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Rossiter Henry Crozier 1943–2009

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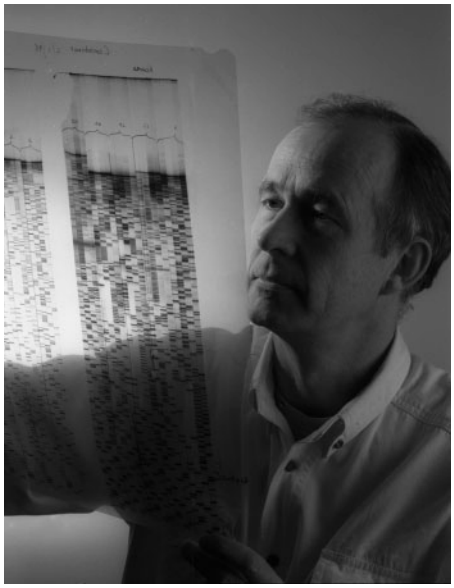
Ross Crozier, population geneticist and leader in the study of the evolutionary genetics of social insects, was born on 4 January 1943 in Jodhpur, India. He died of a heart attack in his office at James Cook University in Townsville on 12 November 2009. He is survived by his wife Yuen Ching Kok, who was his inseparable companion and collaborator in life as in the laboratory. Crozier was a pioneer in the application of molecular genetic markers to the analysis of social insect populations, and generated much of the theory that made these analyses possible. Ross and Ching Crozier produced the first sequence of the honey bee mitochondrial genome—the second insect mitochondria to be fully sequenced. From the sequence Crozier produced fundamental insights into the nature of DNA evolution, particularly directional mutation pressure towards particular nucleotides. Crozier contributed massively to the development of kin selection theory, which remains the most potent explanatory theory for the evolution of social behaviour in insects.

Ross's Father's Family

Ross's grandfather Robert Henry Crozier (better known as Harry) migrated to Australia from England in 1910. Harry was a mining engineer. He married Elsa McGillivray. There were three children: Cecily, Brian, and the eldest, Ross's father, Laurence, known as Laurie. Up to 1923 the family lived in Melbourne but enjoyed (or perhaps endured) frequent and lengthy placements at remote mines including Kuridala near Mt Isa (where Laurie won a baby contest for 'best baby in North Queensland') and three years near Rangoon, Burma.



Harry Crozier was the inventor of the Crozier Retort, a device for extracting oil from shale. Several were built in Tasmania during the 1920s. Elsa was a schoolteacher, but it is unclear that she worked as one after the birth of her children.

In 1923, Elsa and the family moved from Melbourne to London, but the children suffered greatly from the cold and the air pollution, so she moved the family again, to southern France. There they lived in various places including Grasse, Nice and Montpellier (B. Crozier 2002). Cecily, Brian and Laurie all became bilingual in French and English, and fluent in Spanish. In 1930, Elsa and the children moved back to London, eventually settling in Preston Road, Wembley. The Depression hit the family hard, with cancelled contracts for Harry's company 'Mineral Oils Extractions'. Harry went back to Australia and worked in Tasmania, sending money to Elsa and the children in Wembley.

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After her children had grown up, Elsa returned to Australia where she lived in Melbourne. In 1939, Harry was working in the Gold Coast of Africa (now Ghana) where he contracted a microfilarial infection and died, tended in his final illness by his son Laurie.

Brian, the youngest child, went on to have an illustrious career as a journalist, author and polemicist against communism and the Soviet Union. In the late 1960s, Brian was director of Forum World Futures, an organization with links to, and funds from, the CIA. In 1970, he founded the Institute for the Study of Conflict—the world's first think-tank devoted to the study of terrorism. In the 1970s, he and his family lived in Sydney, where he was a correspondent for *The Sydney Morning Herald*. In the 1980s, he returned permanently to London where he was a regular leader writer and sometime Foreign Editor for *The Economist*.

By all accounts Cecily was a ravishing beauty, and in the early 1930s she worked as an artist's model in London. She had a de facto relationship with Nikita ('Niko') Stroumzi, whom she had met in Montpellier. They lived together in Alexandria, Egypt, in the 1930s. Later she moved back to Australia and married Ernst Heideman.

Because of tensions over Harry Crozier's estate, Cecily had little contact with Laurie's family, including her nephew Ross. She was, however, noteworthy in illustrating the talent in Ross's gene pool. She was a breeder of dachshunds in great number, publisher of a literary magazine *A Comment* (1940–1947), a feminist and one-time lover of the Pulitzer Prize winning American poet Karl Shapiro. Indeed, she published a collection of Shapiro's poems, well before his career took off. Old Harry's funds were put to interesting use.

