Celebrating 75 years:
the eclectic origins of the Society for Reproduction and Fertility

Stuart R Milligan & Suman Rice

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Abstract

The birth of the Society for the Study of Fertility (now the Society for Reproduction and Fertility, SRF) in 1950 represented the crystallisation of an eclectic mix of scientific, political, economic and social interests operating in the scientific, agricultural and medical communities in the UK in the first half of the 20th century.These interests broadly fell into three categories. Firstly, major advances in the understanding of basic reproductive physiology and endocrinology. Secondly, the development of reproductive technologies, especially artificial insemination, in livestock production. Thirdly, a growing interest in the medical community in controlling human fertility and intervening in cases of infertility. This review will focus on how these interests interacted and led to the formation of the SRF, with a particular focus on some of the major players involved. It will also give an overview of how the Society subsequently developed and the Society as it exists today.

Introduction

The Society for Reproduction and Fertility (SRF) [formerly the Society for the Study of Fertility (SSF)] is the oldest reproductive sciences society in the UK and one of the oldest in the world. Its remit is to serve its members and the wider community through conferences, grant and scholarship programmes, high quality journals and education. This review, written to celebrate its 75th anniversary, will outline how the Society came into being and how it got to where it is today.

The SSF held its inaugural meeting in June 1950 at the meeting rooms of the Zoological Society of London (ZSL). To an outsider, the first meeting might have seemed an extraordinary collection of individuals: the presenters included two academics from Cambridge who cooled animal sperm, a family planning pioneer who ran a birth control clinic in Exeter, and a genito-urinary surgeon who was also a children's author (Fig.1). From its earliest days, the SRF was characterized by a mixture of scientists and clinicians exchanging ideas on a remarkable mix of reproductive topics, from comparative biology, farm animal breeding, human fertility and infertility, gamete biology, through endocrinology to behaviour. How did this breadth of interests come about and what made it coalesce into a coherent scientific society?

The first half of the 20th century in the UK was a period of transformation in both society and science. These changes were driven in no small part by the economic, social and political pressures created by two world wars and included the emancipation of women, increasing urbanisation, dramatic changes in agricultural practice and a plethora of technological and medical advances. In the biological sciences, emphasis shifted from the observational and descriptive approaches of the Victorian era to more experimental, physiological investigations. There was a growing general acceptance of Darwinism which, with the new science of genetics, helped support a rise of the eugenics movement in the UK.

CONFERENCE ON FERTILITY—JUNE 1950

Programme

FRIDAY, 16th JUNE

10.00 a.m.

Business Meeting:—

Inauguration of the Society for the Study of Comparative Fertility.

"The Diagnosis and Treatment of Male Infertility."
KENNETH WALKER, Esq., F.R.C.S.

"Pathological Changes in the Rat Testis following Ischemia."
R. G. HARRISON, Esq., D.M., and A. G. OETTLÉ, Esq., M.D.

2.00 p.m.

"Storage of Mammalian Spermatozoa at Low Temperatures." A. S. PARKES, Esq., SC.D., D.SC., F.R.S.

"Comparative Studies on Semen Ejaculate and Testis Biopsies." C. A. JOËL, Esq., M.D., PH.D.

"Artificial Insemination in Fowl." C. POLGE, Esq.

SATURDAY, 17th JUNE

10.00 a.m.

"Reflections upon some Aspects of Fertility."
SAMUEL L. SIEGLER, Esq., M.D., F.R.C.S.

"Sterility: Its Causes, Investigations and Treatment."
Film: SAMUEL L. SIEGLER, Esq., M.D., F.R.C.S.

"Some Observations on the Breeding of Dogs."
I. W. ROWLANDS, Esq., PH.D.

"The Significance of Round-cell Infiltration as seen in Endometrial Biopsy Sections."
MARGARET C. N. JACKSON, M.B., D.R.C.O.G.

2.00 p.m.

"Hysterosalpingography in the Diagnosis and Treatment of Sterility." Film: CLAUDE BÉCLÉRE, Esq., M.D.

"Activity of Spermatozoa *in vitro*."
A. WALTON, Esq., PH.D.

"Some Conclusions about Infertility."
BETHEL SOLOMONS, Esq., M.D., F.R.C.P.I., F.R.C.O.G., F.A.C.S. (HON.)

Notes on the speakers:

K. Walker: genito-urinary surgeon, author of *Physiology of sex and its social implications*; worked with Mary Barton. R.G Harrison: just appointed Chair of Anatomy, Liverpool, aged 29.

AS Parkes*: National Institute of Medical Research, London.

C.A Joel: German medical scientist.

C. Polge*: PhD student, aged 24, working with Parkes.

S.L Siegler: American physician and surgeon, author of *Fertility in women* (1944);

I.W Rowlands*: scientist worked with Parkes; ARC Institute Animal Physiology, Babraham; appointed 1964 First Director of the Wellcome Institute of Comparative Physiology, ZSL;

Margaret Jackson*: medical scientist, family planning pioneer and advocate for widely accessible sexual health services in the UK.

C. Beclere: French clinician, son of Antoine Beclere who developed medical radiology;

A Walton: expert in sperm physiology and AI in animals;

B Solomons: gynaecologist and former irish International rugby player, authored Handbook of gynaecology (1919), President of the Royal College Physicians (1946–8) . (* later SSF Marshall Medallist).

Fig 1 (opposite page). *The programme of the inaugural meeting of the Society for the Study of Fertility, 1950 (from Parkes, 1971)*

It was from this shifting societal and scientific environment that three main elements emerged which crystallised into the SRF. The first was the advance in scientific knowledge and understanding of the physiological processes controlling reproduction. This was supported by, and contributed to, the increasingly experimental approach to studies of biological mechanisms. The second was the increasing focus on the practical and economic need to improve productivity in the livestock industry, in part by the use of artificial insemination (AI). The third reflected the growing societal interest in controlling human fertility and family size, as well as the medical interest in treating human infertility.

This article will focus on some of the key characters, and the scientific and societal landscape in which they were operating, that led to the formation of the SRF. The subsequent growth and evolution of the nascent Society will be briefly described to allow it to complement the previous reviews of the Society and its associated journals (Clarke, 2007b; Cook, 1994; Parkes, 1971).

