SYMP14: Changing selection pressure on avian annual cycles due to climatic change

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With climatic change becoming increasingly evident, investigations of its impact on organisms have exploded over the last years. Various aspects of birds' life histories have already been found to be affected. However, comprehensive predictions for the effects of climate change on birds are presently still difficult. Climate change simultaneously affects different parts of the annual cycle, and, in addition, differ between species and geographical regions. So far, many results stand on their own as they single out changes in particular aspects of birds' lives, e.g., the onset of laying date. The purpose of the symposium is to present to a general ornithological audience an overview of effects of climate change on birds. Eight oral contributions, framed by short introductory and concluding remarks, and three poster contributions emphasize an integrated approach that acknowledges avian life cycle stages as mutually interdependent. The symposium sets out by specifying predictions for changes in the climate, and then the implications of these changes for different life cycle stages are addressed. Contributions include studies of changes in life cycle stages, based both on field work and on experimental approaches. A related workshop is held to enhance exchange among those actively working on effects of climate change on birds.

SYMP14-1 Projected climate change: Global and regional aspects that may have a noticable influence on ecosystems

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Since 1860, global mean temperature has warmed up 0.6°C and land surface precipitation has increased up to 1% per decade over most Northern Hemisphere higher latitudes. These changes reportedly are already associated with ecosystem changes, and climate change as projected by climate models (GCMs) is expected to increasing affect ecosystems. The IPCC Third Assessment Report summarizes knowledge on the climate system, assesses capabilities of climate models, and presents predictions for a future climate based on several emission scenarios.

GCMs predict significant changes in earth climate systems but their magnitude depends on the intensity and quality of human activities. As these are not exactly known, some IPCC scenarios evaluate the range of expected impacts. All models predict changes in temperature (between 1.4 and 5.8 °C for all 35 scenarios) and hydrological cycle. Physical changes are not homogeneously distributed over the globe and also show seasonal variations. Although the resolution of global models does not allow small scale predictions yet, regional impacts can be gathered differently. Focus is set to Europe and to quantities that may characterize an ecosystem, for instance temperature, water availability, and extreme events. Regional warming for Europe is expected to exceed global average warming. Some key perceptions for Europe, resulting from scenario runs, imply higher maximum and minimum temperatures, more hot days and heat waves, fewer cold days over land areas, in-

creased precipitation in the north and increased pressure on water resources particularly in the south, increased risk of flooding, erosion, wetland loss and degradation in coastal zones.

SYMP14-2 Annual survival in Mediterranean populations of sedentary blue tits co-varies with tropical and local climatic summer factors

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In Western Europe, the influence of the North Atlantic Oscillation (NAO) on winter climate and on ecological systems sensitive to winter environmental conditions is well established (STENSETH et al. 2002 – Science 297: 1292–1296). On the other hand, the large-scale climatic phenomena important in summer are less well known, although recent findings indicate major tropical influences (FOLLAND et al. 1986 – Nature 320: 602–607; HURREL et al. 2001 – Proc. U.S. CLIVAR Atlantic meeting, D. LEGLER ed., Boulder: 111–114). In the Mediterranean basin, winter is characterised by a mild and moist climate which makes the region quite favourable. By contrast, the summer dryness and hotness are likely to be highly constraining. Animal populations from the Mediterranean Basin thus provide ideal biological models for assessing the ecological impact of large scale climatic phenomena in summer.

Using a long-term population biology study, we provide here the first quantitative evidence for influences of both large-scale and local-scale summer climatic factors on demographic response in a European bird. Future investigations of impacts of climate change on European ecosystems and sedentary populations should therefore also focus on climatic summer phenomena both at local scale and at larger scales beyond their distribution range.

