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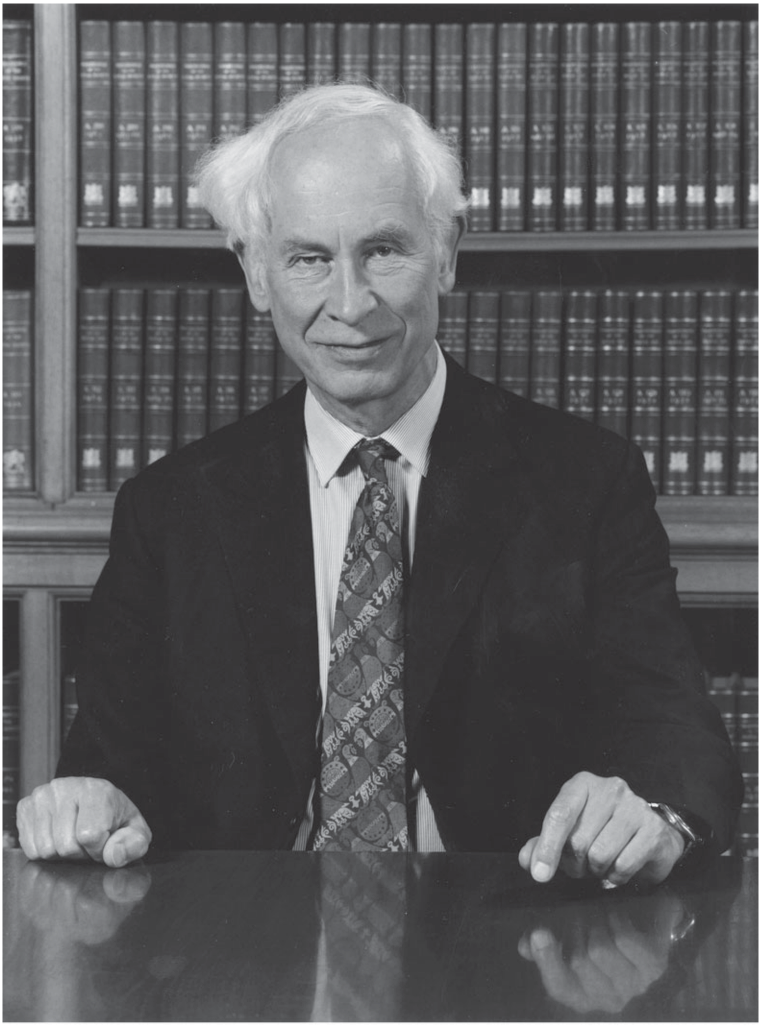

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Elected FRS 1983

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Patrick Bateson made outstanding contributions to the study of animal behaviour over a 50-year period, a field in which he was regarded as a world leader. His research involved analyses of the development, causal mechanisms, function and evolution of behaviour, and combined work in the experimental laboratory with observations of the natural behaviour of animals and theoretical analyses. With particular expertise on behavioural development, Bateson made seminal contributions to several topics, including filial imprinting, mate choice, developmental plasticity, the roles of behaviour and development in evolution, animal welfare and animal play. His research on imprinting in birds pioneered new methods, set new standards for behavioural research and shed new light on the interplay of internal and external factors during behavioural development. Recognizing that a complete understanding of behaviour requires investigation at a number of levels, Bateson's interactionist perspective led him to be highly critical of reductionism and of simple-minded use of terms such as 'instinct' and 'innate'. Bateson published several influential books and well over 300 scientific articles, including a substantial number in flagship journals such as *Nature* and *Science*. His contribution to science was recognized with many honours, including a knighthood, the Frink Medal of the Zoological Society of London and the Distinguished Animal Behaviorist Career Award of the Animal Behavior Society. Bateson was also provost of Kings College Cambridge, president of the Zoological Society of London and biological secretary and vice-president of the Royal Society. A leading public intellectual in the early part of the twenty-first century, Bateson