Ross's Mother's Family

Sheila Goss was the youngest daughter of Arabella (née Bull) and Harry Goss.

Harry Goss was an Anglican clergyman who held various positions in rural Victoria, his last post as the vicar of Rushworth. He is said to have looked a lot like his grandson Ross. Someone described Harry Goss as being 'selfish, dogged and pedantic', another called him a 'highly committed Christian'. He died on 30 January 1943, when Ross was a few weeks old.

Harry, understandably, did not like the idea of his daughter Sheila marrying Laurie Crozier, especially when it required her travelling alone to Egypt to meet up with him. His instructions were that she should be 'cold and distant' with him. Then, Harry further instructed, after she had recovered her senses and abandoned Laurie in Egypt, she should continue her journey onward to England where she should present herself to the Bishop of London. Laurie never quite forgave the vicar for his opposition to the marriage.

Arabella Goss was an accomplished singer—she won the Melbourne Sun Aria competition, and was complimented by Dame Nellie Melba herself. Before she married, she was much in demand as a singer around Melbourne, and it was in that role that she met Harry Goss. After their marriage she performed much less often, but continued to practise throughout life. After her husband died, she remained in Rushworth for some time before moving to one of a small block of flats owned by Ross's parents in Fernhill Road, Sandringham, a beachside suburb of Melbourne. The Crozier boys Ross and Brian often stayed there with their grandmother during school holidays.

Sheila died in 1980.

Ross's Father, Laurence Crozier

After Montpellier, Laurie attended Brentwood School in Essex, 1927–30, where he showed varied talents. However, because of the Depression he was obliged to leave school before matriculating, getting his first job at the Heinz cannery at the age of 17.

Laurie was working with his father on the Gold Coast (now Ghana) when the latter died in 1938. Laurie immediately returned to London, where there were robust negotiations to retrieve what was owed to Laurie and his father from the company that owned the Gold Coast mine. Laurie and Brian eventually obtained a payout of £7,000 from the company. This estate allowed Elsa to buy five houses in Melbourne, and Brian one in London. Elsa lived in one of the Melbourne houses and lived on the proceeds of the others. Laurie was unhappy with this outcome, feeling that he should have shared in the estate.

Laurie met his future wife Sheila in Australia in 1938 and they were engaged in 1939. In 1940,

Figure 1. The Raub mine's guest house at Fraser's Hill in the early 1950s. Some of Ross's earliest memories would have been of this house.

Laurie was offered a job as the underground shift manager at Mawchi Mines in Burma. Laurie cabled Sheila in Australia that she should meet him in Alexandria in Egypt, so they could travel to Burma together. They duly met in Alexandria and sailed to India, where they were married in St Thomas's Cathedral in Bombay (now Mumbai), with a couple of cleaners as witnesses. They travelled on by ship to Rangoon, and thence to Mawchi.

The Japanese invaded Burma in December 1941. Two months later, Sheila was evacuated to India. Laurie followed overland two months after that, joining Sheila in Calcutta in early 1942. By 1943, they had moved to Degana in Rajasthan and another mine, and it was in nearby Jodhpur that their first child, Ross, was born. Ross's brother Brian was born in 1948 in Bolivia, and his sister Judy in 1954 in Malaya (now Malaysia).

In 1950, Laurie accepted a position as mine manager for the Raub Australian Gold Mining Co. in Raub, Malaysia. It was here that Ross spent his early childhood (Figure 1).

In 1955, Laurie returned to Mawchi with a brief from Gold Fields, a London-based company, to rehabilitate the mine. By then Burma was extremely unstable politically, and not a safe place to raise a European family (L. Crozier 1994). The mine was under sporadic attack from bandits and insurgents, from whom it was the job of police and army units (themselves at war) to defend it. Brian was sent to join Ross at boarding school in Australia, though Sheila and Judy remained at the mine. By 1958, the mine was forced to close and the entire family returned to Melbourne.

The mine's status and future were complicated by the fact that the Burmese government had proposed a joint venture with Gold Fields. There was political manoeuvring related to the partial buy-out, leading to the replacement of the board of directors. Laurie defended the old board and was thereafter blackballed from mining. After an anxious period of unemployment in Melbourne, in 1960 he accepted a position advising the Australian government on aid projects in Asia and spent the rest of his career working in similar capacities (L. Crozier 1994).