The first ingredient of the eclectic mix: advances in basic reproductive physiology and endocrinology

A clear starting point for this part of the story is Walter Heape FRS (1855–1929) (Fig. 2). Heape was affiliated with the Department of Zoology in Cambridge where he developed a remarkably broad range of interests in basic, comparative and applied science, but particularly "*mammalian development and generation*" (Biggers & Kountz, 2016). Following a trip to India where he attempted (but failed) to collect embryos from langur and rhesus monkeys, he described the detailed uterine changes during their menstrual cycles and he compared these to the cycles in women. His studies on fertility in sheep provided the basis for his important paper "The '*sexual season' of mammals and the relation of the 'pro-oestrum' to menstruation*" (Heape, 1900) and the introduction of the now familiar terminology associated with oestrous cycle stages. Perhaps his single most remarkable achievement was the first successful embryo transfer in rabbits on the 27 April 1890 (Biggers, 1991). Heape also recognised that "heat" alone was not sufficient to cause ovulation in rabbits. This stimulated his interest in artificial insemination (AI) and in 1897 he reported the use of AI in rabbits, dogs and horses. Heape had a background in business and he recognised the importance of understanding animal breeding for improving livestock: in 1897, he was appointed by the Royal Society to their Evolution

Committee, and published a book "The Breeding Industry. Its value to the Country and its Needs" in 1906. Heape retired from Cambridge in 1907, but Heape's contributions to reproductive biology and animal breeding were acknowledged, continued and expanded by the next major player in the field, FHA Marshall.

Francis Hugh Adam Marshall (1878-1949; Fig 3) studied science (Zoology, Geology, Chemistry) in Cambridge but the course bored him (he later complained that there was not enough physiology) and he finished with a 3rd Class in Part II in 1900. Before he left Cambridge Marshall had obtained an introduction to Walter Heape and Heape told him some of his ideas about reproductive processes. This sparked a real interest in Marshall and despite his mediocre academic record he went to Edinburgh as a research assistant with the zoologist James Cossar Ewart FRS (Professor of Natural History). He initially undertook research on the reproduction and experimental breeding of animals on Ewart's private experimental farm. Ewart was a pioneer in animal breeding and genetics and had been investigating the theory of "telegony" (a theory of heredity holding that offspring can inherit the characteristics of a previous mate of the female parent). His experiments His experiments on

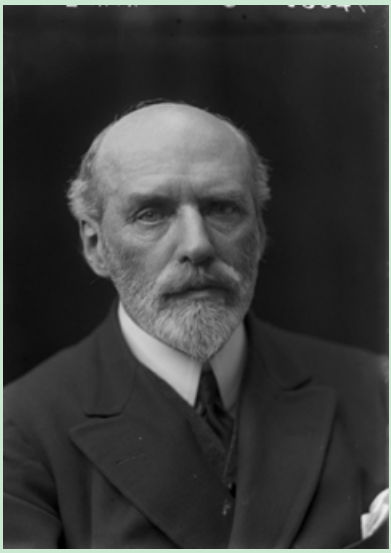

Fig 2. ***Walter Heape,*** *FRS (1855–1929) (in 1918; National Portrait Gallery)*

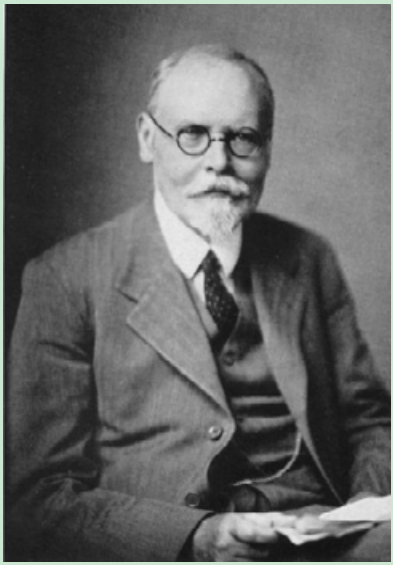

Fig 3. ***FHA Marshall****, CBE, FRS (1878-1949) (from Parkes, 1950)*

the hybridisation of species, some of which involved crossing a zebra stallion with mares of various breeds, provided no support for the theory (Ewart, 1899) and he shifted some of his attention to cross-breeding sheep and for fleece improvements. Marshall acted as a research assistant to Ewart for about a year (1903-4) but then became Lecturer in the Physiology of Reproduction (1905-8) and Assistant to the Professor of Physiology (EA Schafer) (1906-8). Marshall later recalled his '*lasting sense of gratitude*" to Ewart "*for the facilities he enjoyed at the Penicuik experiment station… at a time when such facilities did not exist elsewhere*" (Marshall, 1934).

If Heape and Ewart provided the initial sparks for Marshall's interest in reproduction, it was Edward Schafer (1850-1935; Fig. 4) in Edinburgh who provided the intellectual and physical space for the fire to ignite. Schafer is acknowledged as a great physiologist and was a founding member of the Physiological Society in 1876. Schafer's observations in 1894 on the immediate and dramatic effects of adrenal extracts on heart rate and blood pressure (in contrast to the slow and often variable, and therefore problematic, effects of other ductless gland extracts in other systems) opened the door to the role of endocrinology in physiological investigations. He moved from University College

London to Edinburgh in 1899. The results of the work of Marshall and Jolly in his Department on the oestrous cycle of dogs and rats (Marshall and Jolly, 1905) changed Schafer's previously long-held view that the gonads influenced other tissues through nervous connections and instead convinced him that the gonads secreted hormones (Borrell, 1985). Schafer became the chairman of the Committee on the Ductless Glands of the British Association for the Advancement of Science; during the years 1904-1920 over one-quarter of all the funds allocated by the Association for Research in Physiology went to studies of endocrine systems.

During his time in Edinburgh, Marshall studied the ovarian events associated with oestrous cycles in sheep, dogs, ferrets as well as the effects of ovariectomy and ovarian transplantation. He clearly identified the role of the ovary in producing two hormones: one controlling the oestrous cycle and another from the corpus luteum controlling the early stages of pregnancy. However, it was not this early experimental work that pushed Marshall to the forefront of reproductive biology. It was his publication in 1910, at the age of just 32, of the encyclopaedic, 700 page *The Physiology of Reproduction* (Marshall, 1910).

Schafer had pointed Marshall

Fig 4. ***Sir Edward Albert Schafer****, FRS (1850-1935) (Wellcome Collection)*

towards an intellectual vacuum which needed filling. In 1898 Schafer had produced the first volume of a huge, multi-author Textbook of Physiology, but he admitted in the Preface that "*The subjects of generation and reproduction have been omitted in this text-book because although strictly speaking appertaining to physiology, they are studied almost entirely by morphological methods and are more conveniently treated in connection with morphology*" (Schafer, 1898).