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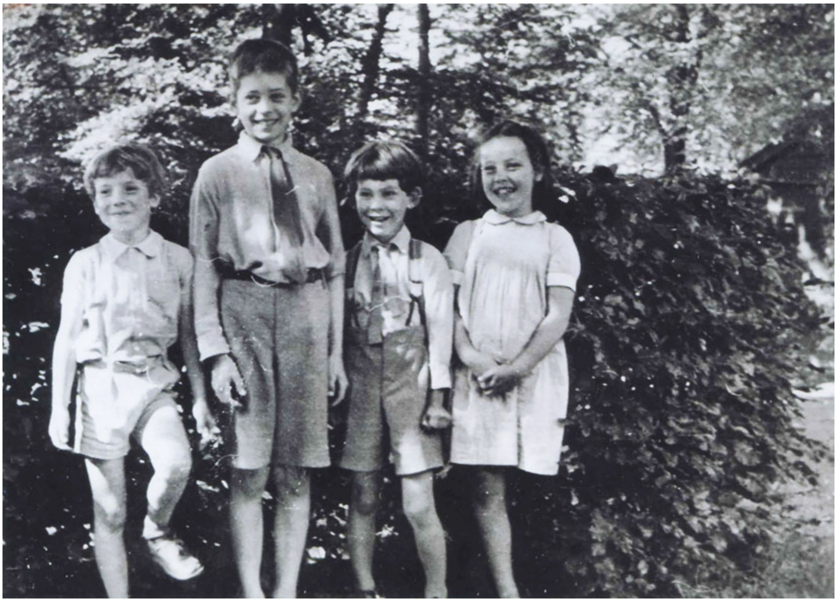

Figure 1. 'Wartime orphans' at Chinnor Hill. From left to right, Mons Lie (a lifetime friend of Bateson and best man at his wedding), Jon Bateson (Pat's older brother), Patrick Bateson, aged five, and Bente Lie (sister to Mons). Photograph taken in 1943.

brought leadership and balanced judgement to many difficult issues, including the use of animals in medical research, dog breeding and hunting.

Childhood, upbringing and family background

Paul Patrick Gordon Bateson (known as 'Pat') was born on 31 March 1938. Although appearing quintessentially English, three of his four grandparents were Norwegian. With his older brother Jon, he was born and brought up in a house designed and built by his father, Richard, a timber expert, at Chinnor Hill in Oxfordshire. During World War II his mother, Sölvi, worked for the Norwegian government in exile in London. Unfortunately, he saw little of his father before reaching age seven, as the latter fought in the British Army during the war, was captured at Dunkirk and spent five years in a German prisoner-of-war camp. Meanwhile, at home, the family at Chinnor Hill grew with the addition of evacuees from occupied Norway and Denmark (figure 1).

Bateson decided from an early age that he would be a biologist, influenced by the legacy of William Bateson FRS, his grandfather's famous cousin, who had coined the term 'genetics' and championed the work of Gregor Mendel. William Bateson had died before Patrick Bateson was born, but the entire family took pride in this aspect of their ancestry. Bateson did, however, get to know William's younger brother, and later acknowledged that 'hearing about the research carried out by his brother from this marvellous old man planted in me an ambition to become a biologist'. Patrick Bateson was later to write an article arguing that William had been ahead of his time and that the latter's views, including some that were contentious

Figure 2. First VIII at Westminster School, 1955–1956. Bateson is seated on the right.

at the time, had largely been vindicated (41)*. Both men argued forcefully that evolution requires an understanding of developmental processes, particularly the interactions among genes, and between genes and other developmental resources, as well as the interplay between the individual and its environment.

In an autobiographical article, Bateson (54) acknowledges a second early influence that stayed with him throughout his life, namely a love of natural history. He describes how a well-known naturalist, Richard Fitter, came to live nearby, and helped culture in Bateson an enthusiasm for ornithology. This interest grew in his teenage years, and led to his spending several holidays in bird observatories, where he proved a precocious observer. At the age of 14, he spent two weeks learning how to trap and ring birds at an observatory on the Northumberland coast. Later, in his professional life as an ethologist, Bateson emphasized repeatedly that there was no substitute for simply observing animals.

