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SYMP12 Biological timing mechanisms in birds

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The most important environmental information to coordinate seasonal rhythmicity of physiology and behaviour in birds is the annual cycle of photoperiod. Changes of the environmental light/dark cycle are measured by circadian systems and have to be encoded as well as decoded within the animal to finally synchronize circadian and circannual mechanisms with the environment. Besides photoperiodic information, a large number of external and internal factors may influence daily and annual rhythmicity in birds. The goal of this symposium is to review existing knowledge about regulatory mechanisms and provide new insight into molecular and genetic as well as physiological and behavioural phenomena associated with the coordination of daily and annual rhythms in birds.

SYMP12-1 Time coding mechanisms in songbirds: News about avian circadian systems

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Birds have the capacity to perceive information about the photic environment by retinal, pineal, as well as deep encephalic photoreceptors and there are at least three neural circadian oscillators involved in the regulation of circadian rhythms at the whole-organism level: the retina, the pineal gland, and a hypothalamic oscillator. In the house sparrow, a model species in circadian research, the pineal gland plays a major role in circadian time-keeping by encoding time of day as well as time of year and transdcuing environmental information into a particular melatonin signal. Additionally, a complex spatio-temporal pattern of clock gene expression can be found in the SCN and in the lateral hypothalamus suggesting the presence of one or several hypothalamic clocks that may be involved in regulating both daily and annual rhythms. Rhythms of clock genes can also be found in other brain regions, including the tectum opticum and the cerebellum, as well as in many peripheral non-neuronal tissues, including liver, heart, lung, and gastro-intestinal tract. Complex communication mechanisms between individual components of the circadian system may play a major role in coordinating and synchronizing rhythms on a daily but also seasonal basis. These data provide the basis for a better understanding of the hierarchical organisation of the circadian pacemaking system of birds and the role individual circadian oscillators may play in regulating daily and annual rhythmicity of birds.

SYMP12-2 Annual rhythms in birds with special reference to timing of reproduction in the great tit (*Parus major*)

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Timing of reproduction is a under strong selection in species where favorable food conditions are only available for a short period of time. Great tits provide their nestlings with caterpillars that are only abundant for 3–4 weeks and have to initiate laying a month before this peak in food abundance. They therefore have to rely upon cues from the environment that predict this food peak. We use field

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studies as well as controlled environment aviaries to assess which cues the great tit uses and how the 'response mechanism' translates these cues into a phenotype (laying date). We show that bud burst of oak trees is not used as a cue while temperature is found to affect laying date in a controlled temperature aviary set-up where the only difference between the treatment groups is temperature. This finding is supported by a statistical model on laying date using our long-term population studies (1955 – present) in which laying date is affected by temperature in interaction with photoperiod. Furthermore we show that spatial variation in territory quality plays a role in timing of reproduction and also that the response mechanism is shaped by experience. Field experiments show that birds adjust their laying date to the perceived mistiming in the previous year. These finding are also relevant for the question how populations can respond to the increased selection for early laying due to large scale climate change.

SYMP12-3 Reaction norms of egg laying date in Mediterranean populations of blue tits: a genetic basis for responses to photoperiod and non-photoperiod factors?

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Blue tits (*Parus caeruleus*) from Corsica and mainland southern France show remarkable variation in their onset of egg laying, even at a micro-geographic scale. Population differences in the timing of reproduction are often closely linked with spatial variations in the peak-date of caterpillar availability, key prey to raise chicks. To test whether these population differences in egg laying dates have a genetic basis, a special experimental design was set up such that captive blue tits can breed with success in large outdoor aviaries at similar latitudes and altitudes to their wild counterparts. Both comparative and experimental studies indicate that individual responses to photoperiodic and non-photoperiodic factors are responsible for genetic differences in average reaction norms between three Mediterranean blue tit populations.

SYMP12-4 Optimal timing and density-dependent factors influence nest survival in the hooded crow *Corvus corone cornix*

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Factors influencing survival of eggs and nestlings of the hooded crow *Corvus corone cornix* were studied in „Ujście Warty" National Park, W Poland. During the years 2000–2002, fates of 108 nests (containing at the start of incubation 467 eggs) were tracked. Data setup of the form (t_i, β_i) was used, where t_i is the observed survival time of an egg or nestling in the nest and $\beta_i = 0$ if the observation is censored (i.e. nest was not visited or its fate was unknown) and $\beta_i = 1$ if death is observed. Thus, survival estimates made here concern probability of survival of an egg, and later nestling, to fledging (53 days). Survival functions over time were estimated for each year (as stratum) separately. Several factors possibly influencing survival were tested: height of the nest, date of laying the

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first egg (expressed as residual from yearly median), water depth and population local density index (the mean distance to the 5 nearest neighbours). For testing the influence of covariates, the nonlinear extension of proportional-hazards model was used.

Totally, survival of the whole nesting period ranged from 0.410 till 0.576 with the 3–year mean of 0.486 (95% CI: 0.443–0.534). Differences between years were significant. Mean survival rate for incubation period only (till the 21 day) was 0.891 (0.863–0.920), without significant differences between years. The most critical period was hatching. In each year, there was a remarkably drop in survival during this short period, reaching from 19% to 22%.

Two factors significantly influence survival: timing and local nest density. Hazard function is nonlinear in the domain of nest initiation date, showing the global minimum corresponding to maximum intensity of egg laying. The local nest density is less important, with hazard function reaching a maximum and steep decrease for small population densities. However, the bulk of crow population nests was situated in places of greater nest density, associated with higher risk.
We conclude, that crows can precisely estimate the best (in terms of their progeny survival) timing for reproduction. The majority of population starts egg laying exactly within the short period connected with the lowest risk. The choice of place of reproduction, unlike the time, is not constrained by the progeny survival.

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