is a journey into ways of seeing and challenges to the transition from seeing to scientific understanding and belief.

Indeed, the long history of research on bird migration is one of understanding being limited by what we can or can not see. While Aristotle and his fellow Greek philosophers were able to observe the movements of many birds, such as cranes and geese, to warmer areas in winter, other species simply disappeared and were speculated to spend the winter hidden in torpor, for instance at the bottom of lakes – a belief which was held through the Middle Ages and perpetuated by naturalists as late as the 18th and 19th century. By the late 19th century migration was, however, generally accepted as the main reason for birds' disappearance in winter, and knowledge was accumulating on the environmental impacts on the progress and timing of bird migration. With the establishment of bird ringing schemes and bird observatories around the turn of the century knowledge on migration routes and wintering areas accelerated. Today, hundreds of millions of birds have been ringed worldwide, forming the most general and often the most important source of knowledge on coarse-scale movements in birds. Yet this knowledge is coarse with many big gaps to fill in, such as intracontinental movements within Africa and Australia [6]. Expectations for technological advances in biotelemetry allowing us to track the position of small birds throughout their annual cycle are certainly great [7, 8].

If the early history of bird migration research is as a tale of what can not be seen, the history of phenological research is a tale of what can be seen. 'Phenology' can be defined as the timing of periodically recurring events in the life histories of plants and animals. With many of the most conspicuous ones following the annual cycle, the existence of records stretching far back in historical time on the timing of flowering or harvesting of culturally or agriculturally important plants is not surprising. The oldest systematic records of the phenology of arrival and departure of migratory birds are from early 18^{th} century Great Britain, and Linné himself promoted systematic phenological observations, with his contemporaries noting the close association between springtime arrival and local temperatures and the timing of ice break-up (see [9]). Today, thousands of birdwatchers record arrival dates of birds in spring, and this has also become a popular activity for citizen science.

With effects of recent climate change becoming clear, and the relative consistency of its signature on phenology, there has been renewed interest in phenology as a scientific endeavour. Advances in the phenology of spring events in birds have been noted for their consistency and strength [3]. This was easily picked up by ornithologist, who already had a long history of interest in the timing of annual events in birds [10]. Today, the study of changes in bird phenology has nearly become a separate field of research, hosting its own conferences and mainly populated by ornithologists from various lines of research. The current work on changes in migration phenology represents the fusion of lines from bird migration research with phenological research, increasingly embedded in global change dimensions. In Paper IV we provide our view of the state-of-the art of the field, rooted in what we see as the more important research questions.

The central challenge

The historical overview above illustrates facets of what can be perceived as a central challenge: Given a noisy time series of the number of birds recorded daily during a fixed period at a fixed point in space, what can we say about variability and change in phenology, and the causes for such, over time scales of years? Our focus is on data from standardized monitoring at bird observatories, mostly in Scandinavia. These are typically located at hotspots for passerine birds along the migratory route, and birds are trapped and ringed daily during the migration periods using approximately constant effort mist-netting and sometimes other trapping methods. A description of the bird observatories and trapping methods is given in the supplementary online material for Paper I, and characteristic features of the data are treated in Paper II.

In a sense the challenge is very fundamental. The birds recorded are on the move, many of them at intercontinental scales. We do not know their exact origin or destination; we only have a record of daily numbers from which we can estimate population parameters (Paper II, VI). There is both a spatial and a temporal component of the birds' movements, and since we know so little about both outside the short observation window, it is very hard to separate phenological change from spatial change, and inference on the former frequently has to rely on the assumption that the latter is not occurring (see Paper IV). From a deterministic point-of-view the coupling between space and time is not problematic, and can for instance be approached in terms of partial differential equations. However, there is a large stochastic component in bird migration signals (Paper II); birds are neither machines nor drifting particles, but make individual- and species-specific movement decisions in a spatially and temporally varying landscape context (Paper III). Furthermore, sample sizes are often small and phenological records hence prone to sampling error as well as year-to-year fluctuations in weather conditions (Paper II, V).

From a pragmatic perspective, this is not necessarily so complicated. We define our biological objectives, choose a measure of the data suiting our needs, such as the sample median, or some early or late sample quantile, and simply go for it (Paper I). However, the quality and representativeness of the data are sometimes questioned, and a closer inspection reveals a number of problematic issues (Paper II). Some of these can be dealt with by appropriately modelling the seasonal distribution curve and robust modelling of changes over time (Paper II). Others may be related to a lack of precise biological knowledge, for instance on movement strategies during migration and in the wintering areas (Paper III, V). Indeed, it is important to put animal movement into its proper ecological and evolutionary context (Paper III) – unfortunately, we often lack important bits of information and hence our attempts to explain for instance responses to climate change remain inconclusive and of poor predictive power (Paper IV). Nevertheless, proper statistical modelling of data from bird observatories can account for the various sources and levels of variability. State-space time series modelling can provide new insight into the dynamics of bird migration phenology and the role of phenotypic plasticity and environmental conditions along the migratory flyway (Paper V). Unknown structure in the data, such as mixtures of populations of different origins, can be dealt with using finite-mixture models and model averaging (Paper VI).

Summary of papers

Paper I

A large number of studies have demonstrated consistent (but varying across species and regions) change towards earlier timing of spring migration and arrival in birds [9, 11, 12], and the selection pressure on the timing of arrival is believed to be high [13-17]. Hence, the question arose whether changes are due to phenotypic plasticity or microevolutionary change in the timing of migration [18]. In principle, changes due to plasticity in the timing of migration and arrival can occur quickly but might be rather limited, while microevolutionary change is likely to take more time but can continue for longer. Plasticity has been the favoured hypothesis, since microevolutionary change is hard to observe and most studies show larger responses to climate change for short-distance migrants, which winter close to their breeding grounds and hence might respond to cues enabling them to adjust their timing of migration in response to breeding site conditions, in contrast to long-distance migrants wintering in Africa (Paper IV).

However, by combining data from four Scandinavian bird observatories into a mixed-effects model with both time and (detrended) NAO as covariates, we in Paper I demonstrated not only more consistent trends over time for long-distance migrants compared to short-distance migrants; trends were also at least as strong as for the latter group. Moreover, the arrival of short-distance migrants in Scandinavia was associated with high NAO index only in the early part of the distribution of arrival times, while the arrival of long-distance migrants was associated with high NAO index also in the mid and late parts. By estimating passage times for six of the species also occurring at an Italian bird observatory, we showed that these northern-breeding species also cross the Mediterranean progressively earlier, and trends are at least as strong as for the Scandinavian bird observatories. This, along with an opposing effect of NAO at Capri compared to Scandinavia, suggested that changes were occurring in the timing of migration onset or speed of migration through Africa, possibly due to climate-driven microevolutionary change in the timing of spring migration. In the supplementary online material, we present species- and observatory- specific parameter estimates and a novel method of fitting a truncated normal distribution via Bayesian Markov chain Monte Carlo (MCMC) estimation to data where the tails of the migration period are missing.

Not surprisingly, the suggestion of microevolutionary change arose controversy; as correctly pointed out in a response [19], our data do not demonstrate microevolutionary change, and there are ample opportunities for phenotypic adjustment along the migratory route. However, [19] also suggested a lack of selection pressure at breeding grounds and earlier arrival to Scandinavia possibly being due to changing mixtures of northern and southern populations or improved conditions in Africa. In our response to [19] we were able to refute the latter suggestion by an auxiliary analysis also controlling for Sahel rainfall and Tunis temperatures; also, ringing recoveries suggest breeding areas where spring phenologies have indeed advanced, and there are no indications of overall differential population growth between northern and southern populations [20]. The issue continues to be at the centre of much research [21]; later studies have not demonstrated microevolutionary change either, although indications acknowledging its possibility are accumulating ([22], Paper IV), and studies of correlation patterns in environmental variables *en route* weaken the notion that long-distance migrants do not have any opportunities to adjust their timing of migration in response to conditions at breeding grounds [23].

Paper II

Data from standardized trapping and observation at bird observatories have been instrumental for demonstrating shifts in the timing of bird migration, and metrics derived from these data have many advantages compared to, for instance, first arrival dates [9, 24]. Paper II provides an overview of problematic issues in the analysis of these data, suggests ways of taking these into account, and reviews methods for modelling the seasonal distribution of migrating birds and trends in metrics derived from these models or from raw data. Particular emphasis is put on methods for getting closer to the ’true’ underlying phenological distribution of migrating birds, either by smoothing the daily data, or by fitting a parametric seasonal distribution curve. As shown in the paper’s Fig. 1, most of the within-year variability in the data is found at a scale of one or a few days, and at scales characterizing the overall seasonal pattern of occurrence. Smoothing can be seen as a way of ’looking past’ the noise, yielding a characterization of the phenological distribution curve as suggested by the data, but does not account for the observation process and will hence be sensitive to observation error, truncated or missing data. Fitting a parametric seasonal distribution curve may be more robust, but assumes a model of the underlying phenological distribution and does not pick up between-year variability in the ’waviness’ at intermediate scales. Choosing between the two methods is hence a matter of data quality and research aims, as well as personal preference. If the data are fairly complete and of good quality, smoothing methods represent a powerful exploratory tool that can be used for suggesting the shape of seasonal distribution curves, multimodality and between-year variability in such. Also, some smoothing methods, such as wavelet analysis, offer a scale-by-scale decomposition of variance – which is interesting in itself, but also can stimulate thinking regarding fundamental aspects of the nature of the data and suggest important structuring processes.

