In Memoriam Eberhard Gwinner 1938 – 2004
Drent, Rudi; Daan, Serge

Published in:
Ardea

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2006

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.
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 Löhr (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 Löhr. 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 & Vouos, 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.
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)
subsidiary, and the long-distance migrant sub-
species 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
270: 2383–2388). This rapidly expanding program
provided niches for interlocking PhD projects
(König, Schueerlein, 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 real-
ized that he could not neglect daily timing mecha-
nisms, crucial in the measurement of daylength,
and thus indispensable in maintaining proper syn-
chronization 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
daylight. 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 ener-
gectics 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 col-
leagues from Switzerland combining radar track-
ing 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 individ-
ual 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 loy-
alty to the ornithological societies, publishing in
their journals (17 papers in JOURNAL FÜR ORNI-
THOLOGIE alone, and contributing to AUK, CONDOR,
IBIS, VOGELWARTE among others) and often lectur-
ing 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 clar-
ity 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 philosophy 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 forefront 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


The authors acknowledge the special help provided by Dr Barbara Helm of Max Planck Institut für Ornithologie, Erling-Andechs.

Rudi Drent and Serge Daan, Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands