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OBITUARY

Walter Crozier Jordan (Bill) 1962–2011

Walter Crozier Jordan (Bill) passed away unexpectedly on Wednesday, 25 May 2011 at his home in London, after a short illness. Bill was born in September 1962 in Ballymena (County Antrim, Northern Ireland) and obtained his BSc in Biology at the Queens' University of Belfast. He then went on to gain a PhD, also at Queen's, under the supervision of Andy Ferguson, though he did most of his doctoral work at the Marine Laboratory, Aberdeen, where as a fellow doctoral student I first met him.

Bill has some 50 papers listed in the ISI web of Science, and a very high citation ratio. His papers are cited an average of 36 times, an unusually high ratio. And three of his papers have been cited in excess of 100 times, which testifies to the quality of his research and the sort of topics Bill was involved on. A man averse to pomposity, Bill nevertheless took his science seriously and was positively not interested in what he called 'mundane' topics. He was Senior Research Fellow at the Institute of Zoology (Zoological Society of London, ZSL) and was the Theme Leader on Genetic Variation, Fitness and Adaptability, a position he held since 2001. He joined ZSL in 1995 as Research Fellow, following postdoctoral positions at the University of Aberdeen (1990–1991), Queen's University of Belfast (1991–1992), University of Louisiana at Lafayette (1992–1994) and the Institute of Molecular Biology and Biotechnology in Crete (1994–1995). He spoke warmly of all the places he lived in and often referred to his American experience as 'when I lived in the States'. There, at Joseph Neigel's laboratory, Bill spent the best part of 2 years looking for genetic variation in duckweeds, and not finding any, he concluded that this must have been due to purifying selection. This turned out to be correct, and his paper in the *American Journal of Botany* has been cited 135 times (Jordan *et al*., 1996).

Bill's list of collaborators is extensive, and he worked with colleagues in Canada, U.K., Ireland, Norway, U.S.A., Spain, The Netherlands and the Czech Republic, to name just a few.

Perhaps Bill's greatest contribution to fish biology was to show that there is nothing intrinsically special about fishes in general, or about salmonids in particular. To Bill, Atlantic salmon was just a very good evolutionary model. Bill was one of the first to see that the study of Atlantic salmon could shed light on the way natural selection operated in the wild (Verspoor & Jordan 1989; Jordan & Youngson, 1991), and that the species' remarkable homing behaviour (Youngson *et al*., 1994) should result in reproductive isolation and locally adapted populations, since no two populations would be subjected to exactly the same evolutionary forces. It is easy to forget that although natural selection is something that is now usually associated with salmonids [in 2004 a whole book (Hendry & Stearns, 2004) was dedicated to this topic], back in the 1980s and 1990s most papers on salmonids were very much fisheries and management oriented. Bill was a fervent Darwinist and an avid reader of popular science; he was particularly fond of Steve Jones, he listed *Almost Like a Whale* as one of his favourite books, and gave me *Coral – A Pessimist in Paradise* by the same author (Jones, 2000, 2008). Gifted with a prodigious memory, Bill knew John Endler's (1986) seminal book inside out, and often pondered how Endler's evolutionary approach might be applied to unlock some of the most puzzling aspects of the salmonid life cycle such as the evolution of homing behaviour or the co-occurrence of resident and migratory males within the same population.

Bill's thesis (Jordan, 1990) was carried out at the Girnock Burn (a tributary of the River Dee, in Aberdeenshire) and represents one of the first attempts at estimating the connectivity of wild Atlantic salmon populations using molecular markers, and thus to determine the extent of homing. This represented a radical change from the use of physical tags, at a time when much of resources were being spent in costly tagging programmes. Bill's early allozyme work was crucial in starting a paradigm shift on the way salmonid populations should be conserved and managed (Youngson *et al*., 2003). It was the realization that some of the markers Bill was using were under selection (and thus not really suitable for estimating gene flow), which led Bill to focus his interest on non-neutral markers, such as malic enzyme (MEP-2*). This was spurred by the arrival of Eric Verspoor from Canada to Aberdeen at the time Bill was doing his PhD. Along with Eric Verspoor and Alan Youngson, Bill was the first to examine in detail how malic enzyme and other salmon allozyme polymorphisms were affected by natural selection (Verspoor & Jordan, 1989; Jordan & Youngson, 1991; Jordan *et al*., 1992, 1997, 2005). Bill then went on to show how this polymorphism was related to age at maturity (Jordan *et al*., 1990), and by extension to timing of return of adults from the sea into fresh water. He also used allozymes to estimate the contribution of mature male parr (he never liked the term 'precocious' parr, then in vogue) to the progeny of anadromous females in the Girnock Burn (Jordan & Youngson, 1992). I remember this well because I accidentally dropped an unscreened female in the wrong part of the stream, thereby making his subsequent parentage analysis more difficult than it should have been.