Inspired and encouraged by Schafer, Marshall worked to fill this gap in physiological understanding. Perhaps reflecting the earlier Victorian vogue for collecting diverse biological specimens, Marshall assembled a huge array of information on the reproductive biology of a wide range of species (mainly, but not exclusively mammals), with topics ranging from gametogenesis and gonadal function through to reproductive patterns, pregnancy, the placenta, parturition and lactation, and even the human birth rate.

The resulting *The Physiology of Reproduction* was hailed as a masterpiece. It firmly established reproductive physiology as an important system in its own right and helped define the breadth of reproductive science. It provided both a stimulus and essential source of information for reproductive studies in laboratories across the world and produced widespread recognition for Marshall. The Preface written by Schafer opened with "*This is the first time that the Physiology of the Organs of Reproduction has been presented in a complete form*". Marshall dedicated the book to Walter Heape "*through whose influence I was first led to realise the importance of generative physiology both in its purely scientific and in its practical aspects*". A new edition appeared in 1922, and greatly expanded, multi-volume, multi-authored 3rd and 4th editions (now entitled "Marshall's Physiology of Reproduction") in the 1950-60's and 1980s-90s (edited by A.S. Parkes and G.E. Lamming, respectively). Marshall was elected a Fellow of the Royal Society in 1920, awarded a CBE in 1933, gave the Croonian lecture in 1933, awarded the Royal Medal by the Royal Society in 1940. Marshall was one of the four honorary members of the Society for Endocrinology and an original member of the Council of Management of the Journal of Endocrinology.

Two years before *The Physiology of Reproduction* was published, Marshall returned to Cambridge as University Lecturer in Agricultural Physiology. Marshall remained in Cambridge at Christ's College for the rest of his career and played a major part in establishing the School of

Agriculture as a world leader in agricultural science. In 1919 he became Reader in Agricultural Physiology. He developed a particular interest in the seasonal reproductive phenomena and their links with external environmental factors (e.g. climate, light etc.). In 1943, Marshall officially retired on account of age, but he consented to carry on with his duties during the war period. Sadly, he died of appendicitis in 1949, one year before the inaugural meeting of the SSF (now SRF). The Marshall Medal of the SSF was established in 1963 following the suggestion of Sir Alan Parkes, to commemorate the life and work of Marshall. It is the Society's premier award, given to outstanding contributors to the study of fertility and reproduction. The fact that the award was instigated some 14 years after Marshall's death and 13 years after the Society was established reflects the deep impact that Marshall had both on the subject and on his fellow scientists.

The 1920s-1950s saw an extraordinary rise in the study and understanding of reproductive biology, particularly reproductive endocrinology. Looking back at this period, Sir Solly Zuckerman recorded "*We were then in the heyday of the growth of endocrinology, and of reproductive physiology in particular. Almost any experiment seemed to produce fascinating results*" (Zuckerman 1984). The dynamic changes in the reproductive tracts of animals at puberty, during oestrous cycles and pregnancy, and during seasonal cycles provided a clear focus for studying how hormonal systems operated. A particular advantage of studies of reproductive systems over other endocrine organs was that the former were amenable to experimental manipulation without threatening essential life processes. In addition, the effects of such manipulations on their various target organs (reproductive tract, brain and behaviour) could be easily recognised and quantified.

Marshall quietly influenced the scientific paths of many individuals during his career. For present purposes, Alan Parkes (1900-1990; Marshall Medal 1970; Fig 5) deserves particular mention. Parkes was not only a remarkable scientist in his own right but also became a particularly adept 'mover and shaker' in the biological sciences. Parkes has been described as "*one of the most influential figures in the field of reproductive biology in the 20th century*" (Polge, 2006). Among many other roles, Parkes was to be the central catalyst for the eventual formation of both the Society for the Study of Fertility and its associated Journal of Reproduction and Fertility (JRF).

Fig 5. ***Sir Alan Parkes****, FRS (1900-1990) (from Polge, 2006)*

Parkes went to Cambridge to study agriculture and was tutored by both Marshall and John Hammond (of whom more later). Marshall asked Parkes to index the second edition of *The Physiology of Reproduction* (1920) and this helped establish a long and productive friendship with Marshall (Polge, 2006). Marshall was also the external examiner for Parkes' thesis. In 1921, Parkes moved to Manchester to study the sex ratio in mammals. This was in the days when animal work was much freer from legislative oversight: he purchased some mice from a local pet shop to form the basis of a small breeding colony. He later took these mice to University College London and then to the National Institute for Medical Research (NIMR) London where the strain became known as the 'Parkes mouse'! Probably reflecting his experience in indexing *the Physiology of Reproduction*, he realised that the variety of reproductive patterns in wild mammals provided a rich insight into reproductive mechanisms. Together with Rogers Brambell (1901-1970; Marshall Medal 1969), he collected material from a wide range of wild species (including voles, shrews, woodmice, hedgehogs, squirrels, moles, bats, stoats and weasels) to study their reproductive patterns and characteristics (Polge, 2006).

But Parkes could switch his focus quickly. Initial chance observations on the effects of X-irradiation on ovarian function led him to develop an interest in the nature and source of gonadal hormones. His first book Internal secretions of the ovary was published in 1928. He was involved in the standardisation and nomenclature for gonadotrophins extracted from sources such as human pregnancy urine, human placentae and pregnant mares serum and he worked on the activities of oestrogens, progesterone and androgens. This was in the heyday of hormone discovery: Parkes himself noted: "*the naturally occurring oestrogens and androgens as well as progesterone were all isolated, characterized and their biological properties extensively investigated between 1929-1935. In addition, the hypophyseal, placental and endometrial gonadotrophins were discovered between 1926-30*" (Parkes, 1985). Amongst other studies, Parkes went on to investigate why the apparent activity of preparations varied with the method of administration: this led him to develop, with his wife Ruth Deanesly, the first sub-cutaneous drug-eluting implant to deliver therapeutically relevant concentrations of hormones (Deanesly and Parkes, 1938).

As the numbers of scientists engaged in research in reproductive studies and endocrinology expanded in the inter-war years, pressure grew to provide an intellectual "home" for their interests and exchanges of ideas. Parkes was one of the major driving forces in the developments that followed. The Journal of Endocrinology " ... *to advance knowledge concerning the glands of internal secretion* ... " came first. It was conceived on a bus in 1937 by Sir Alan Parkes, Sir Solly Zuckerman and others on their way to the first ever international symposium on the physiology of reproduction. The Journal of Endocrinology was first published in July 1939, with Parkes as Chairman of the Management Committee and Marshall as a founding member. The dominance of reproductive studies in endocrinology at this time is reflected by the contents of the first issue, in which 38/44 (i.e. 86%) of the papers were related to reproductive hormones. The formation of the Society for Endocrinology followed in 1946 after the second world war had ended, with Parkes as its first Chairman and Marshall as a founding member. However, while the Society for Endocrinology and its journal were suitable homes for many of the reproductive studies at the time, this was not the case for topics such as gamete and embryo biology.

The second ingredient of the eclectic mix: developments in applied reproductive technology in agricultural production

Changes within the agricultural sector in the UK in the first half of the 20th century provided a different focus on reproductive biology. Throughout this period, political and economic pressures continually focused attention on the need to increase productivity in UK agriculture to provide food security, especially in the dairy industry (Clarke, 2007a; Wilmut, 2007a, b; Woods, 2007). These pressures included the withdrawal of many working men and horses from the land during WWI, the economic depression of the 1930s, the threatening approach of WWII, and a generally poor understanding by both farmers and veterinarians of the control of growth and reproduction in the livestock they managed. New 'animal breeding research' centres were established at Cambridge (~1908), in Edinburgh (Institute of Animal Genetics, in the late 1920s) and in Reading (the National Institute for Research in Dairying, in the 1930s). Food rationing in WWII led dairying to be seen as a vital "war service" (Wilmot, 2007b). In the wake of WWII, the Agricultural Research Council (UK) created the national Institute of Animal Physiology at Babraham, Cambridge. The work of these centres helped broaden the boundaries of reproductive biology to include its wider interactions with development, growth, metabolism, body composition, nutrition, behaviour, health implications and genetics. By the end of WWII, British agriculture had been transformed into a modern industry underpinned by growing scientific knowledge (Woods, 2007).

John Hammond (1889-1964; Fig 6) became a leader in this field. He came from a well-educated, practical farming background with veterinary connections and started his studies in Cambridge in 1907. He attended some of Marshall's lectures which stimulated his scientific interest in fertility, milk secretion and growth in cattle, pigs and sheep. After service in WW1, he joined the School of Agriculture in Cambridge headed by Marshall (Sanders, 1965; Slater & Edwards, 1965). Hammond's background in practical farming continuously focused his research towards understanding farm animal physiology and reproduction and providing practical solutions to improve livestock and husbandry. His dictum was "*science isn't science until it is applied*" (Slater and Edwards 1964).

Hammond's interest in fertility and infertility in cattle and the need to provide practical information to farmers and veterinarians on

problems such as sterility, abortion, management and feeding led to the publication of the detailed "*The Physiology of Reproduction in the Cow*" (1927). He attracted postgraduate students and scientists in agriculture from all over the world.

Hammond's observations on the size and growth of fetuses led him to suspect that the prenatal maternal environment had a major influence on fetal development. The experimental results from crosses of small and large breeds of rabbits confirmed his ideas. Hammond and Arthur Walton (of whom more later) then combined their expertise to up-scale in remarkable reciprocal-cross experiments between Shire horses and Shetland ponies. The results were clear: the mother exerted a major controlling influence on fetal and later development (Walton & Hammond, 1938). These pioneering studies of Hammond were many decades before the concept of the developmental origin of health and disease (DOHaD; Barker, 2007) was developed.

But it was in relation to the development of another, more practical approach to animal breeding that Hammond had the most far-reaching influence in the UK: artificial insemination (AI). At the start of the 20th century, cattle breeding in the UK (like elsewhere) was dependent on natural matings. The logistics

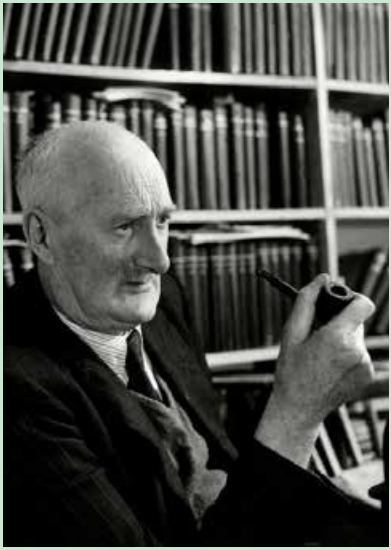

Fig 6. ***Sir John Hammond****, CBE, FRS (1889-1964) (National Portrait Gallery)*

of this meant that matings with individual high quality ("pedigree") bulls were restricted to a limited pool of elite farmers (Wilmot, 2007b). As a consequence, genetic improvements were slow to spread and this severely limited the growth of a high-yielding dairy industry in particular. AI offered the opportunity of rapid, inexpensive improvement in stock by inseminating females with semen obtained from high quality sires. By eliminating natural mating, it also reduced the risk of transmitting some of the main diseases associated with sterility. The potential benefits of AI to improve the quality of the geographically fragmented national dairy herd were clear to Hammond.

Work to establish AI as a practical procedure had begun in Russia in 1899 by Ilya Ivanovich Ivanow and AI was used on a large scale in horses, sheep and cattle in Russian experimental breeding stations from the early 1920s (Ombelet & van Robays, 2015). AI research programmes were started in a number of countries in the 1930s and 1940s. Hammond led the field in the UK, going on a trip to Russia in the early 1930s to bring back the necessary equipment. However, for widespread practical use the technique required the ability to store sperm and allow it to be transported to its distant points of use. Arthur Walton (1897-1959; Fig 7) now becomes a key figure in the story. Walton joined Hammond in the mid-1920s after studying the physiology of mammalian sperm for his PhD in Edinburgh. In Cambridge, Walton continued to focus on sperm physiology and methods for keeping sperm alive in vitro. In 1926, Walton reported success: he had sent cooled rabbit sperm in the post from Cambridge to Edinburgh and successfully produced live young in artificially inseminated does. Walton subsequently sent cooled ram semen to Poland in a thermos with chipped ice (1935) and bull semen to Holland (1938) (Lonergan, 2018).

