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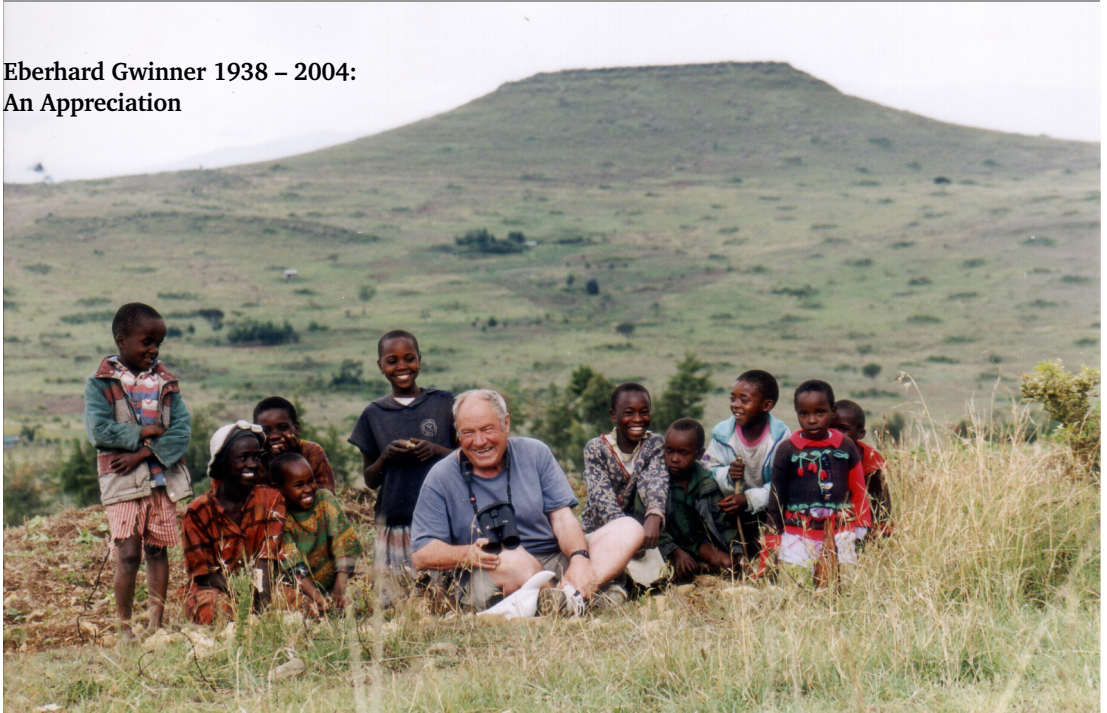
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In Memoriam

Eberhard Gwinner 1938 – 2004: An Appreciation



Ebo during his last field trip to Kenya in 2002, at home among children. Courtesy of Ingrid Schwabl.

Born in Stuttgart 26.12.1938, Ebo Gwinner was fascinated by birds from an early age. His first publication – on a mixed clutch of gull and coot eggs – appeared when he was 18 years of age (1956, *Orn. Mitt.* 8: 215). Hans Löhrl (Vogelschutzwarte Ludwigsburg) propelled him into scientific ornithology and provided the inspiration to acquire skills such as learning to observe living birds minutely, and mastering the tricks involved in hand-raising nestlings. His PhD studies started auspiciously under the guidance of another ornithological giant, Gustav Kramer. The Max Planck Gesellschaft had decided to provide Kramer as well as Jürgen Aschoff each with a department of their own at Walddorf near Tübingen, as units of the Institut für Verhaltensphysiologie. In 1959 Ebo embarked on a study of social behaviour of the Raven at Walddorf, observing intensively 18 tame individuals (some of which had been raised

by Kramer himself). In the early stages of the study Kramer lost his life climbing to reach the nest of wild rock pigeons to obtain birds for his orientation work and Gwinner completed his thesis (published in 1964 in *Z. für Tierpsychol.* 21: 657–748) under the inspiring supervision of Konrad Lorenz and with the support of Aschoff and Löhrl. With his unerring flair in spotting talent, in December 1964 Professor Aschoff invited Gwinner to join his group at the Max Planck Institut für Verhaltensphysiologie (meanwhile established in Erling-Andechs not far from Munich). Here commenced a highly fruitful career that was to end with Ebo himself at the helm of the Institute, now renamed the Max Planck Institute for Ornithology.

