

## PROFESSOR SUE NICOLSON 1950-2023: SWEET SOLUTIONS: POLLINATORS AND THEIR PHYSIOLOGY

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Journal of Pollination Ecology,  
36(9), 2024, pp 104-111

DOI: [10.26786/1920-7603\(2024\)800](https://doi.org/10.26786/1920-7603(2024)800)

Received 30 April 2024,  
accepted 06 May 2024

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**Obituary**—On 27 April 2023 the scientific community lost an inspirational and influential biologist of rare quality following the death of Professor Sue Nicolson and we have lost a dear friend and colleague. Sue's most recent paper (Wei et al. 2023), which reports on how honey bees drink, was published in PNAS just a few months after her passing. It seems a fitting coda to such an illustrious career in science since it captures her research interests in the last two decades on pollination and related topics following a lifetime studying the biology of insects.

Sue was born in 1950 in Dargaville, New Zealand and was awarded a B.Sc. (Hons) degree in Zoology at the University of Auckland with distinction in 1971. She published her first paper on the osmoregulation in larvae of the New Zealand salt-water mosquito *Opifex fuscus* Hutton in 1972 (Nicolson 1972). She proceeded to the University of Cambridge for her Ph.D., where she was one of the first women to be admitted to King's College. She published work on the permeability of insect cuticles in *Opifex fuscus* (Nicolson & Leader 1974), and the effect of starvation on osmoregulation in *Carausius morosus* (Nicolson et al. 1974). Sue went on to complete her Ph.D. in Insect Physiology with her doctoral research focused on comparative aspects of osmoregulation in insects (Nicolson 1976a; b; c), a field of study in which she developed an international reputation.

Sue moved to Cape Town in the late 1970s with her South African husband, John Sharp, where her interests and expertise led her to the unforgiving Namib Desert where her studies on beetles provided novel insights into the physiological mechanisms that enable some insects to survive in even the most inhospitable environments on the planet.

Sue was interested in water balance, osmoregulation and oxygen consumption in a

number of taxa, including tenebrionid beetles (Nicolson 1980; Nicolson et al. 1984a; Nicolson et al. 1984b; Nicolson & Hanrahan 1986; Nicolson 1991), protea beetle (Fielding & Nicolson 1980; Nicolson & Louw 1980) scorpions (Robertson et al. 1982), reed frogs (Withers et al. 1982), carpenter bees (Nicolson & Louw 1982; Louw & Nicolson 1983; Nicolson 1990) and spiders (Moloney & Nicolson 1984). Sue's studies in the latter 1980s focussed more on respiration and Malpighian tubules in a variety of insect groups (Louw et al. 1986; Nicolson & Hanrahan 1986; Hanrahan & Nicolson 1987; Nicolson 1987; 1990) culminating in an important review article in 1993 on the ionic basis of fluid secretion in insect malpighian tubules (Nicolson 1993a).

Sue's interest in osmoregulation resulted in her exploring the way in which nectar-feeding carpenter bees deal with excess water in their food and conserve ions and inspired a shift towards pollinators and questions about the importance of nectar composition for pollinators that would influence the rest of her life in science (Nicolson & Worswick 1990). Sue looked at this interaction from both the plant – how nectar concentrations are affected by a dry atmosphere (Nicolson 1993b) – and the requirements of the pollinator/nectar consumer (Nicolson 1994a; b). Sue adopted an

integrative approach, complementing studies of nectar composition (Barnes et al. 1995; Nicolson 1995; Van Wyk & Nicolson 1995; Jackson et al. 1998b; Nicolson & Van Wyk 1998) and production among plants with investigations of the digestive physiology and nutritional ecology of sunbirds and other avian pollinators (Lotz & Nicolson 1996; Leon & Nicolson 1997; Franke et al. 1998; Jackson et al. 1998a; Lotz & Nicolson 1999; van Tets & Nicolson 2000), including some excursions into mammalian pollinators (Johnson et al. 1999; van Tets et al. 2000; Fleming & Nicolson 2002; Johnson et al. 2006a). And Sue was not constrained by dogma illustrated by her posing the question about whether giraffes are pollinators or flower predators (Fleming et al. 2006).

Sue's work has yielded fundamental insights into the interactions between flowering plants and their diverse pollinators and in the latter part of her life in science, her work focused almost exclusively on the study of nectar and the bees and sunbirds that use nectar as a primary source of food. One interest was how foraging birds and bees deal with the excess nectar water. For example, she showed that honey bees can remove most of the water from nectar droplets at the flower and in flight, thereby reducing flight energy costs for individual bees as well as for the colony. Her approach encompassed all sides of the interaction of plant and pollinators ranging from nectar secretion (Nicolson & Nepi 2005) and nectary structures in *Aloe* spp. (Nepi et al. 2006), over energetic regulation (Köhler et al. 2006) or water management (Nicolson 2006) in nectar feeding birds to humidity regulation in honey bee nests (Human et al. 2006; Ellis et al. 2008; 2010).

The composition of nectar was a key research interest including how this affects pollinator physiology and behaviour and included the importance of xylose in nectar (Johnson et al. 2006b) which was an interest of her's throughout her career (Van Wyk & Nicolson 1995; Johnson et al. 1999; Jackson & Nicolson 2002; Johnson et al. 2006a)

Sue was on the National Steering Committee for the Global Pollinator Project South Africa from 2009-2014, which shifted her interest even more towards insect pollinators (Human & Nicolson 2006; Human et al. 2007) and ecological aspects, such as biodiversity in natural areas and within



**Professor Sue Nicolson (1950-2023)**

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farmland to enhance crop productivity (Carvalho et al. 2010; Carvalho et al. 2011). She explored the role of native flowers in agricultural landscapes (Carvalho et al. 2012), and commented on the geographic bias in doing research on pollinator ecology (Archer et al. 2014b).

