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## **Obituary: Rainer Rosengren**

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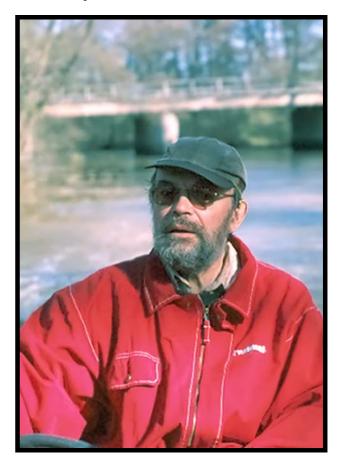
One of the pioneers in ant research, Rainer Rosengren, passed away on February 4th, a couple of months before his 70th birthday. Rosengren's work focused on red wood ants and his work on route fidelity, visual memory and recruitment behaviour in these ants has gained much attention among students of social insects. A lesser known part of his literary production concerns humans as biological creatures. In this vein he wrote several essays on ethology and evolutionary biology in a true Darwinian spirit during the 1960s. These essays build on a Lorenzian tradition and picture him as a persuasive writer eager to engage in debates. Indeed, these essays brought into focus issues that later were championed by E.O. Wilson and set off the sociobiology controversy.

During his entire career he worked in Helsinki University at the Department of Zoology, later renamed to the Department of Ecology and Systematics, where he held a position as a lecturer. In 1999 he was awarded the title Professor by the president of Finland, for his scientific achievements. His own work centered on red wood ants in the Formica group, and his interest in these ants began long before he began his studies at the university. Despite his strong focus on social insects, he had an extremely broad interest in all issues related to evolutionary biology. Being a broadly educated person, he also was an inspiring teacher. Consequently he attracted a number of gifted students who were not afraid to tackle also difficult problems. The research topics encompassed orientation, memory and diurnal rhythms as well as reproductive allocation and sex ratio studies. In collaboration with Pekka Pamilo, he published several seminal papers on the reproductive biology of Formica ants, among the first ones to use genetic markers in assessing colony kin structure and population structure in these ants. In a paper published already in 1983 together with Pamilo in Acta Entomologica Fennica, he outlined many of the ideas and concepts that were to become central to social insect research a decade later. This paper focused on the causes and consequences of polygyny and polydomy.

Rosengren acted as a catalyst for social insect research in Finland. Without his initiative and inspiration ant research in Finland would probably not exist.

Among his first PhD students were Kari Vepsäläinen and Pekka Pamilo, both internationally well known, and others were to follow later. During the 1990s he was actively participating in several research projects. Most of his efforts he devoted to experimental work on learning and memory in ants, but also several projects on the genetic population structure of *Formica polyctena* and *Formica rufa* were on his agenda.

Rosengren's most recent literary contributions comprise an extensive essay on the Finnish philosopher Edward Westermarck's relation to Darwin. This essay was finished already a few years ago, but still awaits publication. It uniquely captures Rosengren's scientific qualities, including his perpetual willingness to learn new concepts, to adopt new methods and to question conventional wisdom. This atti-



Rainer Rosengren, 2001 (photograph by Christine Johnson).

tude, combined with an exceptionally broad general education, a kind understanding of all things human and a wonderful sense of humour made him a truly inspiring colleague and dear friend. His multifaceted character and interests were perhaps best captured by the literature he had on his bedside when he died – The Book of Job and a 500 page manual for advanced statistics.

## **List of scientific publications by Rainer Rosengren** (except abstracts of congress contributions and purely popular work)

- ROSENGREN, R. 1969: Orientering och signalering hos myror. Nordenskiöld-samfundets tidskrift 29: 62-73.
- ROSENGREN, R. 1969: Notes regarding the growth of a polycalic nest system in *Formica uralensis* RUZSKY. Notulae Entomologicae 49: 211-230.
- ROSENGREN, R. 1971: Route fidelity, visual memory and recruitment behaviour in foraging wood ants of the genus *Formica* (Hymenoptera, Formiciade). Acta Zoologica Fennica 133: 1-106.
- Pamilo, P., Vepsäläinen, K. & Rosengren, R. 1975: Low allozymic variability in Formica ants. – Hereditas 80: 293-296.
- ROSENGREN, R. 1977: Foraging strategy of wood ants (*Formica rufa* group) I. Age polyethism and topographic traditions. Acta Zoologica Fennica 149: 2-30.
- ROSENGREN, R. 1977: Foraging strategy of wood ants (*Formica rufa* group). II. Nocturnal orientation and diel periodicity. Acta Zoologica Fennica 150: 1-30.
- ELGERT, B. & ROSENGREN, R. 1977: The guest ant *Formicoxenus nitidulus* follows the scent trail of its wood ant host (Hymenoptera, Formicidae). – Memoranda Societatis Fauna Flora Fennica 53: 35-38.
- ROSENGREN, R. & PAMILO, P. 1978: Effect of winter timber felling on behaviour of foraging wood ants (*Formica rufa* group) in early spring. Memorabilia Zoologica 29: 143-155.
- PAMILO, P., ROSENGREN, R., VEPSÄLÄINEN, K., VARVIO-AHO, S. & PISARSKI, B. 1978: Population-genetics of *Formica* ants. 1. Patterns of enzyme gene variation. Hereditas 89: 233-248.
- PAMILO, P., VEPSÄLÄINEN, K., ROSENGREN, R., VARVIO-AHO, S. & PISARSKI, B. 1979: Population-genetics of *Formica* ants. 2. Genetic differentiation between species. Annales Entomologici Fennici 45: 65-76.
- ROSENGREN, R., VEPSÄLÄINEN, K. & WUORENRINNE, H. 1979: Distribution, nest densities and ecological significance of wood ants (the *Formica rufa* group) in Finland. Bulletin SROP 2: 181-213.
- ROSENGREN, R. 1979: Labialkörtlesyndromet som "epidemi" i en tät stackpopulation av *Formica aquilonia* (Hymenoptera, Formicidae). Memoranda Societatis Fauna Flora Fennica 55: 73-84.