Hammond, together with Joe Edwards and Walton, developed a practical method of AI for use in commercial cattle. In 1940, this increased the potential number of cows fertilised per ejaculation from one to between ten and fifteen (Wilmot 2007b). Hammond became the driving force behind establishing the AI service for cattle in the UK in 1942, helped by the pressures on milk and meat production associated with the war. This was despite much resistance from farmers as well as some government committees to such an "unnatural" technique. The Milk Marketing Board (MMB) became the central organiser of the scheme and by 1950, 20% of UK cattle were being artificially inseminated (Wilmot, 2007b). The success of AI and applied reproductive physiology in the dairy industry

resulted in the establishment of the ARC Unit of Animal Reproduction in Cambridge in 1949 led by Hammond (who had succeeded Marshall in the Readership in Animal Physiology at the School of Agriculture). The MMB later (1959) recognised the importance of reproductive scientists in improving the dairy industry by giving money to help establish a permanent chair (the Mary Marshall and Arthur Walton Chair) in the Physiology of Reproduction at Cambridge, of which Alan Parkes was the first recipient (Parkes, 1985). In 1980, the SSF established the Hammond Lecture which was presented annually at the Society's winter meeting by a scientist recognised for their contribution to the practical application of reproductive research to agriculture. The Hammond Lecture was later subsumed (along with the Parkes, Amoroso and Arthur Walpole Lectures) into the Anne Mclaren Distinguished Scientist Lecture.

Fig 7. ***Dr Arthur Walton*** *(1897-1959) (from Polge, 2005)*

Meanwhile, WWII had resulted in the disruption of Parkes' reproductive endocrinology programmes at the NIMR. Inspired and intrigued by sporadic observations in the literature, he started his own research into trying to prolong the life of sperm in vitro by freezing. He reported successful revival of human sperm frozen in bulk (rather than as a thin film or in capillary tubes) in 1945. With considerable

prescience he wrote: "*Artificial insemination of humans will no doubt become increasingly common, and the elaboration of a method permitting of prolonged storage and transport of the semen without affecting the genetic properties of the spermatozoa would open up remarkable possibilities*" (Parkes, 1945). To progress, he required an animal model that could provide an easy access to semen. Chickens were in good supply at the NIMR and in 1948, he invited a young agricultural graduate (Chris Polge, 1926-2006, Marshall Medal 1988) from Reading to join his staff. Following a remarkable set of circumstances, they fortuitously discovered the potential of glycerol as a cryoprotective agent. In October 1949, nine months before the inaugural meeting of the SSF, they published their findings in Nature (Polge et al, 1949). This unlocked the door to the new world of cryobiology to science in general and to reproductive biology in particular.

The third ingredient of the eclectic mix: a growing interest in human fertility and infertility.

The final essential ingredient for the formation of the SRF was a medical interest in fertility. This gradually developed in the first half of the 20th century alongside huge changes in the social, cultural and political environment, particularly the status of women. At the start of the 20th century, talk about sex or birth control was largely taboo and the consensus of many (predominantly male) doctors was that birth control led to prostitution and immorality (Association of the Directors of Public Health, 2023). At the same time, the use of selective breeding to enhance desired traits in other species led to the concept of eugenics being widely held, especially in the upper echelons of society which included many scientists, medical professionals, politicians, social reformers and leading members of the Church of England (English Heritage, 2024).

But change was in the air. During WWI, women streamed into the occupations which previously had been largely the reserve of men. In 1918, women aged over thirty, who met specific qualifications (owning a house, or married to a houseowner), obtained suffrage. In 1928, suffrage was extended to all women. In 1918, Dr Marie Stopes (1880-1958), a paleobotanist but also ardent campaigner for women's rights, published her controversial (at the time) book "Married Love". The preface states that it was geared toward teaching married couples how to have a happy marriage, including "great sex". In 1921, Marie Stopes and her husband

Arthur Roe opened the first birth control clinic "The Mothers' Clinic for Constructive Birth Control". The clinic was free and open to all married women and offered birth control advice (especially abstinence and withdrawal) and dispensed cervical caps. In the 1920s the numbers of clinics increased across the country. Marie Stopes even operated two horse-drawn Caravan Clinics that travelled to small towns.

The general aim of the birth control movement was to improve the living conditions and health of working-class women through the provision of efficient female-controlled birth control. Because of this, there were links between many in the birth control movement and the Eugenics Society as many eugenicists believed that working-class people were reproducing at a far greater rate than their middle- and upper-middle-class counterparts (Rusterholz, 2020). In 1927, the Birth Control Investigation Committee (BCIC) was established "to promote the scientific investigation of birth control" (Rolleston, 1927). This Committee had very strong links to, and was partly funded by, the Eugenics Society. The Committee included a number of eminent scientists, including FHA Marshall and Julian Huxley. The BCIC commissioned Dr John R Baker (a student of Julian Huxley) to test potential chemical contraceptive preparations (vaginal suppositories, gels, pastes etc.) for both their spermicidal properties and safety (irritation of the vagina of dogs). Over the next decade, Baker went on to develop "Volpar" (for "Voluntary Parenthood") which became a widely used chemical contraceptive.

In Exeter, the first birth control centre in the south-west was opened in 1930 after a local councillor Rachel Allen persuaded the authorities to open a clinic for sick and needy patients to receive contraceptive advice free of charge. Margaret Jackson (1898-1987; Marshall Medal 1979; Fig 8) had qualified as a doctor in the 1920s but there were limited jobs available at this time for women doctors and she was asked to run the Exeter clinic voluntarily. While the initial focus of birth control clinics was to offer practical advice on limiting family sizes, the expertise available began to attract increasing numbers of women who wanted to become pregnant but seemed to be unable to conceive: in 1933, the percentage of women who visited Margaret Jackson's clinic with sub-fertility issues was just 0.5%; by 1946, this had risen to 33% (FPA papers). In addition to the accepted causes of infertility in women (e.g. anovulation, tubal, uterine and cervical damage), there was also a growing recognition that male fertility problems, particularly poor-quality semen, were a significant factor (Beers, 2021). Gradually, this led to the expansion of National

Birth Control Association clinic services to include gynaecology and infertility (Beers 2021). In 1939 the Association was rebranded into the "Family Planning Association" (FPA) (Association of the Directors of Public Health, 2023).

Through her work with the FPA, Margaret Jackson developed a career that led to her being recognised internationally as an expert in both family planning and fertility treatment. In her clinic, Jackson insisted that the husbands of all sub-fertile couples should be examined. Mrs Clare Harvey (1903-1996) joined Margaret Jackson as a volunteer "assistant secretary" soon after the clinic started. However, Clare was a biologist and also started to undertake the semen analyses. Fortuitously, Clare's husband Leslie Harvey was a lecturer (and later Head of Department) in the Department of Zoology in the University of the Southwest (Exeter) and had access to laboratory facilities and technical help in the University. Leslie Harvey also had expertise in cytology and undertook the preparation and staining of endometrial biopsies from the clinic. In 1937, Jackson arranged for Clare Harvey to learn the spermicidal testing procedures used by John Baker in Oxford so that this work for the FPA could instead be done in Exeter. This was facilitated by the fact that Clare Harvey had access to the essential dog kenneling required through her husband's work at the university on silver foxes. Margaret Jackson and Clare Harvey became a powerful team, with Harvey doing the laboratory tests and experiments on sperm and vaginal mucus, while Jackson saw the patients. In 1939, 700-800 women were in more or less regular attendance. Their first publication together was "Assessment of male fertility by semen analysis: an attempt to standardise methods" (Harvey and Jackson, 1945).