In the late 2000s Sue's interests on behavioural and ecological aspects of pollinator biology increased and her work looked at the effects of nectar composition and concentration on sunbirds (Köhler et al. 2008; Köhler et al. 2010), Australian honeyeaters (Fleming et al. 2008) and more in honey bees (Nicolson 2009). The role of macro nutrients in nectar and pollen were explored to understand how composition affected behaviour and physiology of bees (Altaye et al. 2010; Pirk et al. 2010; Nicolson 2011) and she applied the geometric frame work to birds (Köhler et al. 2012c) and bees (Paoli et al. 2014; Stabler et al. 2015). She linked the nutritional aspects of the pollinator to the plants by adding secondary metabolites to the mix.

Sue became interested in nectar secondary metabolites and used nicotine as a research model compound (Köhler et al. 2012a) studying the interactive effects on simultaneous stressors (Köhler et al. 2012b; Archer et al. 2014a; Archer et al. 2014c) in honey bees. She also investigated the effects of pesticides in nectar on pollinator behaviour and physiology (Human et al. 2014; Demares et al. 2016; Demares et al. 2017; Demares et al. 2018) and studied aspects of detoxification in bees which expanded her interests into biochemistry and metabolomics (du Rand et al. 2015; du Rand et al. 2017; du Rand et al. 2020). Her nutritional work resulted in a patented diet for honey bees (Wright et al. 2022).

Sue's research was largely supported through the National Research Foundation of South Africa, but she was also successful in international partnerships winning a grant through the Insect Pollinator Initiative of the UKRI's BBSRC from 2011-2014. This led to a very highly cited paper that was one of the first to identify key threats to insect pollinators and the increased risks due to their interacting effects (Vanbergen et al. 2013). Another BBSRC grant followed on the macronutrient regulation in adult worker honeybees from 2017-2019 with Geraldine (Jeri) Wright, Sharoni Shafir and Phil Stevenson. This led to a comprehensive and highly cited review on the functional role and impact of floral secondary metabolites on pollinators (Stevenson et al. 2017) which was part of a special issue she co-edited for *Functional Ecology* on "Plant-pollinator interactions and threats to pollination: perspectives from the flower to the landscape (Nicolson & Wright 2017) and which was financially supported by the Royal Society (London). This was followed by what will undoubtedly be one of her most enduring science outputs – a review on the nutritional physiology of honey bees in *Annual Review of Entomology* (Wright et al. 2018).

Sue's research was always underpinned by her interests in physiology, be it how green tea helps honey bees with excess protein intake (Archer et al. 2014a), or if bees prefer warmer nectar (Nicolson et al. 2013; Shi et al. 2020) or how honey bees dehydrate nectar while flying (Nicolson et al. 2022).

Despite her health challenges Sue took on a major endeavour in 2021 co-editing a special issue of *Philosophical Transactions of the Royal Society* entitled "Natural Processes influencing pollinator health". This was an outcome of an international conference which she also co-chaired with over 400 registered participants. The meeting was held online as a consequence of the travel challenges of the COVID-19 pandemic but Sue's engaging and inspiring nature shone through despite the unfamiliarity at the time of the new approach to meeting. The conference brought together world leading scientists in the field of pollinator biology and chemistry and reported new research and reviews on the role of nutrients, toxins, parasites and disease and floral diversity as natural drivers of pollinator health. Her own contributions included two important articles: Sweet solutions: nectar chemistry and quality (Nicolson 2022) and how natural process affect pollinator health (Stevenson et al. 2022) which proposed a rethink on pollinator health; that it should focus more at the community level rather than the level of individual, colony or even species.

Sue was the author of 185 scientific publications that established her as an internationally recognised research scientist. She and her co-author Steven Chown wrote *Insect Physiological Ecology: Mechanism and Patterns* ((Chown & Nicolson 2004), Oxford University Press) that was rated as one of the top 10 academic titles for 2005. The work reflected the depth of their insights into Physiological Ecology and their comprehensive grasp of the field. The strong interest and the expansion of knowledge in pollination biology, prompted the book *Nectaries and Nectar* (Springer, Dordrecht, (Nicolson et al. 2007), which she co-edited with Massimo Nepi and Ettore Pacini.

Both at the University of Cape Town and at the University of Pretoria, she made very significant contributions to the teaching of undergraduate students and mentoring of postgraduate students and post-doctoral fellows. In the case of her doctoral candidates and post-doctoral fellows, she published extensively in collaboration with them, and they serve as a legacy of her enlightening influence. She was able to maintain her research initiatives and her teaching responsibilities while contributing to the administration of the

Department of Zoology and Entomology as departmental head from 2003-2011. The period of her tenure was one during which the department was the most research-intensive department in the University and served as a role model for research and teaching excellence.

She was a fellow of the Royal Society of South Africa, a fellow of the Royal Entomological Society (London) and the Cambridge Philosophical Society. She annually received the Exceptional Academic Achiever award from the University of Pretoria for the years 2003-2016. During that period she received the Gold Medal of the Zoological Society of Southern Africa and received the Chancellor's Award for Research from the University of Pretoria for 2013.

She was a warm, engaging and challenging colleague who will be sorely missed by her colleagues in the Department of Zoology and Entomology and the Centre for the Advancement of Scholarship of the University of Pretoria where she was a senior research fellow as well as numerous colleagues, collaborators and science friends across the world. In her spare time, Sue was a gifted artist who produced many paintings drawing on her experience of New Zealand and South African landscapes.

Sue is survived by her husband, her children and grandchild.

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