In his new surroundings Ebo was soon at home in the theme of bio-rhythms, one of the core problems attacked by Aschoff's group. Aschoff himself

had predicted in a 1955 review that annual timing might be largely under endogenous control, but in the 1960s the issue of whether for example early breeding was controlled by circannual rhythms, or simply tracked seasonal cues in the environment, was hotly debated. The problem of seasonal timing in long-distance migratory birds wintering under the uniform photoperiod of equatorial Africa was especially puzzling. In a brilliant series of experiments with caged Willow *Phylloscopus trochilus* and Wood Warblers *P. sibilatrix* kept under constant conditions of an artificial 12:12 LD cycle in Germany, Gwinner demonstrated that the annual program of "Zugunruhe" (nocturnal restlessness reflecting migratory motivation) reappeared year after year. Importantly, this shifted incrementally with regard to the natural seasonal cycle outdoors that the birds could not perceive. This was sure proof that the annual cycle was endogenously anchored in these birds (taken into isolation at 4 months of age, before their first migratory journey). In parallel experiments, warblers flown to the Congo when at the height of their migratory restlessness, kept up their "Zugunruhe" just as long as birds that had not experienced the environmental stimuli of the wintering areas. By a clever calibration of the amount of migratory restlessness of his caged birds against known timing of the first (European) portion of their actual migratory journey, Gwinner proposed that the naive warblers were completing an endogenous migratory program that would carry them on a defined route at a given speed until it "ran out" and deposited them in their winter quarters (see Fig. 1). This work (Gwinner 1968, *J. Ornithol.* 109: 70–95) revolutionized thinking on the role of endogenous programs in migratory organisms, and was deservedly crowned with the Erwin Stresemann prize of the Deutsche Ornithologen-Gesellschaft when first awarded in 1973 (Glutz von Blotzheim, Immelmann, Mayr, Thielcke & Voous, 1974, *J. Ornithol.* 115: 495–496). In the meantime Ebo had spent almost two years working in the laboratories of Donald Farner (University of Washington, Seattle) and Colin Pittendrigh (Stanford University). He had thus absorbed the fine points

of both experimental techniques and the underlying theory of endogenous rhythms from the three groups at that time dominating the field of chronobiology worldwide. Although he confided to one of us at the time that he found the severe regime at Farner's lab somewhat harrowing, Ebo gave a milder view in retrospect (Gwinner 1989, *J. Ornithol.* 130: 393–395) and emulated Farner himself in keeping abreast of novel techniques and incorporating them smoothly in his own work. This intensive period abroad laid the seed for Gwinner's spate of reviews and his 1986 monograph on circannual rhythms.

Another major breakthrough came when Gwinner teamed up with Wolfgang Wiltschko (1974 *Naturwissenschaften* 61: 406, 1978 *J. Comp. Physiol.* 125: 267–273, 1980 *Behav. Ecol. Sociobiol.* 7: 73–78). Together they examined how avian migrants following a route necessitating change of compass heading along the way, dealt with this problem. They demonstrated that these long-distance migrants were equipped with an *endogenous* program that regulated appropriate adjustments in preferred heading keyed in to seasonal time and the amount of motor activity expended in Zugunruhe. This work was carried out with Garden Warblers *Sylvia borin* that held centre stage in Gwinner's laboratory for many years. By the mid-1980s ten bird species studied in elegant experiments by Gwinner and colleagues were found to conform to the pattern of an endogenous circannual rhythm governing the complex seasonal pattern of reproduction, moult and migration. The question of how this endogenous program is synchronized in nature with the environment led to new experiments. Gwinner chose the *Phylloscopus* sibling species *trochilus* Willow (long-distance migrant) and *collybita* Chiffchaff (short-distance migrant) and showed that exogenous, environmental factors exert a greater influence on the short-distance migrant compared to the predominantly endogenous control of the long-distance migrant in faraway Africa (Gwinner 1972 *Proc. XV Int. Ornithol. Congr.* 218–236). Photoperiod was considered the prime clue, and in a revealing comparison Gwinner (1989 *J. Ornithol.*