Bateson was educated at Westminster School (1951–1956) where he excelled at rowing (figure 2) and the sciences, where his school reports note a flair for biology. Before going to Cambridge as an undergraduate in 1957, Bateson spent several months in the Zoology Museum in Oslo, Norway, reading about systematics and learning how to skin birds. He also conducted a field trip to the Arctic Circle studying geographical variation in the morphology of the ringed plover (*Charadrius hiaticula*), which led to his first paper (1).

Early influences: Niko Tinbergen and Robert Hinde

In 1957, Patrick Bateson was offered a place at King's College, and began a natural sciences degree at the University of Cambridge. His exam performance in his first year was poor, principally because Bateson spent much of his time rowing (figure 3). Eventually, his exasperated director of studies told him to 'Get off the river or get out!' Bateson took this

* Numbers in this form refer to the bibliography at the end of the text.

Figure 3. First VIII at King's College, 1958. Bateson is fourth from the right.

advice and, having specialized in zoology, he graduated with a first class degree and the Frank Smart Prize, awarded to the best-performing zoology student of the year (figure 4).

Bateson's early career was greatly influenced by two luminary ethologists, Niko Tinbergen (FRS 1962) and Robert Hinde (FRS 1974), the latter supervising his PhD in the sub-department of animal behaviour at the University of Cambridge on the topic of behavioural imprinting.

Tinbergen's sway on Bateson arose from a shared passion for natural history, particularly bird behaviour. In his first year at Cambridge, Bateson attended a student conference in Oxford (an Edward Grey Institute meeting organized by David Lack FRS), where he gave a presentation about his avian research in the Arctic Circle. Tinbergen was also present, and Bateson took the opportunity to discuss with Tinbergen a plan that he had hatched with some other Cambridge students to return to the Norwegian islands to study a rare bird—the ivory gull. Tinbergen, an expert on gull behaviour, was so enthusiastic about this project that he agreed to lead the expedition, although ill health later forced him to withdraw. Nonetheless, the expedition went ahead and succeeded in its objective of producing a detailed record of the gull's reproductive behaviour. When Bateson wrote up these observations for publication (2, 3), Tinbergen wrote a highly complimentary commentary on the work and subsequently invited Bateson to join him in another expedition to study black-headed gulls in Cumbria, UK. These interactions proved formative, and Bateson resolved that, once his undergraduate studies were complete, he would pursue a PhD under Tinbergen's supervision. Later, however, the prospect of winning a graduate research scholarship from King's eventually tipped

Figure 4. Bateson had two great passions—mountains and birds—which he brought together in a 1960 undergraduate birding expedition to Greece. Here he stands at the summit of Mount Parnassus. (Online version in colour.)

Bateson's decision towards remaining at Cambridge and working with Robert Hinde instead, based at the sub-department of animal behaviour.

The sub-department, situated in the small village of Madingley, five miles outside Cambridge, was originally an ornithological field station, established by William Thorpe (FRS 1951) in 1950. At the time, Robert Hinde was emerging as a leading figure in the field of ethology, and Bateson describes him as 'a superb supervisor' and 'formidable critic' who 'taught us how to think' (54). Hinde specialized in behavioural development, and Bateson was to follow in his footsteps. It was Hinde who first encouraged Bateson to work on behavioural imprinting—the process by which an animal learns to recognize its parents and members of its own species. Together with Thorpe, Hinde had carried out experiments on imprinting in newly-hatched coots and moorhens, showing that these birds could imprint on a variety of objects, with object movement an important stimulus (Hinde *et al.* 1956). Bateson continued this line of research, which was to become an enduring interest.