Paper III

Migratory birds breeding at northern latitudes spend a large part of their year on the move or in wintering quarters. Since most species of passerine birds are too small for equipping them with satellite transmitters, we know very little about their detailed movements. Wintering areas and patterns of intracontinental movement, for instance within Africa, vary greatly across species [6], and the simplified view of migrants breeding in northern Europe, then flying more or less non-stop all the way down to their wintering site in Africa and back again in spring might represents the exception rather than the rule. It may take months to get there, with alternations between periods of rapid movement and periods of staying, and life in the winter quarters may for many species be more nomadic than resident. In Paper III we call for a unified view of animal movements. We envision a continuum of movement strategies ranging from migration to nomadism, and invoke the niche concept in order to ask under what conditions either strategy should be expected to evolve. Arguably, the statistical properties of the resource environment hold the key to understanding the relative merits of movement strategies. In particular we focus on variability and predictability in space and time. Migration is frequently seen as an adaptation to avoid severe conditions and exploit predictable spatiotemporal variation in resource abundance. In contrast, nomadism can be seen as an adaptation to variability and unpredictability. In order to understand the selection pressures shaping movement strategies, we need to consider temporal dynamics of resources, spatial heterogeneity at a range of scales, as well as how animals integrate information about their environment into spatiotemporal movement decisions. We explore some of these ideas using movement strategies of Australian birds and space-time data on rainfall as an illustration. Even such simple explorations might be helpful for linking the diversity of movement patterns to characteristics of the environment. On the other hand, animal movements can not be fully understood in isolation; we also need to consider life history constraints such as those enforced by the spatiotemporal organization of the annual cycle.

Paper IV

In rapidly developing fields such as the study of recent changes in spring phenology of birds, key statements proliferate rapidly, and claims might be made on insufficient grounds or assumed to hold in general. In Paper IV we review the evidence basis regarding ten central issues, in the form of more or less articulated claims pertaining to the timing of spring migration. We assess the basis for the claims, ask whether the claims hold in general, and suggest how to proceed in order to improve our scientific knowledge and predictive power regarding these issues.

Claims were subjectively classified as pertaining to patterns, mechanisms or consequences of climate change effects. Overall, patterns of change seem to be well established, although causes for the large variability in responses across species and regions need to be elucidated, and there are interesting general patterns such as differential timing between sexes that need further investigation. The large amounts of data available could be better utilized, for instance by more and more proper meta-analyses. On the other hand, further research on methodological issues is also needed. The data typically available might, however, not be well suited for resolving the basic mechanisms for change. There has been big disagreement among researchers of the field regarding, for instance, the relative roles of phenotypic plasticity and microevolutionary change, and although it is well known that birds respond to weather conditions *en route* and there is overall agreement that the timing and progress of migration is constrained by the organization in space and time of the annual cycle, we are not able to say much about how climate change effects add up during the course of migration or, more generally, over the course of a year. In order to properly address microevolutionary change, we need genetic data [21], and the genetic basis for the timing of migration is not known in any detail. Long-term data on individuals allow sorting out variance components and apply methods rooted in quantitative genetics, but there simply is too little of these data around, and the data are restricted to a few, well-studied species. Technological advances allowing tracking of individual small migrants will be helpful for resolving uncertainties regarding the spatiotemporal progress of migration; on the other hand, sample sizes will always be small compared to population-level data, and progress in modelling [25] might be needed. Theoretical progress might be needed regarding ways of integrating annual cycle constraints and phenological responses to climate change, and we need more empirical studies investigating flexibility in annual schedules across individuals, populations and species.

As to the consequences of climate change for populations and communities of migratory birds, the field somehow seems to be in its infancy. Efforts have been made to investigate whether climate change increases mismatch with resource phenology, but empirical as well as theoretical studies are still few, and the variability across species and populations is poorly understood. There are a few indications of lacking or insufficient responses being reflected in population declines, but scaling up from local mismatch to population consequences is at best a risky venture, and population responses may be due to a multitude of other factors. Particularly regarding community consequences of climate change, knowledge is scattered and the field appears rather undeveloped, lacking general coherency and focused either on sweeping claims or predicting future distributions using climate change scenarios and habitat suitability modelling.