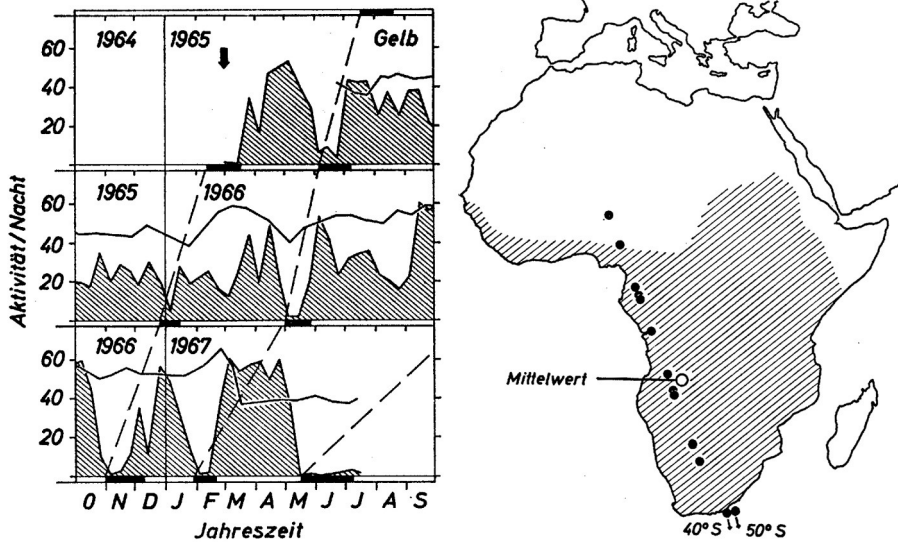


Figure 1. Illustrations from Gwinner's 1968 classic on circannual rhythms in willow warblers. The left panel depicts registrations of an individual ("Gelb") originating in Germany and raised by hand and kept under constant conditions of LD 12:12 for three successive years. Shown are migratory restlessness (hatched blocs, nocturnal activity score) body mass (line) and moult (black bar). On the right, the calculated endpoints of autumn migration in 13 caged individuals, where registrations of migratory restlessness have been calibrated against short-term migratory performance of ringed individuals in free flight. Mean falls neatly within the known winter range (hatched).

130: 1–13) examined the species pair Pied *Ficedula hypoleuca* and Collared Flycatcher *F. albicollis*. Both are long-distance migrants wintering in Africa, but while Pied Flycatchers winter around 5–10°N, Collared Flycatchers winter further south, mainly below the equator. When maintained in captivity through the winter under the light regimes typical of wintering at either 10°N, 0° or 20°S, Collared Flycatchers showed gonadal growth and commenced migratory restlessness in spring on schedule. Pied Flycatchers, on the contrary, showed the normal response only under the photoperiod of 10°N, the annual rhythm being suppressed under the other light regimes. Gwinner reasoned that the daylength needed to end the refractory period and thus reset the annual clock was set differently in these two species, reflecting the wider latitudinal spread of the Collared Flycatcher in winter. This raises the question why some species are saddled with narrower tolerances

regarding the cues needed to reset the program and set spring events in train, but in any case both Pied and Collared Flycatchers reacted appropriately to the photoperiod typical for their normal wintering zone. These problems Gwinner (1990) discussed at length in his contribution to the symposium volume *Bird Migration: Physiology and Ecophysiology* that he organized (convened at Tutzing in 1988).

At about this time (mid-1980s) an ambitious new program was undertaken when Gwinner decided to capitalize on the variation existing within a wide-ranging species by bringing differences between four subspecies of Stonechats *Saxicola torquata* into focus (there is currently debate in taxonomic circles about elevating some of these subspecies to full species). African stock from the sedentary subspecies (Kenya) were raised side by side with the central European (migratory) to which were added the Irish (partial migrant)

subspecies, and the long-distance migrant subspecies breeding in Kazakhstan. This 'common garden experiment' in which Barbara Helm played a key part allowed explorations of the genetic basis of the endogenous program as well as life-history features such as nestling growth rate and clutch size by interbreeding experiments (genetic contribution and phenotypic plasticity). Fieldwork in Kenya (Nakuru) and Tanzania added extra spice to these efforts, that also impinged on the broader implications of the classic concept of the "pace of life" (Wikelski et al. 2003, Proc. Roy. Soc. Lond. B 270: 2383–2388). This rapidly expanding program provided niches for interlocking PhD projects (König, Scheuerlein, Roedl, Canoine, Helm, Raess, Geue) and was at the heart of Ebo's planning at the time of his sudden death. Indeed he had intended hosting a planning session to map avenues onto the future for us all in October 2004 but by then Gwinner was no longer with us.

Intent on unravelling the *annual* organization of migration, moult and reproduction, Ebo realized that he could not neglect *daily* timing mechanisms, crucial in the measurement of daylength, and thus indispensable in maintaining proper synchronization between internal and external annual time. Through the years his department kept up a strong program on avian circadian biology. Unlike the leading role of work on birds in circannual rhythms, most of the current action in circadian rhythms is in mammals. Nonetheless, Ebo achieved several classic breakthroughs widely acknowledged by the chronobiological community worldwide. Notable was his early demonstration of endocrine sensitivity of circadian pacemakers (1974, Science 185: 72–74) and the revelation of the internal feedback from melatonin (1978, J. Comp. Physiol. 127: 209–213) which plays such an important role in how animals measure daylength. Numerous other studies, including recent probing into the underlying molecular-genetic mechanisms consolidated the position of the department in Erling at the pinnacle of research in avian chronobiology.

Ebo's abrupt demise (7 September 2004) due to a catastrophic illness leaves a sorry gap in the

international scene, but his team at the MPI in Erling is still in the midst of publishing insightful results (see PLoS Biol. April 2006: e110) and will doubtless follow up the work on hormonal control of the endogenous program that has already proven so fruitful. The future of the line of research initiated at MPI in Erling-Andechs is in capable hands and we can look forward to many surprises both at Erling and elsewhere.