The field station became the sub-department of animal behaviour in 1960, just as Bateson joined, and grew substantially to become a leading centre for behavioural research, with many eminent student alumni, including Dorothy Cheney, Tim Clutton-Brock (FRS 1993), John

Crook, Dian Fossey, Jane Goodall, Sandy Harcourt, Peter Klopfer, Phyllis Lee, Peter Marler, Robert Seyfarth, Kelly Stewart, Richard Wrangham and many others, who came to Madingley as postdocs or staff.

While finalizing his PhD thesis, Bateson secured a prestigious Harkness Fellowship that he was to spend in North America, and he hurriedly completed his writing up. In July 1963, Bateson and Dusha Matthews, whom he had met as a student at Cambridge, got married and travelled to the United States together. Bateson spent much of this time at Stanford University working with neuropsychologist Karl Pribram and studying perceptual learning in rhesus monkeys. The Harkness Fellowship allowed Bateson to travel and interact with several eminent scientists, including developmental psychologist Harry Harlow, at the University of Wisconsin, Madison, and comparative psychologist Daniel Lehrman, at Rutgers University in Newark, New Jersey.

Bateson returned to Cambridge in 1965 as a junior lecturer in the Department of Zoology and a junior research fellow of King's College. His subsequent career centred on these two Cambridge institutions—the sub-department of animal behaviour at Madingley and King's College, with Bateson eventually becoming director of the former (1976–1988) and then provost of the latter (1988–2003). He later remarked that his work benefitted from 'some superb graduate students', including David Chantrey, Jeremy Cherfas, Patrick Green, Patrick Jackson, Paul Martin, Mike Mendl and Dafila Scott (54). He was also an enthusiastic lecturer, and taught many generations of students the principles of behavioural development, as well as supervising countless final-year undergraduate projects. At home, Pat and Dusha had two daughters, Melissa, born 1968, and Anna, born 1972.

The study of imprinting

Imprinting is the process of rapid learning whereby a newly-born mammal or newly-hatched bird forms an attachment to the first prominent moving object it sees, typically its mother. Imprinting occurs only during the first few hours or days of a precocial animal's life—described as the sensitive period—and not thereafter. The study of imprinting was pioneered by the Austrian ethologist Konrad Lorenz (ForMemRS 1964), whose film of young goslings, imprinted on his boots and following in his footsteps, became famous. Lorenz regarded imprinting as a unique phenomenon, unlike learning in older animals. Bateson became interested in what ends the sensitive period for imprinting and, along with others, argued that it was due to a process of competitive exclusion. Experience with one class of objects made it more difficult for the birds to form attachments to another class, and the greater the stimulus value of the first class, the more rapid would be the exclusion effect (5, 15). As he describes in his autobiographical notes (54), Bateson's view that imprinting is not unique, but just one form of perceptual learning, brought him, as a young researcher, into open conflict with Lorenz at the 1963 International Ethological Congress (figure 5).

Bateson employed carefully designed lab experiments to elucidate the environmental and developmental conditions facilitating imprinting in domestic chicks (4) (figure 6). His imprinting apparatus involved placing newly-hatched chicks in a fixed but freely running wheel facing a flashing red light—a strong imprinting stimulus. To test the strength of imprinting following the training, the wheel could run on a reversible geared track, with the imprinted stimulus at one end and a novel, yellow light at the other (figure 7). As the chick

Figure 5. Participants at a scientific meeting on animal behaviour in the 1960s. Bateson is top right, while Konrad Lorenz is seated third from right on the front row. Others present include Erik Salzen, Klaus Immelman, Gilbert Gottlieb, Erik Fabricius and Eckhard Hess.