Although neither of us ever met Laurie, we can see many aspects of Ross in his writings (L. Crozier 1992, 1994). He apparently had a fierce sense of right and wrong and an inability to allow wrongs to go unchallenged—often to the detriment of his own happiness and health. Both father and son were particularly incensed by bureaucratic inefficiency and cronyism. Laurie and Ross suffered some of the same health problems, particularly an allergy to sulphur that sadly precluded Ross from drinking white wine, and that almost killed Laurie when he was administered an antibiotic for an abscess in Burma. Of Laurie's three children, Ross, the scientist, was the closest to him.

Ross's Mother, Sheila Goss

Sheila and Laurie met in Melbourne while Laurie was a student studying mining and metallurgy at the University of Melbourne. Sheila trained as a secretary at Stott's Business College in Melbourne, but didn't work outside the home after she married. She was a gifted writer and also enjoyed drawing and painting in water colours. She was very close to all her children, and was a weekly correspondent with Ross and Brian while they were at school in Geelong. This habit continued with Ross when he moved to Ithaca. Ross's strong interests in things artistic, cultural, historical and literary reflect his upbringing in a household that valued all these things as well as the sciences.

Ross's Early Years

When Ross was five the Croziers were living in Malaya. Ross's mother suggested that if Ross opened up a termite mound with a knife, he would discover the termites' secret little world

Figure 2. Ross's family in 1963, probably in Melbourne. From left to right: Brian, Sheila, Ross, Judy, and Laurie.

Figure 3. Ross and Ching at Ching's graduation from the University of Melbourne, ca. 1966.

of tunnels and chambers. This exploration was apparently an epiphany and the beginning of Ross's life-long love of social insects.

The conditions in Mawchi meant that Ross had to go to boarding school at the age of nine, at Geelong Grammar School. Laurie was also keen that his children should have a stable school environment and not be moved from school to school as he had been. Nonetheless, sending Ross away to school must have been dreadfully difficult for both parents and child. Ross hated boarding school but spoke fondly of his time at Timbertop, a rural branch run by the school near Mansfield, where all students in year 4 of high school stayed for the entire academic year.

From the beginnings of his time at Geelong Grammar, Ross regularly made solo trips to visit his parents in Asia, in the care of airline staff. The destinations were often in politically unstable places, including Vietnam during the hostilities. On one extraordinary occasion, the young Ross flew to Rangoon (after a stopover in Singapore) to meet his father. But on arriving, where was Dad? Ever resourceful, Ross sat down and had a think, before deciding to hire a taxi to convey him to The Strand, the only ex-pat hotel in the city. Sure enough, he found his father in the bar, who murmured 'Hello old chap' before continuing his story.

As mentioned above, Ross wrote from school to his parents on a weekly basis, and perhaps this habit of regular communication with family members was the harbinger of or at least training for Ross's regular correspondence with colleagues around the world (Figure 2).

University of Melbourne

After finishing school Ross briefly considered a career in journalism, but instead studied genetics and zoology at the University of Melbourne from 1961 to 1965. He then enrolled in a Master's degree under Professor M. J. D. White, the influential evolutionary cytogeneticist and former student of J. B. S. Haldane. Ross's thesis was entitled 'Cytotaxonomic studies on Australian Formicidae' and the degree was awarded in 1966. White had a hands-off approach to student supervision and his laboratory was very small, so Ross was left pretty much to his own devices.

As part of his Master's research, Ross developed a new technique for fixing and examining ant chromosomes (1), versions of which are still in use today. The other papers to emerge were brief descriptions of the chromosomes of various Australian meat ants *Iridomyrmex* (2, 3).

While an undergraduate, Ross met his future wife, Yuen Ching Kok (Figure 3). Ching was in the year after Ross's, also studying genetics and zoology. A Malaysian of Chinese descent, Ching had come to Melbourne to study. She was funded entirely by her mother. Ching's and Ross's first date was at Genevieve's, an Italian restaurant in

Carlton that was much in vogue with students and affordable, according to Ching, provided you only had minestrone soup. Their second date was at an ice skating rink, a cunning choice given that Ching had never skated before so that gallant rescues and fallings into each other's arms were required.

Cornell University

Ross applied to Harvard to study for his PhD under the eminent myrmecologist and sociobiologist Edward O. Wilson, but was not accepted. Instead he started his PhD with William L. Brown in the Entomology Department at Cornell University in the autumn of 1966, on the topic of ant chromosome evolution. Brown was an excellent ant systematist but knew nothing of cytogenetics or population genetics. Fortunately, this lack was amply compensated by the presence of Bruce Wallace, the eminent population geneticist, on Ross's advisory committee. Wallace, a former student of Theodosius Dobzhansky, was a pioneer in the application of molecular markers to population genetics, and was no doubt highly influential on Ross's approach to evolutionary biology. Bill Brown and Ross never published together, a matter of regret to Ross. While at Cornell, Ross and Ching, who had joined him at Cornell, began their first foray into molecular population genetics of social insects, setting up an electrophoresis apparatus and looking for polymorphisms in esterase proteins within and between ant populations. Ross's thesis, 'Genetic and phylogenetic studies on ants', was completed in 1969.