Gwinner's 'type locality' was undoubtedly the battery of sophisticated environmental chambers at Erling. Here some critical experiment or other seemed always on the brink of a breakthrough as he explained in his lucid and infectious manner what was going on against the background of the restlessly hopping subjects, a few stray feathers in his hair. But Ebo was equally at home in fieldwork, which he enjoyed immensely. Gwinner gave his team strong support (director since 1991, from 1998 recognized as the Max-Planck Institut für Ornithologie) and supported whole-heartedly the construction of a wind-tunnel for the flight energetics line developed by his colleague Herbert Biebach. This work followed on from enterprising Africa expeditions (aimed at elucidating the Sahara crossing) undertaken by Biebach and colleagues from Switzerland combining radar tracking with short-term experimental manipulations of birds 'caught on the road'. These adventures resulted in models of fat deposition and depletion, defining stopover decisions in relation to individual stores, and led to the need to evaluate flight energetics directly (see Biebach & Bauchinger p.269–280 in Berthold, Gwinner & Sonnenschein 2003).

Throughout his career Ebo showed great loyalty to the ornithological societies, publishing in their journals (17 papers in *JOURNAL FÜR ORNITHOLOGIE* alone, and contributing to *AUK*, *CONDOR*, *IBIS*, *VOGELWARTE* among others) and often lecturing at ornithological meetings. Hallmark of his impressive presentations was the enormous and often visible effort Ebo devoted to providing an up-to-the-minute overview, taking endless care to enunciate with compulsive logic and absolute clarity where the urgent next steps could be expected.

This unfolding of complex vistas was a special feature of his way of thought, and the many reviews Gwinner contributed (14 at least) share this special ingredient and must have greatly aided in bringing new recruits into his school. Gwinner held a teaching appointment at Munich University and went to great pains to kindle enthusiasm in those as yet uncommitted, and given the intellectual and practical expertise collected in his team, his institute appeared underused. In fact Ebo's style towards students and visiting scientists emphasized the intensity of collaboration in a highly focussed team. The PhD students he coached (fifteen in all) now sprinkled over the world and the many postdoc researchers who were attracted to Erling represent a powerful scientific legacy that over the coming decades will disseminate and elaborate on Gwinner's ideas (documented in more than 250 publications) and justify his holistic approach. We all acknowledge a debt to his wife Helga, a trained ornithologist in her own right, who with the family of one daughter and two sons provided the understanding and backing Ebo needed to throw himself wholeheartedly unto his work. Gifted with a spontaneous nature Ebo was a good companion under all circumstances and we treasure our memories of impromptu discussions and joint field excursions tracking down elusive birds.

Throughout his long career Ebo interacted with his friend from student days Peter Berthold who became head of the Vogelwarte Radolfzell of the MPI and also enjoyed the benign support of Jürgen Aschoff as its official director (1967–1981, see Gwinner 2000 in *Ibis* 142: 181). Berthold's group was eventually administratively united with Gwinner's unit as section of the Max-Planck-Forschungsstelle für Ornithologie. Berthold (who retired in 2004) has told his side of the story (*Vogelwarte* 43: 59–60) and the extended collaboration of these 'scientific twins' had a stimulating but also corrective influence as the two investigators kept each other on their toes. In approach and temperament the two differed but in many ways their efforts were complementary and we must acknowledge the wisdom of the Max Planck phi-

losophy in allowing the two sister departments an existence of their own providing the ideal environment for an element of healthy rivalry. In retrospect the three constellations (The Wiltschkos at Frankfurt with their brilliant pupil Helbig, Gwinner at Erling and Berthold at Radolfzell) interacted to provide a series of breakthroughs that underlined the special power of imaginative experimentation with hand-raised birds on a scale never witnessed before. In combination with intensive fieldwork these efforts fired the imagination of ornithologists the world over and transformed the study of bird migration bringing it to the front ranks of experimental biology, a fitting tribute to the unstinting support that made it all possible. With his inquiring mind and facility in making contacts throughout the scientific community Ebo Gwinner powered by his zest for life and unquenchable curiosity has made a lasting contribution that places him in the very first rank of his generation worldwide.

Books and symposium volumes edited by Ebo Gwinner

- Gwinner E. 1986. *Circannual rhythms*. Springer Verlag, Heidelberg-Berlin
- Daan S. & Gwinner E. (eds) 1989. *Biological Clocks and Environmental Time*. Guilford Press, New York & London.
- Gwinner E. (ed) 1990. *Bird Migration. Physiology and Ecophysiology*. Springer Verlag, Berlin.
- Berthold P, Gwinner E. & Sonnenschein E. (eds) 2003. *Avian Migration*. Springer Verlag, Berlin & Heidelberg.

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