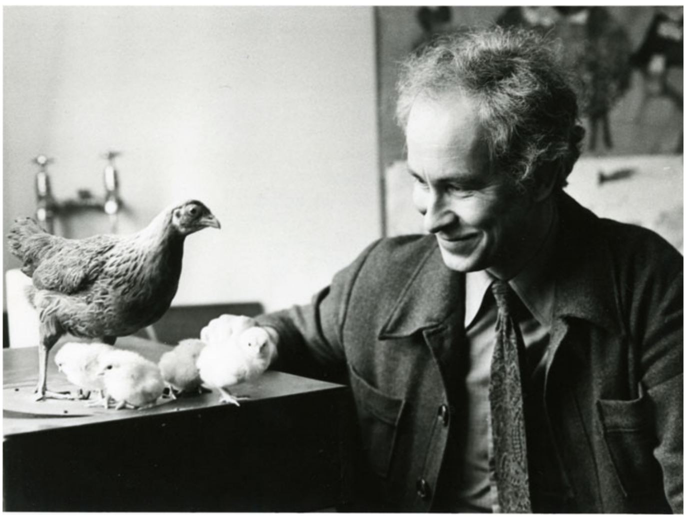

Figure 6. Patrick Bateson with his study system of hen and chicks. Photograph taken in 1976 when Bateson was awarded the Zoological Society of London Scientific Medal.

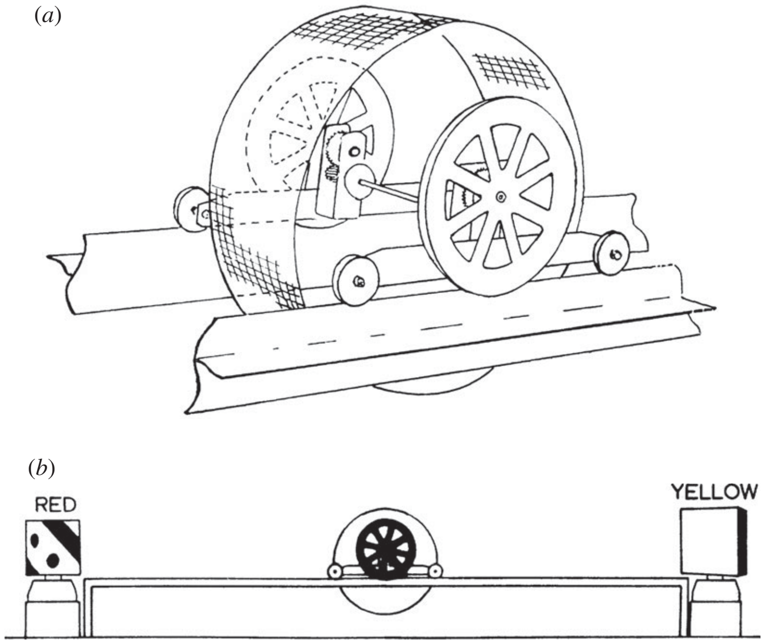

Figure 7. (*a*) Running wheel used by Patrick Bateson in imprinting choice test to measure the strength of a preference for a novel object. (*b*) The chick runs towards the object on which it has imprinted, with the relative strength of alternative imprinting stimuli measured by its final position. This and similar apparatuses were used by Bateson in numerous imprinting experiments. Figures adapted from (9).

ran towards the red light on which it had been imprinted, the reverse gearing moved the wheel steadily further away. Eventually a stationary point was reached when the attractiveness of the yellow light matched that of the now distant red. The strength of imprinting could thus be measured in centimetres from the chick's starting midpoint of the track. This seemingly simple but effective experimental apparatus was characteristic of his approach throughout his career.

The 1960s was a period in which interest in the possibility of identifying the molecular and cellular processes involved in learning and memory formation was gathering strength, and a chance meeting with the neuroscientist Gabriel Horn (FRS 1986) (figure 8) at a college dinner in 1967 stimulated his interest in the possibility of using imprinting in chicks as a model system (54). In 1968, Bateson and Horn began a highly productive collaboration that was to last several decades. A year later, Bateson met with Steven Rose at a Royal Society symposium where Rose had been speaking about his work on the neurochemical events associated with first visual experience in the rat. From 1969, a three-way collaboration was forged, and a ground-breaking series of studies resulted. The experiments that followed were planned over lunchtime sandwiches in Bateson's rooms at King's, with the behavioural studies carried out at Madingley and the brain samples frozen, coded and taken to Rose's lab for analysis, first at Imperial College in London and then at the Open University. Dusha recalls joining the triumvirate in helping to freeze the samples, and Ann Horn (Gabriel's then wife) was a co-author on some of the early papers (7, 8). Imprinting in chicks was to become an important model system for exploring the neural, cellular and molecular bases of behaviour and memory