SYMP14-3 ‚Cues or constraints?' – Timing of breeding in great tits and the consequences of climate change

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Globally rising temperatures might disrupt whole ‚food chains' by changing the phenology of e.g. plants, insects and insectivorous birds differently with possible severe fitness for the higher trophic levels. In one Dutch great tit population the synchrony between food demands and supplies has been disrupted. While caterpillars, the food supply for the chicks, appear now earlier the birds do not laying earlier. There are two hypotheses explaining the birds' lacking (or imperfect) reaction to the changing climate. (1) Timing of breeding is determined by the reaction to ‚cues' which signal favourable in the near future. If the birds are currently reacting to wrong ‚cues' selection towards a modified response mechanism would lead to a restoration of the synchrony. (2) Timing of breeding is constrained by resources – others than the food for the chicks – which means that birds simply breed as early as possible. Under this hypothesis we would expect no full restoration of the synchrony and a negative effect on population viability. By ‚tricking' birds into laying earlier it would be possible to discriminate between the two hypotheses. Under the ‚cue'-hypotheses birds could advance laying dates without fitness costs. However, under the constraint-hypothesis birds could only advance laying dates by paying a fitness cost, e.g. in-

creased mortality during laying. To adress this question we manipulated laying dates in a field-experiment making use of the learning ability of the birds and looked at fitness consequences.

SYMP14-4 Long-time effects of spring weather on phenotypic structure of a pied flycatcher population in the Moscow region

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Near Moscow, spring temperatures increased in late April but decreased during the first half of May over the last 10–15 years. Due to these climate changes, arrival dates of pied flycatchers have advanced ($Rs = -0.84$, $p = 0.001$, $n = 11$ for dates of first arrived males), but laying dates were not affected. The response to climate change was differed between two male colour types (pale or conspicuous; Drost 1936). Over the years, the proportion of pale birds increased among males that advertised nestboxes during the pre-breeding period but not among successful breeders. Return rates of pale and conspicuous males were affected differently by climate. The probability that an adult conspicuous male returned to its previous breeding area was positively correlated with ambient temperatures in late April and therefore gradually increased. It was unrelated to its reproductive success in the current season. In contrast, the return rate of pale males did not change over the years and was strongly affected by their reproductive success in the current season: breeding failure led to consecutive disappearance from the local population for the majority of pale birds. At the same time, the proportion of pale males was higher in old ($> = 2$ ys) immigrants than in established local breeders. We suggest that weather-dependent changes of phenotypic structure in the pied flycatcher population can be explained by differences between conspicuous and pale phenotypes in tolerance of cold temperature during the advertising period and by breeding area fidelity.

SYMP14-5 Is it costly to be attractive? Temperature dependent differences in advertising behaviour of pied flycatcher males as a possible source of changing selective pressures in the pre-breeding period

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Breeding success of passerine males depends on their success in pair-formation. Attractiveness of males is related to both their appearance per se and their advertising activity. In pied flycatcher males conspicuous phenotypes are more attractive than pale ones. In our population near Moscow, the average level of singing activity was similar in males of both phenotypes. We show that females visited territories of conspicuous males, independently of the level of their singing activity, and territories of those pale males that sang intensively. We observed the behaviour of 35 free-living bachelor pied flycatcher males. The average level of energy expenditure of each male in the daytime (without cost of

thermoregulation) was calculated from time budgets by converting coefficients. The rate of energy expenditure was higher in pale males than in conspicuous ones (2.2 x and 2.5 x BMR) mainly due to a larger proportion of time spent on flight activities (10% versus 7% in conspicuous males). This difference was the largest early in the pre-breeding period. Thus, the costs of attractiveness were higher for pale pied flycatcher males than for conspicuous ones. Energy costs of advertising behaviour correlated negatively with ambient temperatures both in conspicuous and pale males. In addition, advertising behaviour of pale males was more sensitive to low ambient temperatures. Consequently, warm weather in the early pre-breeding period could increase the competitive ability of pale males and may lead to an increasing proportion of pale males attempting to enter the breeding population.