- ROSENGREN, M., ROSENGREN, R. & SODERLUND, V. 1980: Chromosome-numbers in the genus Formica with special reference to the taxonomical position of *Formica uralensis* RUZSKY and *Formica truncorum* FABR. Hereditas 92: 321-325.
- ROSENGREN, R. 1981: En tredje fyndort av den svarta hästmyran *Camponotus vagus* (SCOPOLI) i sydvästra Finland (Formicidae) (with English summary). Notulae Entomologicae 61: 227.
- ROSENGREN, R. & CHERIX, D. 1981: The pupa-carrying test as a taxonomic tool in the *Formica rufa* group. In: HOWSE, P.E. & CLÉMENT, J.-L. (Eds.): Biosystematics of Social Insects. Academic Press, London, New York, pp. 263-281.
- ROSENGREN, R., CHERIX, D. & POUTANEN, R. 1981: The pupa-carrying test as a taxonomic tool in the *Formica rufa* group. Memoranda Societatis Fauna Flora Fennica 57: 14.
- ROSENGREN, R., VEPSÄLÄINEN, K. & WUORENRINNE, H. 1981: Distribuzione, densità delle colonie ed importanza ecologica delle formiche del gruppo *Formica rufa* in Finlandia. – Collana Verde 59: 239-259.
- PAMILO, P. & ROSENGREN, R. 1983: Sex-ratio strategies in *Formica* ants. Oikos 40: 24-35.
- ROSENGREN, R. & PAMILO, P. 1983: The evolution of polygyny and polydomy in mound building *Formica* ants. Acta Entomologica Fennica 42: 65-77.
- GYLLENBERG, G. & ROSENGREN, R. 1984: The oxygenconsumption of submerged *Formica* queens (Hymenoptera, Formicidae) as related to habitat and hydrochoric transport. – Annales Entomologici Fennici 50: 76-80.
- PAMILO, P. & ROSENGREN, R. 1984: Evolution of nesting strategies of ants genetic evidence from different population types of *Formica* ants. Biological Journal of the Linnean Society 21: 331-348.
- ROSENGREN, R. 1985: Internest relations in polydomous *Formica*-colonies (Hymenoptera, Formicidae). Mitteilungen der deutschen Gesellschaft für allgemeine und angewandte Entomologie 4: 288-291.
- ROSENGREN, R., CHERIX, D. & PAMILO, P. 1985: Insular ecology of the red wood ant *Formica truncorum* FABR.
  I. Polydomous nesting, population size and foraging. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 58: 147-175.
- ROSENGREN, R. & FORTELIUS, W. 1986: Ortstreue in foraging ants of the *Formica rufa* group hierarchy of orienting cues and long-term-memory. Insectes Sociaux 33: 306-337.
- ROSENGREN, R. 1986: Competition and coexistence in an insular ant community a manipulation experiment (Hymenoptera, Formicidae). Annales Zoologici Fennici 23: 297-302.