Ross and Ching were married on 3 February 1968 in a chapel at Cornell. The chapel was furnished with a revolving panel that could be set appropriately for the theistic proclivities of the ceremony at hand. Ross and Ching chose the blank panel. Ching writes: 'Cornell was a happy time for us'.

University of Georgia

At the end of the summer of 1969, after Ross had finished his PhD, the Croziers left for the University of Georgia where Ross had a one-year postdoctoral fellowship with Peter Thompson that transformed into an appointment as Assistant Professor. Ross finished off cytogenetics papers from his PhD and published an important review of sex determination in the Hymenoptera (11). He also made the interesting discovery in a population of *Aphaenogaster* ants: malate dehydrogenase was heterozygous in queens and homozygous in workers. This was interpreted as differential selection between queens and workers, but in hindsight may better be interpreted as hybridization between two subspecies and genetic caste determination. Ross also wrote a short book on Hymenopteran cytogenetics (19), and made important contributions to the theoretical population genetics of social insects (24).

University of New South Wales

In 1975, Ross and Ching moved back to Australia so that Ross could take up a lectureship at the School of Zoology at the University of New South Wales (UNSW), in Sydney. This was an important time for Ross and Ching because they were able to form collaborations with biochemists (particularly A. G. Mackinlay) that paved the way for their entry into the world of DNA. Nonetheless most of the papers from this period were from the old themes of theoretical population genetics and cytogenetics. Ross and his colleagues and students documented the enormous variability (1–16) in chromosome number within the *Myrmecia pilosula* species complex (60, 108), and worked with Hirotami Imai (National Institute of Genetics, Japan) on a theory that explains chromosome evolution as a process that minimizes the incidence of deleterious chromosome rearrangements (27, 67).

At UNSW, Ross hosted several postdoctoral fellows and students who have gone on to be influential, including Mark Elgar, now of the University of Melbourne; Pekka Pamilo, University of Oulu (Figure 4); Michael Crossland, University of Hong Kong; Christian Peeters, University of Paris; and Robin Moritz, University of Halle. Important visitors were Bernie Crespie (Simon Frazer University), Joan Herbers (Ohio State University), Scott Davies (Texas A&M) and Penny Kukuk (University of Montana).

La Trobe University

In 1989, Ross was offered the Chair of Genetics in the Department of Genetics and Human Variation at La Trobe University in Melbourne.

Figure 4. Ross (in the hole) with Pekka Pamilo digging for ants at the University of New South Wales's field station at Fowlers Gap, ca. 1975.

UNSW matched the offer, but perhaps the opportunity to return to Melbourne and Ross's aging father, and to work with some outstanding colleagues at La Trobe, enticed Ross and Ching south in 1990.

The years at La Trobe formed an interesting time for Ross. At once, they were his most productive years, but also his most difficult. He ran a thriving laboratory, with numerous visitors, postdoctoral fellows and students. But the department itself was in a state of civil war and Ross, as Head, was caught in the crossfire. It is hard to imagine a more dysfunctional academic department, except that, perversely, it had three world-renowned (and extremely collegial) geneticists on staff: Jennifer Marshall Graves (sex chromosome evolution), Ary Hoffmann (ecological genetics) and Ross. None of this trio remained at La Trobe a decade later. All had moved on to more congenial academic environments.

Highlights from Ross's period at La Trobe include publication of the complete sequence of the mitochondrial genome of the honey bee (102), discovery of intracolonial social parasitism in the honey bee (111), publication of the influential monograph *Evolution of Insect Societies. Sex Allocation and Kin Selection* (124), and development of methods for prioritizing conservation effort (96, 132). More on these below.

Influential visitors included Jean-Marie Cornuet and his former student Arnaud Estoup, who had recently pioneered the practical application of DNA microsatellites to issues of sociobiology in the honey bee (Estoup *et al*. 1994). Although Ross was one of the first to recognize the enormous potential of microsatellites for answering questions in social evolution, his group had not been particularly successful in applying the technology. The arrival of Cornuet changed that and fostered a very exciting period in which much of the low-hanging fruit of social insect biology was plucked. Exactly how many times does a honey bee queen mate (118)? Do the workers ever lay any eggs and if so are they reared (111)? Is there a genetic component to caste determination in social insects (171)? There was good work done on birds, too, revealing hitherto unanticipated cuckoldry (175, 210). Gordon Luikart, then a PhD student, also joined the group as a visitor. Gordon has gone on to do pioneering work in conservation genetics.