Society often calls upon researchers regarding effects of climate change, asking for 'expert opinions' or consensus views. Considering ourselves as a group of 'experts', we assessed our ability to provide such services. We (the group of co-authors) individually and for each claim scored our opinion regarding the amount of support, as well as the amount of research effort that has been put into investigating the claim (the 'knowledge basis'). There was poor agreement regarding the support for most claims, but a somewhat better agreement regarding the knowledge basis enabled consensus regarding broad patterns and likely causes. With increasing knowledge, the overall support ('consensus view') for a claim increased and between-researcher variability in support ('expert opinions') decreased; hence it is important to assess and communicate the knowledge basis.

Paper V

The relative roles of phenotypic plasticity and microevolutionary change for recent changes in the timing of bird migration remain elusive (Paper IV). Disentangling environmental and genetic components is a hard task requiring good data at the level of individuals, but it is nevertheless crucial to improve our understanding of the interplay between the two, as well as of how natural selection fluctuates in response to climate change and variability [21]. In Paper V we explore the use of time-series analysis for studying the dynamics of bird migration phenology. By generalizing the concept of reaction norms beyond the level of individuals [26] we show how environmental sensitivity (a component of phenotypic plasticity) can be estimated as loadings in a principal component analysis (PCA) of median migration dates. PCA defines latent environmental gradients, and these principal components were interpretable in terms of environmental conditions along the flyway. When including principal components as covariates in dynamic time-series models (fitted using MCMC methods), we were able to separate between responses to between-year variability in the local environment, responses to winter and flyway conditions and latent long-term fluctuations not representing a common response to the environment. The former two occur instantaneously and were rather synchronized across species, while the latter were out of phase but directionally consistent over time and capable of explaining fluctuations in phenology during periods of weak environmental control. We found indications of positive, negative and stabilizing feedback mechanisms between the latent dynamical components representing long-term dynamics and response to flyway conditions. The role and nature of such intrinsic dynamics needs to be further elucidated. Phenological responses to climate change in birds are generally thought to be driven mainly by rather generic responses to extrinsic factors such as weather conditions, mediated by population- and species-specific factors such as breeding habitat and life history characteristics [27, 28]. Proper time-series modelling seems a natural starting point [29]; yet, there are surprisingly few studies applying time-series models to phenological data. For migratory birds we are aware of one study applying second-order autoregressive models to first arrival dates [30] and one study on population dynamics controlling for effects of overlap in phenology [31]. As in the latter study, we applied state-space models for time series analysis [32], and found this to be a flexible tool allowing direct specification of hypothesized dynamic behaviour under conditions when the stationarity assumption of the Box-Jenkins framework does not hold.

Paper VI

In Paper VI we take the consequence of phenological time series being composed of samples being a mixed bag of often unknown structure and explore how this can be dealt with statistically using finite-mixture models and model selection or -averaging on basis of the model likelihood. Finite-mixture models offer a statistically rigorous and well-founded approach to identifying subpopulations in the data and estimating parameters for these [33, 34]. Through simulations we compare maximum likelihood (ML), penalized maximum likelihood and Bayesian MCMC methods for model fitting. In terms of obtaining consistent parameter estimates, MCMC estimation outperforms the former two, which apparently suffer from problems related to the degeneracy of the likelihood function. For ML estimation, the precision of parameter estimates also depends on the quality of the initial guesses (*i.e.*, how close they are to the true parameter value), and estimates are biased at low sample sizes. We apply Bayesian MCMC fitting for two real-world examples, and illustrate the use of model averaging for inference when there is no obvious 'correct' model in terms of the number of components to fit. Poor separability between component densities and a lack of information on actual mixing proportions might present challenges to the practical usefulness of finite mixture models for identifying subpopulations in phenological data from bird observatories. On the other hand, MCMC fitting seems promising for overcoming this, since it yields consistent estimates, allows great flexibility in model specification, and the performance of the model is improved by applying a more informative prior on the mixing proportion.

Perspectives

In the opening line of a recent book on the effects of climate change on birds [35], the editors state "*No other field in evolutionary biology and ecology has gained so much public attention in recent years as research on the consequences of climate change for plants and animals.*" Yet, they start their concluding chapter with "*This volume provides* *an extensive overview of what we currently know and what remains to be studied in terms of climate change and birds. To conclude we can state without doubt that, although we have accumulated a large amount of knowledge about the consequences of climate change, we know much less than we thought we knew.*" Although the latter realization might be seen as a sign of coming-of-age of a scientific research field, it should not be dismissed as such. It is in fact quite worrying, given the large amount of research effort devoted, the continued public interest and the conservation consequences [36] of rapid climate change.