Diagnosis of the fertility problems by the FPA clinics was not the same as treatment. When female-factor infertility was indicated, women could be referred to a gynaecologist. When male-factor infertility was indicated, options were more limited. Depending on the nature of the male problem, artificial insemination (AI) was a possibility - either using the husband's sperm (if suitable) or more controversially, semen from a donor (AID). There were two main pioneers of AI and AID in the UK: Mary Barton in London and Margaret Jackson in Exeter.

In 1943, the FPA set up an executive subcommittee (including Margaret Jackson) to consider how the organisation could make its impact felt in the field of human sub-fertility. They agreed to establish a Seminological

Centre in London to run tests on the husbands of infertile couples. Crucially, as far as the formation of the SSF/SRF is concerned, they also agreed to organise scientific meetings to exchange ideas with others working in the field (Beers, 2021). The first was in Exeter in 1944.

The meeting of minds: towards the establishment of the Society for Reproduction and Fertility

Margaret Jackson wanted to share and exchange scientific knowledge for clinical benefit. She initiated the bringing together of workers from the human clinical and the animal reproductive world who had interests in semen analysis and artificial insemination. Under the auspices of the FPA she organised a meeting entitled "Conference on Method of assessing Male Fertility" in early September 1944 in Exeter. It is remarkable that the meeting took place at all: D-Day had taken place just 3 months earlier and V1 and V2 rockets were hitting London.

There were just 11 attendees (FPA papers). On the human fertility side, there were Dr Margaret Hadley Jackson and her husband (who was a local GP), Mrs Clare Harvey and her husband and three London fertility specialists. Two other attendees were A Macbeth (from Organon, a pharmaceutical company

Fig 8. ***Dr Margaret Jackson*** *(1898-1987) (in 1972, receiving her Honorary Doctorate from Exeter University; courtesy of Dr Mark Jackson)*

supplying hormone preparations), and another "Margaret Jackson" (who was Margaret Hadley Jackson's sister-in-law) from the Lancet. On the "animal" side of the Conference there were just two: Arthur Walton and MC Chang from Cambridge. Arthur Walton had by now more than 25 years of expertise of semen collection, dilution, storage and in AI in domestic and wild animals. MC Chang (1908-1991; Marshall Medal 1971) was studying the physiology and metabolism of spermatozoa with Walton, having had completed his doctoral degree in 1941 under Walton. Chang was also studying the possibility of cooling and reviving mammalian embryos. He went on to be one of the pioneers in the studies of mammalian fertilisation and worked with Gregory Pincus on the development of the oral contraceptive pill.

This was very much a meeting of open discussions and exchange of ideas. There were practical demonstrations, including the examination of human post-coital cervical mucus, which was a routine procedure in Margaret Jackson's clinic. Summarising the meeting, Dr Jackson wrote "*Everyone expressed satisfaction with the venture, especially bringing together workers in the human and animal fields. It is hoped that similar meetings, dealing with all aspects of the problems of sterility, will be held once or twice yearly in different centres*".

At the invitation of John Hammond and Arthur Walton, a second meeting, entitled "Meeting on Seminology", was held in July 1945 at the ARC Animal Research Station in Cambridge. The attendees increased to 15, and now included Alan Parkes (who was later described by Margaret Jackson to be in "*great form and a great addition*") (FPA papers). Thaddeus Mann (Marshall Medal 1976) also attended: he was an expert in the biochemistry of semen and of male reproductive function and went on to be Director of the Agricultural Research Council's Unit of Reproductive Physiology and Biochemistry at Cambridge (1953-76) and later became the Mary Marshall-Walton Professor of the Physiology of Reproduction (1967-76). It was another hands-on meeting with demonstrations and the value of "*pooling of ideas from findings in both animal and human research in fertility*" was recognised. It was also a very hospitable meeting, with Margaret Jackson recording afterwards "*The Conference was a success – Walton and Hammond were marvellous hosts – we had a kind of bottle party in Hammond's Room at Downing College on Sat night". She also wrote "All seemed agreed that it was a good show and general relief it was a small gathering and one with a friendly feeling and no undue amount of back biting and intrigue*".

Further meetings under the auspices of the FPA were held on "Infertility" (London, 1946, at the invitation of Alan Parkes), Oxford (1947, to tie in with the International Physiological Congress), Exeter (1948; ~ 60 delegates) and Edinburgh (1949). The Conferences were beginning to cover wider topics and the label of "Infertility" was increasingly inappropriate: for example, in 1948 Geoffrey Harris (of hypothalamic releasing factor fame) presented a paper "Coitus and Fertility in the Rabbit", and in 1949 Arthur Walton gave a paper entitled "Patterns of male sexual behaviour". The Conferences were also outgrowing the support that the FPA was able to effectively offer in terms of organisation and publication of the papers presented. At the close of the Edinburgh meeting it was agreed that "*the time might be ripe for the formation of a society for the study of problems in comparative fertility, both from animal and the clinical side*". Margaret Jackson saw it as an opportunity to "*rope in animal reproduction people and researchers who weren't interested in the problem from the FPA angle at all*" (FPA papers). To coordinate the two sets of interests, Dr Arthur Walton and Dr Gerald Swyer (an eminent endocrinologist and expert in reproductive medicine) were appointed as joint secretaries to a new Committee (which also contained Alan Parkes). This was charged with arranging the next conference and with presenting before that conference "*plans for the formation of such a society*" (Conference on Infertility, 1949).

And so it was, on Friday 16th June 1950 at the Zoological Society of London, there was the inaugural meeting of the proposed "Society for the Study of Comparative Fertility" (Fig 1). There was no enthusiasm for the word "comparative" in the title and the Minutes recorded "*The chair was taken by Dr AS Parkes FRS with the unanimous consent of those who had come together for a Conference on Fertility, the Society for the Study of Fertility was called into being*" (SRF papers). Arthur Walton was Biological Secretary, Gerald Swyer was Medical Secretary and the Committee included Clare Harvey and Margaret Jackson. One of the three trustees was Dr John Hammond.