SYMP14-6 Climate change and fitness components of a migratory bird breeding in the Mediterranean region

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Increasing spring temperatures led to advancing spring phenology, and most resident birds have responded by advancing their onset of breeding. The pied flycatcher is a long-distance migrant with a relatively late onset of breeding with respect to both resident birds and spring phenology. In a correlational study, we show that some fitness components of pied flycatchers are suffering from climate change in two of the southernmost European breeding populations. In both montane study areas, temperature during May increased between 1980 and 2000 and an advancement of oak leafing was detected by using the Normalized Difference Vegetation Index (NDVI). This might result in advanced peak caterpillar availability, the main prey during the nestling stage. Over the past 18 years, the time of egg laying and clutch size of pied flycatchers were unaffected by increasing spring temperatures. However, it apparently had an adverse effect on reproductive output over the same period. Our data suggest that the mismatch between the timing of peak food supply and nestling demand caused by recent climate change might result in a reduction of parental energy expenditure that is reflected in a reduction of nestling growth and survival of fledged young in our study populations. The data seem to indicate that the environment has shifted away from the pied flycatcher breeding season. Mediterranean pied flycatchers were not able to advance their onset of breeding, probably because they are constrained by their late arrival and restricted high altitude breeding habitat selection near the southern border of their range.

SYMP14-7 Extended breeding season following global warming may facilitate compensation for nest losses in the blackcap

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Predation is the main cause of nest losses in songbirds and therefore a main selection factor determining reproduction. Songbirds are known to respond to nest predation by quickly replacing lost clutches. However, number of possible replacement clutches and clutch size are limited by the length of the breeding season and the condition of birds. Recently, the period spent on the breeding ground has grown in some migratory species, associated with global warming. Therefore, birds may have more time to compensate for nest losses.

We analysed records from about 2300 nests of the blackcap *Sylvia atricapilla* that were collected in seven woodlots between 1981 and 2000. The data show that today the breeding season starts earlier and ends later than in 1981. Predation was high as indicated by the low probability (0.23) of a clutch to „survive" until fledging. The comparison of clutch sizes among seven study sites revealed that clutch size decreases with increasing predation. Moreover, we found that mean clutch size in the blackcap has on average decreased by 0.2 eggs within the last 20 years. These results suggest that in the presence of strong predation blackcaps may hedge their bets by reducing clutch size and increasing the number of breeding attempts. Improved conditions on the breeding grounds seem to relax time constraints on the number of clutches produced and thereby facilitate the compensation for nest losses. Our study shows that predation may be a major determinant of the consequences of climate change for the reproductive ecology of bird.

SYMP14-8 Plasticity and adaptability of the relationship between timing of postjuvenile moult and migration timing in European songbirds

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Moult and migration are energy-demanding processes and are therefore usually separated from each other. Separation, however, is expected to be compromised when birds are under time stress. These trade-offs between moult and migration and their consequences for the evolution of avian life cycles are largely unexplored.

Here, I present data on the timing of moult and migratory activity in juvenile blackcaps (*Sylvia atricapilla*) and garden warblers (*Sylvia borin*) that were hand-raised and kept under controlled laboratory conditions. Nest-mates were separated and exposed to different photoperiodic conditions in order to assess the importance of environmental and genetic effects on the timing and phase-relationship of these events. In the blackcap, I found strong family effects on the time-lag between termination of moult and onset of autumn migration, and no influence of hatching date on this relationship. In garden warblers from a lowland population, this result was confirmed. In garden warblers from a mountain population, however, there was no indication for a correlation between timing of moult and migration. A comparative analysis of previously published data on moult and migration in European passerines studied under controlled conditions revealed that the extent of overlap is largely phylogenetically constrained. These results suggest that there are physiological and/or energetic trade-offs constraining independent evolution of the timing of moult and migration. Differences among species and populations in the extent and the control of moult-migration overlap may reflect adaptations to different migration strategies and environmental conditions.

SYMP14-P1 Ambient spring temperature and timing of life-cycle stages in the willow warbler and the great tit in Northern Europe

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In the last decade, evidence for ecological effects of climate change in bird populations has increased, particularly regarding changes of dates of arrival and laying. The knowledge of how the

shift of temperature influences other life stages (e.g. timing of moult, autumn migration) in the population is still far from complete.

Our study is aimed at revealing the relationship between spring temperature, date of spring migration, timing of breeding, moult and autumn migration in two species – the willow warbler, a long-distance migrant, and the great tit, a partial short-distance migrant. The analysis is based on 30–years of field data recorded by the Ladoga Ornithological station, as well as on the authors' long-term personal data on breeding. We will discuss the temporal interdependence of different life stages and the influence of temperature on the timing of spring, summer, and autumn life stages.