Another important visitor at La Trobe was Dan Graur, a specialist in molecular phylogenetics. Dan worked with Ross and student Lars Jermiin on the problem of extracting phylogenetic signal from DNA sequence data when the assumption that DNA sequences evolve randomly over time is not met (110, 114, 117, 126).

Ross's achievements and productivity were recognized by the Australian Research Council, and he was given a five-year Special Investigator award in 1991.

It is fair to record that the machinations of the Department of Genetics and Human Variation at La Trobe had a profound and deeply negative effect on Ross. Despite his efforts to be scrupulously fair, the concept of rewarding effort and achievement was alien to some lesser-achieving academic staff and they fought him bitterly at every opportunity. Ross was unable to comprehend how intelligent people could be so truculent, narrow-minded, and parochial. For example, at one point some staff members challenged the notion of hosting postdoctoral fellows (on external funds) because it 'drained the department of resources'! This led to the incredible situation where quite senior postdocs and visitors were crammed five into a room designed for one person, while a couple of PhD students luxuriated in a room built for ten of them.

James Cook University

Fortunately, Ross was offered a personal chair in the School of Tropical Biology by James Cook University in north Queensland, which allowed him to escape the slough of despond that the Department of Genetics and Human Variation had become. At James Cook, Ross recovered his equilibrium and happy disposition. After a couple of attempts, he was awarded a professorial fellowship by the ARC. Ross diversified his interests into some new areas, including marine biology (225, 269), insect immunogenetics (239, 264), and the effects of climate change on tropical reef fish (256, 277).

Ross's Major Scientific Achievements

Molecular Evolution

Ross and Ching were responsible for producing the second complete sequence of an insect mitochondrial genome (102). This was during the days of manual sequencing and was a Herculean task, requiring cloning of the bee DNA into bacterial plasmids, followed by dideoxy chain termination sequencing of the cloned fragments, and piecing together the short sequences into the complete sequence. One of us (BPO) recalls Ching poring over the X-ray plates, which had to be scrutinized laboriously over a light box, so that the sequence could be read off one base at a time. For a 17,000 base pair genome, this was no easy feat.

A remarkable discovery that jumped out of the sequence (at least for the sharp eyes of Ross) was that the honey bee genome is extremely AT-rich relative to that of *Drosophila*. This finding led to some interesting speculations about the causes of mutational bias towards A and T, and launched a series of papers about the detection of directional mutation pressure with Lars Jermiin and Dan Graur.

The mitochondrial project fostered an interest in using DNA sequences to infer phylogenetic history. Phylogenetic inference based on DNA sequences was a blossoming field in the 1990s. The promise was that DNA would provide an objective, simple and rapid basis for clearing up taxonomic uncertainties, untangling evolutionary history and assessing biological diversity. Ross was as keen as anyone to apply the new technologies to ants and other creatures, and was involved in phylogeny projects from such diverse groups as honey bees (262), termites (179, 180), ants (114), birds (139), and octopuses (231). But Ross realised sooner than most people that simply creating a genetic-distance matrix based on the similarity of DNA sequences and then drawing a tree that represented the distance matrix required some simplifying assumptions about how DNA evolves that could not usually be sustained. Thus Ross was one of the first to apply statistical methods to phylogeny construction. In particular, he was an advocate for maximum likelihood approaches. In this technique a sample of possible tree topologies is generated, and each topology is tested to see how well it fits the dataset. By this criterion, the 'most likely' phylogeny is chosen, and with a measurable degree of uncertainty. This approach differed from the distance- or parsimony-based methods in vogue at the time that did not typically take statistical uncertainty into account. An additional feature of the likelihood method is that the user can specify a model for the way DNA sequences change over time, and can even propose a model based on the data themselves, including models that incorporate a bias towards A and T.

Although a phylogenetic tree can be an important end in itself, trees can also be used to understand the evolutionary history of traits via the comparative method (Harvey and Pagel 1991). Ross was a great advocate of the method, and used his phylogenies to understand the evolution of such things as bower bird bowers (139) and the honey bee dance language (262). For the bower birds, student Rab Kusmierski showed that plumage was a poor indicator of evolutionary history (that is, plumage traits are very labile). On the other hand, bower structures (for example, the number of towers) are more constrained by evolutionary history. Species derived from a common ancestor tend to share traits of bower architecture. For the bees, student Rika Raffiudin showed that the ancestral honey bee species most likely nested in the open, with a single comb, and danced vertically on the comb. This conclusion was controversial, because at least one author argues that the ancestral honey bee species was cavity nesting (Koeniger 1976).