After his doctoral work, Bill began to develop a long-lasting interest in the major histocompatibility complex (Jordan & Bruford, 1998; Consuegra *et al*., 2005*a*, *b*, 2011; De Eyto *et al*., 2007, 2011), which he developed with his friend René Stet (1954–2007). He also started pioneering work on the significance of genetic variation

in olfactory receptors (OR) and their role on Atlantic salmon homing behaviour (Dukes *et al*., 2004, 2006).

In addition to his 'salmon stuff', as he referred to it, and which he published first and foremost in the *Journal of Fish Biology*, and in the *Canadian Journal of Fisheries and Aquatic Sciences*, Bill published in high impact journals, including *Nature, Molecular Ecology*, *Molecular Biology and Evolution*, *Proceedings of the Royal Society*, *Biological Reviews*, *Biology Letters*, *Heredity and Evolution*, amongst others. He described his principal interest as the genetics of adaptation. For this, he examined the influence of variation in structure and expression of candidate genes on individual fitness and population persistence. He also used molecular markers to examine social, population and phylogenetic structure in a range of animal species. The breadth of topics Bill addressed in his research was remarkable, ranging from the study of genetic variation of giant otters in the tropical forest of Bolivia to duckweeds in America or lizards in the Iberian Peninsula. He was not fond of giving talks, but in typical Bill's vein, insisted that everybody else did. Thus, he was a regular attendant at the European Society for Evolutionary Biology (ESEB) and at the Population Genetics Group (PopGroup), which he encouraged his students and postdocs to attend.

A modest and unassuming person, Bill's generosity was legendary. Nothing was too much trouble for Bill and he helped many of us in the field. I once asked Bill to give me a hand electrofishing in the headwaters of the Girnock Burn, in a particularly hostile and chilly place called the Hampshire Bridge (the bridge was built by the Hampshire Regiment, hence the name). This was on the very same day he was due to go home to Ballymena for Christmas, so he was understandably reluctant. But after some persuasion, as always, he gave in. 'OK' he said, 'but I must catch a ferry to Ireland tonight, so you must promise that we will be back to Aberdeen on time' 'Do you promise'? 'Yes, of course', I said, 'It will be a quick one, we will just sample 50 salmon fry and will be back in no time', 'It will be easy piece', I added reassuringly. Once there, it seemed to me that it was not really necessary to cross the stream at the Hampshire Bridge and that we could instead steer across the river to save time. Always cautious, Bill warned me that the stream was far too deep to wade, and that if the 'Hampshires' had decided to erect a bridge there it was probably for a reason. 'Nonsense', I said. 'We will be just fine'. But we were not fine. The stream was indeed too deep to wade, water started rushing in, and we watched horrified as the Land Rover was swept downstream until it became wedged between two large boulders. We dismounted and made our way to the bank. Mortified, and still shaking, I tried to cheer him up by pointing that it was a beautiful starry night, and that we were, after all, lucky as it was not raining or snowing. Bill glanced at me briefly and told me to 'b. . . .off'. He spoke no more words and we walked many solitary miles down to Ballater to get a tow and retrieve the vehicle. Bill did miss his ferry.

Bill had a fine sense of humour, though I must admit that understanding him was not always the easiest of tasks. His strong Northern Irish drawl made telephone conversations challenging, and as I suspect he thought the same of my accent, I suppose much of what was said must have been 'lost in translation'. Going to London was always a good excuse to see Bill, and to pay a visit to the Zoo, something Bill always managed to arrange for free. He was very fond of children, and not having any of his own, he served as 'uncle Bill' for many of his friends' children, including mine. Bill is sorely missed and has left a big emptiness that is impossible to fill. Those

of us who were fortunate enough to know him will always remember his kindness, generosity and refined, nonchalant sense of humour. For the rest, the quality of his scientific work survives him.

C. Garcia de Leaniz
Swansea University
Department of BioSciences
Singleton Park
Swansea SA2 8PP
U.K.

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Corrigendum

Garcia de Leaniz, C. (2011). Walter Crozier Jordan (Bill) 1962–2011. *Journal of Fish Biology* **79**, 1089–1093.

Please note that the correct title of the above obituary is: William Crozier Jordan (Bill) 1962–2011.