Figure 8. Patrick Bateson (right), with Robert Hinde (left) and Gabriel Horn (centre). Photograph taken in 1991.

formation. The team pioneered the development of suitable controls that were critical to disambiguate the immediate effects of learning and memory formation in the brain from the consequences of other forms of activity that operated simultaneously.

Biochemical studies on rats from several laboratories had suggested that novel experience, including learning, was associated with protein synthesis in regions of the rat brain, as measured by increased incorporation of amino acid precursors into the protein (Rose 1968). So, the first chick experiments measured the rate of incorporation of ^{3}H-lysine into the chick brain, divided crudely into 'roof' and 'base', and found that imprinting was associated with an increase in incorporation into the 'roof' (6, 7). The finding was intriguing, though insufficient, but pointed to two goals for further research. The minor goal was to locate more specifically the brain region(s) involved in the response. The major goal, which recognized that there might be many behavioural processes other than the neural registration of the imprinting experience responsible for the enhanced synthesis, was to design experiments that systematically excluded such other possibilities—for example, motor activity, visual experience *per se*, or hormonal responses. What was required was to prove that the neuronal changes were the necessary, exclusive and, if possible, sufficient correlates of the formation of memory of the learned response (8, 10). Successive experiments ruled out the possibilities that the changes in synthesis were associated with light exposure, stress or motor activity, and established that they were correlated with the strength of the imprinting as measured in the geared running wheel. A series of 10 papers that followed over the next decade, several in *Nature*, plus a review in *Science* (11), charted the progress towards these goals. By the mid 1970s, however, the interests of the collaborators began to diverge, although they continued to work in parallel.

Bateson and Horn were joined by Brian McCabe, and the site of imprinting-associated neuronal change was localized by autoradiographic (16) and later lesion studies to a region in the left forebrain roof, the intermediate medial hyperstriatum ventrale (IMHV; later renamed IMM: intermediate medial mesopallium) (18). The team concluded that this region of the chick brain was where imprinted memories were initially represented (although at least one additional longer-term store was identified). Chicks exposed to an object learned the stimulus's characteristics, and in doing so, the responsiveness of the IMHV neurons to that object was found to be enhanced. Lesions of the IMHV prior to exposure were shown to impair acquisition, while lesions shortly after resulted in memory loss. Bateson and Horn went on to explore the electrophysiological correlates of the stimulus, while Rose, whose focus was in the biochemical and cellular processes required for the coding of memory, adopted a more amenable experimental model for these studies, one trial passive avoidance in the chick.

Research into behavioural development

Bateson regarded his research into imprinting as providing a tractable model system for studying how one important feature of behaviour develops. However, his interests were much broader than imprinting, extending to virtually all of the biological, psychological, social and environmental influences that collectively explain the transition of a unique organism from conception to adulthood. His understanding of behavioural development was greatly influenced by his own research on play in the domestic cat. Pat and Dusha Bateson had kept cats for many years, and he regarded pets as a means to spend significantly more time observing animal behaviour than was possible under controlled laboratory conditions.