Conservation Biology

Ross's interests in conservation and phylogenetics were merged when Ross weighed into the 1990s discussions about the setting of conservation priorities. Vane-Wright (1991) had argued that conservation effort should be directed at maximizing total biodiversity—not just species richness, but also the total genetic information carried in the species. Thus a taxonomically distinct species like a tuatara should be held as being more valuable than a species that was phylogenetically similar to widespread species, even if it itself is rare. This makes perfect sense. Vane-Wright proposed an index of taxonomic distinctness based on cladistic groupings of taxa. A cladogram is a way of grouping taxa in an evolutionary tree based on their shared ancestry, but does not take account of the evolutionary lengths of the branches: two taxa that have barely speciated might have the same branch lengths as two deeply diverged taxa. In a cladogram, provided two taxa share the same common ancestor, they are represented in the same way; however long ago they diverged and however distinct they may be. Ross objected to Vane-Wright's index for this reason, arguing that a 'cladistic method will err on occasion because it does not take into account the accumulation of genetic divergence along branches of the evolutionary tree' (96). Ross modified Vane-Wright's method to take account of genetic distance, producing a new index that took account of uniqueness as well as ancestry. Crozier's index was influential, in theory if not in practice. In practice, it is much easier to count species than to amass the data required to generate a phylogenetic tree for them as well.

Social Evolution

Perhaps the most important achievements of Ross's career were his contributions to social evolution and kin selection theory. Kin selection theory provides an elegant solution to one of the greatest evolutionary puzzles—the evolution of sterile workers in insects. Consider the problem: how could an allele that makes one sterile spread in a population? The solution to this puzzle came in 1964 when Bill Hamilton developed the concept of 'inclusive fitness'. Hamilton argued that the 'inclusive' fitness of an organism should be measured—not just the number of offspring it has, but also the number of offspring its relatives have (Hamilton 1964, 1972). Inclusive fitness theory formalizes the obvious fact that in evolutionary terms having two sisters is just as good as having one daughter—the genetic legacy is identical. So, an allele that causes an individual to help its relatives and thereby increases their direct fitness can spread in a population because the relatives spread the allele that is present in the helper. This relationship is formalized in what is known as 'Hamilton's rule', $b/r > c$, where b is the benefit to the receiver of the largess, c is the cost to the giver, and r is the coefficient of relatedness between the two.

Ross was fascinated by this simple equation, which is actually not nearly as simple as it seems. In particular, what is r and how should we measure it? Ross's first contribution, developed while he was still a student at Cornell, was to point out an error in the calculation of r for haplo-diploid males in Hamilton's seminal work (8). Ross refined Hamilton's definition by pointing out that 'if you are weighing up (in terms or relationship) the benefits of being altruistic to someone, you should care more about the proportion of your genes present in him, than the proportion of his genes present in you' (38). From this insight one can readily understand that relatedness is asymmetrical for haplo-diploids, where all of a male's genes are present in his mother, but only half of hers are present in him—that is, he is related to her by unity, but she is related to him by only 1/2. This paper was followed by a major theoretical analysis of the best ways to measure relatedness between and within haplo-diploid groups (48). In essence, the approach is to throw out pedigrees as a way of calculating relatedness, and to use data from genetic markers (like allozymes) alone. This idea was truly revolutionary, generating a tsunami of studies on the genetic relatedness of natural populations based on molecular markers, some of which came directly from the Croziers' laboratory (e.g. 52, 64, 72, 189). The approach was greatly facilitated by the development of (relatively) easy-to-use software that can take data on the genotypes of individuals sampled from a population, and generate the usual population-genetic parameters like F_{ST} and F_{IS} (different measures of inbreeding), plus the all important G, the regression coefficient of relatedness (Goodnight and Queller 1999).

Ross's influential monograph *Evolution of Social Insect Colonies. Sex Allocation and Kin Selection* (124) is a *tour de force*, with over 700 citations and rising. It is useful to everyone interested in social insects because, although it is quite mathematical and requires a good grounding in population genetics theory, all the mathematics and population genetics are embedded in a readable text supported by helpful diagrams. It is exhaustively comprehensive, reflecting Ross's broad reading and near-photographic memory for sociobiological and myrmecological minutiae.