Clearly, the challenges have been large. In Paper IV we summarize the challenges researchers in this field face when trying to resolve issues that might seem simple and isolated at first sight. More and better data is the obvious answer, but the paper also highlights the need for doing proper integrative research. Yet there has been no lack of guidance, with books and special issues [6, 35, 37-41] published rather frequently, summarizing fields of research and providing recommendations. In their concluding chapter, [35] express concern that hardly any of their 16 recommended areas of serious need for research they identified in a keystone publication six years earlier have been seriously pursued. Has the field become an arena for affirmative research?

I think not, although we should certainly be aware of the danger. Rather, in the big rush to document effects of climate change, research might have lost sight of some important biological foundations. Also, there is a natural sequence of things; Paper IV indicates that the field's knowledge is best with respect to patterns of climate change effects, poorer regarding the mechanisms of change, and arguably poorest regarding consequences of climate change. There are many exciting new perspectives arising, both in the field of research on climate change effects on birds, and in migration biology. Recent reviews emphasize the need for more knowledge on how ecological interactions [42], community dynamics [43] and range shifts [44] integrate with climate change effects such as phenology shifts. An upcoming edited book on animal migration aims at a new synthesis of the field [45], putting migration into its broader evolutionary and ecological context, where we need to consider areas as disparate as life history strategies, community dynamics and locomotory modes. Perspectives are integrated into new blends such as 'movement ecology' [46] and embraced as new paradigms. Ways of integrating climate change and other impacts such as habitat change are sought [47], and the 'contract' between science and the community at large is taken seriously by applying climate change scenarios and generating predictions for the future [48].

Much research on bird migration and phenological responses to climate change has been data-driven. Indeed, better data might be needed in order to answer some questions [8], but we must not forget the large amounts of data already existing, either [49]. Bird ringing and standardized observation data and the phenological records they provide have been instrumental for bringing us to our current level of understanding on climate change effects on birds. With the large amounts of available data, we might do well by entering the meta-analysis mode now. As with all data, a little soberness and knowledge about the strengths and limitations of the data is, however, needed [9, 12, 49]. There is definitely a lot of information in the phenological data from bird observatories, but it is noisy and can be hard to extract (Paper II, V, VI). The way further could definitely benefit from improved statistical knowledge and extending the toolbox of applied researchers.

A popular Norwegian saying, allegedly from a 19th-century cookbook by Hanna Winsnes, goes "Man tager vad man haver…" (literally translated: "One applies what is available…") Applied biological research is often in many ways 'following the recipe'; since biologists typically lack a deep foundation in statistics, a common approach is to find a recipe, perhaps modify it a little, and apply whatever resources there are at hand. As statistical requirements are getting higher, the trend seems to be toward collaborative work, sometimes with proper statisticians when needed. But perhaps our self-esteem is a little on the low side. It is in fact possible also for biologists to increase their statistical competence [50], hopefully contributing a little to a field's toolbox along the way (Paper II). However, some issues in the analysis of phenological data collected at bird observatories are so complex (see, *e.g.*, Paper VI) that they might better be explored jointly by biologists and statisticians.

On the other hand, researchers working with bird migration and climate change are increasingly realizing that they need more information on what changes in meteorological factors birds are sensitive to *en route* [25, 51] Obviously, birds are subject to a multitude of factors along their migratory flyway and may respond differently according to region and the spatiotemporal correlation patterns created by large-scale weather systems (Paper V). However, much research has focused on temperature or some climate index such as NAO as the only covariate, also overlooking the spatial variability at large [52, 53] as well as small [54] scales, and perhaps without properly thinking about the functional significance of, for instance, temperature [55]. In a sense, this brings us back to the days of the old field naturalists, when researchers simply sought to relate bird migration to day-to-day variability in weather [56]. Perhaps their days are not yet gone – they might be needed in order to do sensible integrative biology, and science might do better by bringing them into the warmth again from their long exile in the realms of amateur and citizen science.

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PAPER II Characterizing bird migration phenology using data from standardized monitoring at bird observatories

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PAPER III Uncertainty and predictability: the niches of migrants and nomads

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PAPER IV Challenging claims in the study of migratory birds and climate change

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PAPER V Phenotypic plasticity, migratory flyways and the dynamics of changing bird migration phenologies

Knudsen, E.*, Jonzén, N. & Stenseth, N.C. (submitted)*

PAPER VI Finite-mixture modelling for assessing climate change effects from samples of unknown structure

Knudsen, E*. & Cardinale, M. (manuscript)*