The development of the SRF (nee SSF)

The early days of the Society and its associated journals have been well described by Parkes in his 1971 review to celebrate 21 years of the Society (Parkes, 1971) and embellished in his autobiography (Parkes, 1985). Clarke (2007) extended the account to take in the changes in 2001 when the Journal of Reproduction and Fertility (JRF)

changed its name to Reproduction, and when the previously separate organisations of the Society and Journal merged to become the Society for Reproduction and Fertility (SRF). Cook (1994) reviewed the first 30 years of the JRF. The current account will not repeat this information but will simply reflect on the general way the Society evolved in parallel with developments in reproductive science.

The early annual meetings of the Society were heavily weighted towards male fertility and infertility in humans and animals, but the representation from the wider "biological" and endocrinological experimental community increased during the 1950s and 1960s. This was without doubt helped by ensuring that the officers (Chairman, Biological and Medical Secretaries, and Treasurer) were representative of the different interests involved (Parkes, 1971). Publication of the proceedings of the early annual meetings was under the heading of "Studies on Fertility" but there was dissatisfaction with the publishers. In 1956, Alan Parkes proposed, on behalf of the SSF that the Journal of Endocrinology should become the official organ of the SSF and that its name should be changed to "The Journal of Endocrinology and Reproduction". However, "*views on this proposal were so divided that it was dropped, and the Society for the Study of Fertility then launched its own journal*" (Zuckerman, 1984). The Journal of Reproduction and Fertility (JRF, now Reproduction) was first published in 1960, with Alan Parkes chairing the Council of Management. In 1993, the Journal established the Parkes Lecture in memory of Sir Alan Parkes, and this lecture was given at the annual conference until 2003 when it was subsumed into the Distinguished Scientist Lecture. Between 1965 and 2000, the JRF also published separate Supplements designed to cater for original papers too long for inclusion in the Journal, for extended reviews and monographs and for the Proceedings of symposia and similar meetings. Many of the symposia were sponsored by SSF. The supplements were extraordinarily wide ranging in topic and covered meetings across the globe: from Immunological aspects of pregnancy (Supplement 3, Edinburgh, 1968), to "the Great Apes of Africa" (Suppl 28, Gabon, 1980) "The environment and reproduction in mammals and birds" (Supplement 19, 1973; symposium in Edinburgh) to "Embryonic diapause in mammals (Supplement 29, 1981, Australia). One remarkable one was Supplement 17: this was an annotated translation of Regnier de Graaf 17thC *Treatises on the Human Reproductive Organs* which contained wonderful facsimile illustrations.

The post-war period saw a worldwide expansion in universities and the

science research base. In the UK, the number of universities more than doubled in two decades. As the Society grew, there were pressures for it to expand its core base beyond the UK (Society for Reproduction and Fertility papers). In 1956, there was an approach from the American Society for the Study of Sterility to see whether the two societies could be amalgamated, but this was deemed impractical. In 1965, the Society was approached by Dr W Ansel suggesting that an American branch of the Society be formed, but the SSF Committee was against any fragmentation of the Society and the practicalities seemed too daunting to consider further. The result was the formation of the Society for the Study of Reproduction (SSR) in 1967: the next year, John Biggers reported that there had been "explosive growth" of the new SSR to about 1200 members with a new journal (Biology of Reproduction) planned. In 1968, Brian Setchell asked whether an Australian chapter of the Society be formed. The response of the SSF Committee was positive this time and the SSF AGM agreed that "the Australians should make their own decision". In the end, the Australians decided to go their own way: the Australian Society for Reproductive Biology (SRB) was formed.

A major strength of the new Society was the bringing together of people with a diversity of interests and perspectives across the breadth of reproductive biology, including clinical and basic science. This provided an enormously stimulating and friendly environment for the discussion and exchange of new ideas. This approach has characterised the Society to the present day. In addition to its traditional 3-day summer meetings held at various locations around the UK, the growth of the Society allowed the introduction of shorter (1-2 days) winter meetings, often at the ZSL, London. Even so, the conference programmes became increasingly crowded. The introduction of parallel sessions was inevitable but was met with considerable resistance because the majority of delegates enjoyed the exposure to topics and ideas outside their own speciality.

The breadth of interests within the Society inevitably overlapped with other scientific societies and this was embraced by organising joint meetings. These included with the Antibody Club (1964), Association for the Study of Animal Behaviour (1971), Blair Bell Research Society (1964, 1969, 1978, 1982), British Neuroendocrine Group (1995); British Society for Animal Breeding (1985), British Society for Developmental Biology (1977), British Society for Population Studies (1975), Nutrition Society (1994); Society for Endocrinology (1962, 1968, 1978); Royal

Society of Medicine (1965, 1967). Occasional meetings were held with the various French, German and Flemish fertility societies, usually in mainland Europe (Aachen 1993, 1998; Utrecht, 2000; Ghent, 1996, 2004; Paris, 1991; Rouen, 1979; Tours, 1975, 2002). The last stand-alone summer SRF meeting was in 2016 in Winchester.

But it was not all work! The 3-day summer conferences were a great mix of science and social activities. For example, the Conference in Reading in 1984 included "an Irish Ceilidh on Wednesday evening, a river trip to an Elizabethan mansion on Thursday, and a Civic Reception preceding the Banquet on Friday". There is no doubt that such activities were important in helping to break down social barriers and favoured the free and friendly exchange of scientific ideas. However, increasing financial pressures on individuals, hosting institutions, local councils and sponsors of the Society began to impact the jollities. In 1985, the AGM Minutes recorded "*Professor Hearn noted that the supply of (free) beer at meetings appeared to be drying up. This was unfortunate, as scientific (and other) interaction at Society meetings was enhanced when individuals congregated together. An adequate supply of beer ensured that this happened*". The Committee agreed to do what it could! Their efforts were obviously temporarily successful: the next year, the meeting was in Nottingham and included a Civic Reception on the first night, "activities" on the Sports field on the second, with free beer and a barn dance, and a Conference Dinner on the last night (SRF papers).

Membership numbers grew steadily: 50 (in 1950), 271 (1961), 757 (1971), 984 (1981), 1276 (1991), 1418 (1995), 1288 (1997). But this situation reversed rapidly: by 2000, there was concern about the falling attendances and increasing costs of winter meetings and it was decided that winter meetings were no longer viable. Membership dropped to 600 in 2007, 300 in 2010 and to a low point of 274 in 2015. Since then, numbers have increased again: 457 (2018) and 479 (2023). The marked decline in membership over the first decade of the 21st century reflected the changing focus and research support away from basic reproductive biology towards issues associated with assisted human reproduction.