Some have argued that there has been too much focus on the *r* part of Hamilton's Rule, and not enough on the *c* and *b*. To some extent this situation arose because, after Ross's insights, the discovery of microsatellites (Queller *et al*. 1993) and the development of the software to analyse the data (Goodnight and Queller 1999), *r* became relatively easy to measure objectively. In contrast, measuring *c* and *b* with any sort of objectivity is a lot trickier. Indeed, in recent years kin selection has come under sustained attack as a general theory to explain the evolution of eusociality (Wilson 2005; Wilson and Holldobler 2005; Hunt 2007; Nowark *et al*. 2010). Ross was outraged by these challenges, despite the fact that some of them came from some of the greats of sociobiological research whom he had admired for years. One of his last big papers is a patient, well-reasoned defence of kin selection theory (270).

Evolution of Polyandry

One of the challenges to kin selection theory (which in reality is not a challenge at all) is the fact that, in most of the clades where eusociality has reached the zenith of complexity, either the queens mate many times (honey bees, army ants, harvester ants and many wasps) or there are multiple queens in the nest (many ants). In these species, where the 'single queen mated to one male' model has been replaced by greater intra-colonial diversity, the *r* part of Hamilton's rule approaches 0.25 (or less in multi-queen species). Polyandry (multiple mating) and polygyny (multiple queens) are secondarily derived in the Hymenoptera (Hughes *et al*. 2008), and an important evolutionary question is why in these sophisticated societies there has been a shift to lowered relatedness.

In a seminal paper, Crozier and Page (55) drew up eight hypotheses for the evolution of polyandry. Three of these they saw as 'front runners', and set out testable predictions for them. These predictions laid out much of the agenda for social insect research in the next decade. Microsatellites started to reveal how widespread polyandry actually is in the eusocial Hymenoptera and how extreme it can be. For example in the giant honey bee, *A. dorsata*, a queen can mate more than a hundred times (Wattanachaiyingcharoen *et al*. 2003).

One of the three hypotheses favoured by Crozier and Page was that polyandry generates behavioural and morphological variance among workers, and that this variance enhances colony fitness by allowing workers to specialize in different jobs. This idea led to a small industry (of which BPO was an active member) in which parentage was determined for workers found performing different tasks based on molecular markers. As predicted, there is a strong tendency for workers of different patrilines or matrilines to specialize in different tasks (reviewed in Oldroyd and Fewell 2007). Modelling studies have now shown how this variance can enhance fitness by dampening steep swings in task allocation that might occur if all workers were exactly the same (Graham *et al*. 2006).

Ross retained his interest in the evolution of polyandry throughout his life. In 2001, he expanded the original eight hypotheses to fourteen, suggesting that five were now plausible (184). He very sensibly pointed out that a unifying hypothesis is unlikely, and that multiple factors must have contributed to the evolution of polyandry, the relative importance of which varies between clades.

Nestmate Recognition

A social insect colony is packed with nutritious larvae and pupae, and in the case of bees and some ants a food store as well. Social insect colonies therefore need strong defences against robbers of their own and other species. Colonies also need to defend themselves against social parasites—workers from other nests that lay eggs to be reared in a cuckolded host colony (Beekman and Oldroyd 2008).

What social insects need is a system for recognizing nestmates and non-nestmates so that the former can be admitted to the nest and the latter forcibly ejected if required. But while it is easily demonstrated that social insects have evolved such systems, the mechanisms behind them are poorly understood. What is clear is that social insects seem to use the odours of the cuticular hydrocarbons to determine whether an individual is a nestmate or not. But is the variation in hydrocarbon profiles entirely genetic, entirely environmental or both (Downs and Ratnieks 1999)? Crozier and Dix (34) assumed that there is a genetic basis to colony odour and proposed two models for how nestmate recognition might come about. Under the Individualistic model, a guard worker recognizes another individual as a nestmate if she shares an allele at all odour-generating loci. Under the Gestalt model, odour molecules become mixed between nestmates via physical contacts, thus creating an overall colony odour that the guards learn to recognize. Crozier and Dix favoured the Gestalt model, because it better explains empirical observations, and works in multi-queen nests.

Despite preferring a genetic component to nestmate recognition systems, Ross noted a potentially fatal flaw in the concept that has become known as the ‘Crozier paradox’. A nestmate recognition system based on genetically based cues is unlikely to evolve, because kin discrimination selects against rare alleles so that the required genetic diversity cannot evolve. That is, if a new allele arises at a recognition locus, its bearer is likely to be the subject of aggression, potentially preventing the spread of the allele (59, 69, 89). Ross was particularly chuffed about having a paradox named in his honour.