- ROSENGREN, R. 1986: Nest founding in *Camponotus herculeanus* and *Formica fusca* (Hymenoptera, Formicidae). Notulae Entomologicae 66: 121-123.
- ROSENGREN, R. & PAMILO, P. 1986: Sex-ratio strategy as related to queen number, dispersal behavior and habitat quality in *Formica* ants (Hymenoptera, Formicidae). Entomologia Generalis 11: 139-151.
- ROSENGREN, R. & FORTELIUS, W. 1986: Light-dark-induced activity rhythms in *Formica* ants (Hymenoptera, Formicidae). Entomologia Generalis 11: 221-228.
- ROSENGREN, R., CHERIX, D. & PAMILO, P. 1986: Insular ecology of the red wood ant *Formica truncorum* FABR. II. Distribution, reproductive strategy and competition. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 59: 63-94.
- ROSENGREN, R. & FORTELIUS, W. 1987: Trail communication and directional recruitment to food in red wood ants (*Formica*). Annales Zoologici Fennici 24: 137-146.
- ROSENGREN, R., FORTELIUS, W., LINDSTROM, K. & LUTHER, A. 1987: Phenology and causation of nest heating and thermoregulation in red wood ants of the *Formica rufa* group studied in coniferous forest habitats in southern Finland. Annales Zoologici Fennici 24: 147-155.
- FORTELIUS, W., PAMILO, P., ROSENGREN, R. & SUND-STRÖM, L. 1987: Male size dimorphism and alternative reproductive tactics in *Formica exsecta* ants (Hymenoptera, Formicidae). Annales Zoologici Fennici 24: 45-54.
- ROSENGREN, R. & SUNDSTRÖM, L. 1987: The foraging system of a red wood ant colony (*Formica* s.str.). In: PASTEELS, J.M. & DENEUBOURG, J.L. (eds.): From individual to collective behaviour in social insects. Experientia, Supplement 54: 117-138.
- Passera, L., Keller, L., Grimal, A., Chautems, D., Cherix, D., Fletcher, D.J.C., Fortelius, W., Rosengren, R. & Vargo, E.L. 1990: Carbohydrates as energy-source during the flight of sexuals of the ant *Formica lugubris* (Hymenoptera, Formicidae). Entomologia Generalis 15: 25-32.
- CHERIX, D., CHAUTEMS, D., FLETCHER, D.J.C., FORTELIUS, W., GRIS, G., KELLER, L., PASSERA, L., ROSENGREN, R., VARGO, E.L. & WALTER, F. 1991: Alternative reproductive strategies in *Formica lugubris* ZETT. (Hymenoptera, Formicidae). Ethology Ecology & Evolution 1: 61-66.

- ROSENGREN, R. & SUNDSTRÖM, L. 1991: The interaction between red wood ants, *Cinara* aphids and pines a ghost of a mutualism past? In: CUTLER, D.F. & HUX-LEY, C.R. (eds.): Interaction between ants and plants. Oxford University Press, Oxford, pp. 80-92.
- GORDON, D.M., ROSENGREN, R. & SUNDSTRÖM, L. 1992: The allocation of foragers in red wood ants. Ecological Entomology 17: 114-120.
- CHERIX, D., FLETCHER, D.J.C., CHAUTEMS, D., FORTELIUS, W., GRIS, G., KELLER, L., ROSENGREN, R., VARGO, E.L.
  & WALTER, F. 1993: Attraction of the sexes in *Formica lugubris* ZETT. (Hymenoptera, Formicidae). Insectes Sociaux 40: 319-324.
- FORTELIUS, W., ROSENGREN, R., CHERIX, D. & CHAUTEMS, D. 1993: Queen recruitment in a highly polygynous supercolony of *Formica lugubris* (Hymenoptera, Formicidae). Oikos 67: 193-200.
- WALTER, F., FLETCHER, D.J.C., CHAUTEMS, D., CHERIX, D., KELLER, L., FRANCKE, W. FORTELIUS, W. ROSEN-GREN, R. & VARGO, E.L. 1993: Identification of the sex-pheromone of an ant, *Formica lugubris* (Hymenoptera, Formicidae). – Naturwissenschaften 80: 30-34.
- ROSENGREN, R., SUNDSTRÖM, L. & FORTELIUS, W. 1993: Monogyny and polygyny of *Formica* ants a result of alternative dispersal tactics? In: Keller, L. (ed.): Queen number and sociality in insects. Oxford University Press, Oxford, pp. 308-333.
- PAMILO, P., SUNDSTRÖM, L., FORTELIUS, W. & ROSEN-GREN, R. 1994: Diploid males and colony-level selection in *Formica* ants. Ethology Ecology & Evolution 6: 221-235.
- ROSENGREN, R., CHAUTEMS, D., CHERIX, D., FORTELIUS, W., & KELLER, L. 1994: Separation of two sympatric sibling species of *Formica* L. ants by a behavioural choice test based on brood discrimination. Memorabilia Zoologica 48: 237-249.
- WALIN, L., SUNDSTROM, L., SEPPA, P. & ROSENGREN, R. 1998: Worker reproduction in ants a genetic analysis. Heredity 81: 604-612.
- SALO, O. & ROSENGREN, R. 2001: Memory of location and site recognition in the ant Formica uralensis (Hymenoptera: Formicidae). Ethology 107: 737-752.
- ROSENGREN, R. & TAKALA, J.-P. 2001: Edward Westermarck's evolutionary approach. Unpublished manuscript.