

Matthew J. G. Gage (1967–2022)

Researcher who studied fundamental questions about sexual selection, and an inspiring and kind colleague and friend.

Professor Matthew Gage died on 15 January 2022 at age 55. His premature death from cancer has robbed evolutionary ecology of one of its most respected researchers. Matt made major research contributions into our understanding of sperm competition, and conducted ground-breaking research into the role of sexual selection in extinction, inbreeding and the effects of thermal stress on fertility. Most significant of all, Matt exemplified how to do it right — how to be an effective and inspiring research leader, colleague and teacher. He had a unique brand of incisiveness, a keen mind, great wit and a seemingly bottomless generosity of spirit. This set of qualities represents a very rare legacy.

Matt had keen and diverse interests in the natural world (Fig. 1), fostered from an early age by his immersion in the beauty and remoteness of the Gage family home on Rathlin Island in Northern Ireland. Many of the major themes of his subsequent research career were informed by this curiosity and were evident in the range of topics and approaches taken in his research programmes. His approach was superbly effective — define the important and ‘big’ research question, get the right approach and system, and have the confidence to develop the (often large-scale) programme needed to get the answer.

Matt studied for his BSc (1989) and then his PhD (1992) at the University of Manchester, UK. He then gained an independent Natural Environment Research Council (NERC) Fellowship, which he took to the University of Liverpool, UK, before undertaking a Fellowship at the University of Western Australia in 1995, which was also the year in which he gained a prestigious ten-year University Research Fellowship from the Royal Society. He held this at Liverpool until 2001, when he moved to the School of Biological Sciences at the University of East Anglia (UEA), UK, where he remained for the rest of his career, becoming professor in 2010.

Matt’s PhD research drew upon his fascination with understanding sperm form and function, and the role of sperm competition in shaping sperm morphometry, themes he then developed during his time at Liverpool as a key member of Geoff Parker’s field-defining



Fig. 1 | Matthew Gage in 2012, flying his peregrine falcon in Caithness, Scotland. Matt excelled in his major hobby as one of the UK’s top falconers. Photograph by Michael Calvin.

sperm competition group in the 1990s. Geoff notes that “Matt was a highly talented scientist, making many original and fundamental contributions, including being one of the first to propose and demonstrate strategic sperm allocation”, using the Mediterranean fruit fly (M. J. G. Gage. *Anim. Behav.* **42**, 1036–1037; 1991). This novel result has since been replicated across diverse animal taxa, supporting the development and predictions of ‘ejaculate economics’ theory (N. Wedell et al. *Trends Ecol. Evol.* **17**, 313–320; 2002). At Liverpool, Matt developed insect models to demonstrate how sperm competition shapes plasticity in ejaculates. He was also among the first to recognize the power of comparative methods to reveal broader taxonomic patterns of sperm form and function, producing influential studies across diverse taxa, including butterflies, fishes and mammals (M. J. G. Gage et al. *Phil. Trans. R. Soc. Lond. Series B* **350**, 391–399; 1995).

At UEA, Matt continued to work on the evolutionary forces that drive sperm evolution. He had great personal interest, and a high level of expertise, in fly fishing. This fed into research on the importance and risks of introgression between wild and farmed trout and of the determinants of fertility in salmonids in general. Important contributions showed the consequences of

sexual selection for sperm form, and that sperm velocity and the timing of entry into the sperm pool are prime determinants of fertilization success. Intriguing and novel contributions of the effect of ovarian fluid on cryptic female choice were also identified (S. E. Yeates et al. *Evolution* **67**, 3523–3536; 2013).

Matt had also become attracted to experimental evolution as a tool to enable the precise delineation of the forces that underpin the evolution of key fitness traits. He established lines of the red flour beetle *Tribolium castaneum* that varied in mating systems and the opportunity for sexual selection, together with sets of thermally adapted individuals. Realizing that line replication was key, these regimes were produced and run at enormous scales and the experiments were conducted over many years.

The possibility that variation between individuals in reproductive choice and success can purge deleterious mutations at a genome-wide scale remains a hot topic. This was the sort of big question that attracted Matt, and he turned his hand to it with great success, using his *Tribolium* lines to show that a history of sexual selection could indeed slow the rate of extinction (A. J. Lumley et al. *Nature* **522**, 470–473; 2015). The evolutionary importance of inbreeding is well recognized and was a major interest of Matt’s — he contributed to this area by showing how inbreeding could drive mating system evolution by promoting promiscuity (Ł. Michalczyk et al. *Science* **333**, 1739–1742; 2011) and highlighting the fitness effects of reduced heterozygosity.

More recently, Matt’s group had started to focus on the effects of thermal stress — including heatwaves — on fertility. This work revealed the magnitude of sex-specific effects of temperature on fertility, striking intergenerational effects of temperature stress (K. Sales et al. *Nat. Commun.* **9**, 4771; 2018), and the importance of plastic responses in mitigating against thermal damage (R. Vasudeva et al. *eLife* **8**, e49452; 2019). This research highlights the fragility of fertility limits and just how perilously close they potentially are as the climate warms.

Matt was also able to demonstrate his accomplished leadership through his strategic and administrative roles

(School Research Director, Deputy Head of School, Associate Dean for Research, NERC grant panel core member and UEA–NERC Doctoral Training Partnership leadership team). He was a committed member of the Association for the Study of Animal Behaviour (ASAB), and was ASAB Trustee and Treasurer for the past 10 years.

For such a hard-working and productive researcher, one might think that Matt had little time for anything else. This was so very far from the truth! Matt had a rich hinterland, a wide circle of friends and deeply profound family relationships. Talking to Matt was always life-affirming. He was funny, warm, irreverent and full of first-class academic gossip. To have received

his compassionate friendship is a prized and wonderful thing. Throughout his last illness, support from his family enabled Matt to keep working, and even shortly before he died, his insights, plans and vision were as cogent and sharp as ever. Our thoughts are with his wife Silvie and two daughters Lily and Tessa, and are aptly echoed in these words from Geoff Parker: “A true gentleman with a unique personality and an amazing (but never cruel) sense of humour, he was always a wonderful friend and colleague.”

It's still a huge shock — Matt was greatly admired and a really lovely man. It was a rare privilege to have known him and we will miss him forever. □

Tracey Chapman¹✉ and Paula Stockley²✉

¹*School of Biological Sciences, University of East Anglia, Norwich, UK.* ²*Institute of Infection, Veterinary & Ecological Sciences, University of Liverpool, Liverpool, UK.*

✉*e-mail: tracey.chapman@uea.ac.uk; p.stockley@liverpool.ac.uk*

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Additional information T.C. thinks she first met Matt Gage at an ASAB winter meeting in the late 1990s, and from 2006 she was lucky enough to have become a fellow colleague at UEA. P.S. first met Matt in 1993 as a colleague in Geoff Parker's Liverpool sperm competition group, and was one of Matt's friends, working with him on ASAB Council in recent years.