In the early days of the Society, the variety of meetings had catered for the interests of most members of the Society, but the clinical interests had proved more of a challenge. The early growth of the Society had seen the animal science element become dominant at the expense of

the clinical. In 1973 a questionnaire was sent out to all clinical members about how to increase their participation. However, the cause had already been lost and only 29/130 clinical members replied. Patrick Steptoe had initiated discussions with others about the possibility of forming a British Fertility Society. The primary motive for forming the BFS was to provide "*a forum for British gynaecologists with a special interest in infertility*" but there was also a general "*dissatisfaction with the SSF which appeared dominated by animal scientists with minimal human clinical concerns*" (Reiss, 1997). The first meeting of the BFS was in March 1974 and it grew rapidly in size. A few years later, Robert Edwards and Jean Cohen suggested the formation of the European Society of Human Reproduction and Embryology (ESHRE) "*to stimulate the study and research in the field of reproductive medicine and science*" and its first meeting was held in Bonn in 1985 (ESHRE, 2024). The British Andrology Society (BAS) was formed in 1977 for scientists and clinicians "*working in the fields of human and mammalian reproduction with a particular interest in the male*". The Association of Clinical Embryologists (ACE) was formed in 1993 "*to promote high standards of practice in clinical embryology and to support the professional interests of clinical embryologists working in the UK*". Such clinically focussed Societies and their associated journals (e.g. Human Fertility from 1998 and Human Reproduction from 1996) inevitably weakened the attraction of the SSF to clinicians. This impacted the Society intellectually and also financially: commercial exhibitors at conferences reduced and stand-alone meetings became less viable. The SSF tried to maintain clinical contact with occasional meetings with the BAS and BFS. The first major joint meeting of all three Societies was in 1997 and this format was repeated in 2000. The SRF began to participate in Fertility meetings biennially from 2003 and then annually from 2017. The last standalone annual meeting of the SRF was in 2016. After this, to mitigate against the increasing financial loss of its standalone meetings, the membership decided to increase the Society's participation in the joint annual Fertility conference, alongside the BFS and the Association of Reproductive and Clinical Scientists (ARCS). Margaret Jackson, in her acceptance speech of the Marshall Medal in 1979 in Glasgow, made the plea that "*the Society should do it's utmost to retain and reinforce in its scientific proceedings the clinical aspects of the study of fertility*". There is no doubt that she would have been delighted to see the breadth of participation in the Fertility meetings and the way that animal model systems became integral in informing clinical research and developments.

Where is the Society in 2025?

The SRF continues to evolve along with the advances and challenges in reproductive biology and fertility. Gone is the dichotomy between human fertility applications and basic reproductive biology interests. Developments in basic science and translational research drive each other. Techniques for assisted reproduction developed for humans and domestic animals are increasingly being used in attempts to conserve endangered species. We are now beginning to understand the intricate web of interactions within and across generations that link reproduction and development with nutrition, metabolism, disease, stress and pollution.

The SRF facilitates both research and the essential exchange of ideas and information in many ways. Participation in the annual *Fertility* meetings has helped to provide financial security and foster collaborations with clinical colleagues in our partner Societies: the BFS and ARCS. The SRF is one of the most generous reproductive societies awarding a wide range of grants and sponsorships, including bursaries to members to attend the Fertility conference. It publishes two journals: *Reproduction* which covers reproductive biology and the open access *Reproduction and Fertility (RaF)* which has a wider breadth, including translational and clinical research. The Society continues to award the Marshall Medal as its premier honour and presents the Anne McLaren Distinguished Scientist Award to scientists that have made pioneering contributions to reproductive biology (this award subsumes various previous honours given by the SSF, including the Parkes, the Hammond, the Amoroso and the Walpole Lectures). Other awards include the SRF-Reproduction Prize (to recognise the best research published in Reproduction).

The SRF has always been an open and inclusive Society – Anne McLaren became the first female chair of the SSF in 1975 and SRF voted in its first female BAME Chair (Suman Rice) in 2025. Three of the last ten Marshall Medallists have been female. A hallmark of the Society has always been its friendliness and the encouragement of younger scientists. Vacation scholarships are awarded to promising undergraduates to foster their research interests, and the Stewart Rhind Communication Prize is available to undergraduate or postgraduate students for outstanding scientific communication on a topic relevant to reproduction and fertility. A RaF-sponsored symposium is held at Fertility meetings to allow undergraduate, Masters and first-year PhD students to showcase their

work. Also reserved for younger members are the PhD and Postdoctoral Prizes. The Emerging Investigator Award is given to a young scientist displaying originality, independence, and conceptual breakthroughs. Formal mentoring schemes have been established, and RaF has created a Reviewing Panel to support young scientists and clinicians who want to gain experience as peer reviewers. In 2025, ~50% of the paying membership are "Early Career Members" with many from overseas. Increasing links with the Society for Reproductive Biology (Australasia) and the Society for the Study of Reproduction (North America) have allowed the creation of the Roger V Short Medal and Lecture to recognise early to mid-career researchers across the globe who have made outstanding discoveries in the field of reproductive science.

SRF is a charity and part of its remit is "*the advancement of education for the public benefit*" (Charity Commission for England and Wales, 2025). It has participated in several "public education" activities in recent years, including the "Sex in 3 Cities" lecture series (2011-2018) and the interactive event "Bits and Bobs: the Anatomy of Sex" (2025). To commemorate the 75th anniversary of SRF it also launched the first of an educational e-book series "Reproduction in a Changing World" aimed at teenagers.

The SRF was formed to bring together people with different expertise and perspectives to solve practical problems in an era when individual physiological systems tended to be considered in isolation. Today the problems are different: the focus on assisted reproduction continues to help solve the fertility problems of millions of individuals but demographic changes across the globe pose challenges to society. Politics and religion are eroding the reproductive rights of women in many countries. At the same time, population-driven environmental pressures, including climate change and pollution, threaten human and animal health, agricultural sustainability and the viability of natural ecosystems. These all come at a time of reduced research funding on reproductive science both in the UK and globally. To address these issues, the SRF is working with other reproductive societies across the world to establish the International Federation of Reproductive Biology Societies (IFRB) "as a single global voice for reproductive biology in humans and animals". The SRF has come a long way in the last 75 years but there are many challenges in the fields of human and animal reproduction and fertility still to face. These make the Society as relevant now as at its inception.

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