SYMP14-P2 Timing of breeding and spring arrival of the pied flycatcher in relation to climatic fluctuation in Finland

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Most of the Passerine bird species breeding in Finland, have their wintering areas far away from breeding grounds. Pied flycatcher is presumed to winter in tropical Africa. Among other things, climatic factors regulate the timing of spring migration – and timing of breeding is strongly dependent on arrival time. After arrival, local weather of the breeding area might affect the timing of breeding. We studied how do variation in North Atlantic Oscillation and local weather regulate the spring arrival and egg laying of pied flycatcher *Ficedula hypoleuca* in SW Finland. Our study is based on LARS VON HAARTMAN's long-term (1941–1994) breeding data from Askainen and a continuation (1991–2002) from Harjavalta. As explanatory variables, NAO-index and daily local temperatures from breeding region and locations along migration route were used. NAO and local temperatures of the breeding region had clear advancing effect on first egg laying days. This was as predicted, but in spite of this the long-term trend was towards later breeding.

SYMP14-P3 Photoperiodic response to wintering latitude in the pied flycatcher

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Climate warming leads to an extended growing period in northern temperate regions. Under these conditions, migratory birds are expected to shorten migration distance and to start breeding earlier. A shortening of migration distance, however, exposes birds to novel daylength conditions which may either constrain or facilitate adaptive changes of the annual cycle. I conducted indoor experiments on the pied flycatcher *Ficedula hypoleuca* to determine how a long-distance migrant responds to latitudinal variation in photoperiodic conditions. Groups of first-year males were subjected to photoperiodic treatments simulating 5 different wintering latitudes ranging from central

Africa to central Europe. The timing of prenuptial moult, spring migratory activity and testicular growth was determined. First results suggest that birds advance springtime events with decreasing migration distance. This response along the latitudinal photoperiodic gradient may facilitate the evolutionary adjustment of migratory behaviour to earlier spring conditions on the breeding grounds.

SYMP14-P4 Climate change and the timing of breeding variability of great and blue tits over the last decades

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In the Western Palaearctic, recent climate change has consequences on avian breeding phenology within populations. Here, laying date variability, measured by the coefficient of variation, of great tit *Parus major* and great tit *Parus caeruleus* among populations over the Western Palaearctic are examined in relation to climatic fluctuations, measured by the winter North Atlantic Oscillation (NAO) index. Within breeding sites, the coefficient of variation of laying date was negatively related to the year-specific mean laying date. Thus, when great and blue tit females lay earlier the coefficient of variation of laying date is larger. The present study shows that across populations there has been an increase of laying date variability over the last decades across Europe. Moreover, egg-laying date variability was also increasing in relation to climatic fluctuations, measured by the winter NAO-index. These combined analyses for the two species controlled for potentially confounding variables such as latitude, longitude, elevation and habitat of each study site. The consequences of climatic fluctuations on breeding phenology of insectivorous passerine birds probably differ among early and later laying pairs. Late laying females, presumably due to a constraint on earlier lay dates, are not able to advance their onset of breeding in response to climatic fluctuations. This fact may be an explanation for the decline in average reproductive success and fledgling condition, and for the increased selection for early laying females observed in some European passerine populations.

SYMP14-P5 Have birds responded similarly to climate warming in two different periods?

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Recent studies concerning climate effects on the arrival times of birds have shown that most species arrive earlier after warm winters. Also an apparent trend that the timing of first arrivals has become earlier has been shown in many species. Most studies have focused on the effects of the recent warming period. We studied the timing of first arrivals of 13 species to Southern Finland using long-term phenology data collected by Societas Scientiarum Fennica and the Ornithological society of Turku. The species selected were those that live close to human settlements or are otherwise well-known species such as cuckoo, skylark, Swallow and starling. I compare the species' responses in two equally long periods of climate warming, one in the beginning (~ 1890–1930) and the other in the end of 20th century (~1960–2000). During both warming periods the mean spring temperature

rose about 2°C. I seek answers to the following questions: (1) Was response to temperature change different in the beginning of 20th century compared to the recent warming? (2) Did all studied species show similar response?