In total, Ross published over 200 papers, which collectively had been cited more than 5,000 times at the time of his death.

Awards, Honours and Service

Ross’s achievements were recognized by a string of research fellowships from the Australian Research Council. He was a Fellow of the Australian Academy of Science (elected 2003) and the American Association for the Advancement of Science. Probably Ross’s proudest professional moment was receiving the inaugural William Hamilton Award from the International Union for the Study of Social Insects at its Washington meeting in 2006. The applause was thunderous and Ross had a hard time keeping his voice steady. He was completely overwhelmed and it was wonderful to see him so happy.

Ross was serving on the Council of the Australian Academy of Science at the time of his death. His was a voice for change, always reasonable but persistent in seeking to improve process and to avoid bureaucracy. He was particularly helpful as the Academy strove to improve the diversity of the Fellowship, for example persuading one leading woman scientist to agree to nomination, when the pleadings of her close friends had failed to move her for years. (She is now a Fellow.)

He served on numerous editorial boards including *Molecular Biology and Evolution*; *Génétique, Sélection, Évolution*; *Annual Review of Ecology & Systematics*; *Journal of Molecular Evolution*; *Australian Biologist*; and *Insectes Sociaux*. He served as Associate Editor for the journals *Evolution*, *Behavioral Ecology & Sociobiology Molecular Biology & Evolution*; and *Ecology Letters*.

He served on the Australian Research Council’s biology panel 1993–95, chairing an ARC committee on access to Australia’s genetic resources. From 1995 to 2002 he served on the board of the Australian Genome Information Centre as ARC representative. He was a member of the Scientific Advisory Committee to the

Zoological Parks and Gardens Board of Victoria. He held two successive Special Investigator awards from the ARC.

And he had one ant named after him *Pheidole crozieri* Wilson 2003.

Ross the Man

Ross was not an easy man to get to know or to communicate with. He tended to be shy, but in a curious way. He had no qualms about ringing up famous people or politicians and chewing their ear, but if one introduced him to someone at a conference he would often be a little awkward. He was no glad-hander or worker of rooms. If Ross knew something, he tended (probably out of courtesy) to assume that everyone else knew it too and conducted his conversations based on that assumption. As Ross knew a lot about many things, it meant that conversations with Ross could be rather one-sided, with the listeners being reduced to nodding agreement to propositions that they did not fully understand.

Ross was generous. He supported charities, characteristically making an annual donation in lieu of his subscription to the University of New South Wales Staff Association, from which he had resigned after a philosophical disagreement; perhaps less expectedly, the donation was to the University of Witwatersrand in South Africa. When BPO left his ARC Research Fellowship at La Trobe to take up a lectureship at the University of Sydney, Ross provided him with a generous sub-grant from his Special Investigator award. Although their projects had been merged by the Australian Research Council, Ross was under no obligation to provide BPO with any money. Ross and Ching's Townsville house was a revolving door for visitors, and they were the most gracious of hosts.

Ross thought the best of people, especially his students, post-docs, collaborators and family. He wrote strong and enthusiastic job references. He was understanding and tolerant of eccentric behaviour. He did everything a good supervisor should: provide ideas and sensible feedback in a timely manner, support the research financially and emotionally, but get out of the way of the day-to-day laboratory work and give full credit where credit was due. He recognized the importance of networking and supported his whole laboratory to go to conferences. He ran a weekly laboratory meeting in his office on Friday afternoons that was always enlivened by wine and food.

Ross had a passion for gadgets, some of which were permanently suspended from his belt, while his shirt pockets were filled with a voluminous collection of pens. He was always one of the first to try out (or write) new software for his beloved Mac computers, and his laboratory was always an early adopter of new computer hardware and new molecular and statistical techniques.

Ross had some health problems. In particular, he was laid low by recurring sinus infections related to allergy. He had his sinuses operated on several times. On the most recent occasion (2003), he haemorrhaged at home afterwards and came close to death through blood loss. He had very pale skin and was prone to superficial skin cancers. Thus, his broad-brimmed leather hat became a trademark that adorned the coffin at his funeral. Ross remained slim to the end of his life and was pretty fit, enjoying 'power walks' along the esplanade in Townsville.

He worked extremely long hours and assumed that everyone else did too. It was not unusual to receive a call from Ross after 11.00 at night or on the weekend with a work-related question or musing. He would never mind if you said it wasn't convenient to talk, but he never asked either!

He was a good bloke, and we sorely miss him.

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