Careful observations, with the help of Priscilla Barrett, led to important insights into how behavioural development responded plastically to circumstances. Barrett and Bateson (13) found that social play typically developed before object play, with object play typically commencing around the time of weaning. Kittens separated artificially from their mothers started to play with objects significantly earlier and more frequently than other kittens; blocking the mother's lactation with drugs, or rationing her feeding, had the same effect (17, 20, 28). The results suggested that the kittens' pattern of development was conditioned by an environmental forecast provided by the mother. Kittens that would have to fend for themselves at an early age learned through play the critical skills they would need at the stage in development when they would have to put these skills to serious use. The play experiments also established that there could be alternative developmental pathways to achieving adaptive outcomes. For instance, cats can acquire and improve their adult predatory skills by catching live prey when young, by playing at catching, by watching their mother catch prey, by playing with siblings and by finally catching prey as an adult. Thus, a kitten deprived of the opportunity to play can still develop into a competent predator. The twin ideas that development was adjusted flexibly to environmental contingencies, rather than following a scripted trajectory, and that the mother could provide adaptive information about the state of the environment were to become central themes in Bateson's thinking, e.g. (57, 64). These ideas connected development and evolution in ways that challenged traditional nature–nurture distinctions.

In 1988, following a conference on the topic, Bateson, together with Dennis Turner, published an edited volume of articles on cat behaviour, entitled *The domestic cat: the biology of its behaviour*. The book was highly successful, and led to a second edition (38). Pat and

Dusha Bateson had been breeding cats for many years, and that experience, combined with his behavioural experimentation and the book's popularity, led to him becoming known as the world's leading authority on cat behaviour. However, Bateson went on to study play in several other species, including humans (45), and to write an important book on play, *Play, playfulness, creativity and innovation*, in which he and his co-author Paul Martin argued that play functions to generate creativity and stimulate innovation (61). They suggested that play was an adaptation that functioned to motivate individuals to get out of the rut and discover better solutions to life's challenges.

The flexibility and contingency of development, manifest in the skill learning of cats and his experimental work more generally, exacerbated certain concerns that Bateson had about the validity of the ethological concepts of 'instinct' and 'innate'. The idea that behaviour could be understood as an instinct—a behaviour that had evolved through natural selection to fulfil an adaptive goal—had fluctuated in popularity throughout history, and was resurrected by ethologists in the 1930s–1950s. To the ethologists, instinct was an inherited and adapted system of coordination within the nervous system. However, at the time Bateson began his own behavioural experiments, the concepts of 'instinct' and 'innate' behaviour were starting to be recognized as problematic. It had become clear that both of these terms were commonly deployed with several distinct meanings, including (i) present at birth, (ii) a behavioural difference caused by a genetic difference, (iii) adapted over the course of evolution, (iv) unchanging throughout development, (v) shared by all members of a species, and (vi) not learned. Later, in a paper entitled 'Taking the stink out of instinct' (36), Bateson identified no fewer than nine distinct uses of the term 'instinct' in common practice.

This plurality might have proven workable had the different qualities attributed to instinct always occurred together, as Konrad Lorenz had originally envisaged. However, studies conducted in the 1960s and 1970s revealed this was not the case. For instance, Hailman (1967) established that the accuracy with which a newly-hatched gull chick pecks at its parent's bill to initiate feeding improves after hatching (i.e. the behaviour is present at birth and species-typical, but modified throughout the lifespan). Similarly, Gottlieb (1971) had shown that a newly-hatched duckling's preference for the maternal calls of its own species is affected by hearing its own vocalizations in the egg (i.e. the preference is present at birth, but not unlearned). Further experiments had revealed how internal and environmental factors worked together, such as Lehrman's (1965) demonstration that the male dove's courtship dance triggers the release of a female dove's hormones prior to mating and reproduction (i.e. an external factor elicits an internal change).

The findings of such studies resonated with Bateson's own experimental work conducted in the 1970s and 1980s, and he played an important role in bringing the complexities of development to prominence through an influential series of articles (31, 36, 44, 48–51, 58) and a highly successful and popular book co-authored with Paul Martin, *Design for a life: how behaviour develops* (35).

Bateson argued that all the different definitions of 'instinct' and 'innate' were unsatisfactory, either because they are based on simplistic and empirically outmoded views of development, or because they commonly led to inferential mistakes (49, 51, 58). Researchers had treated the various scientific notions that capture some aspect of innateness as equivalent to each other or at least as tracking properties that are strongly correlated with each other. Bateson pointed out that whether these correlations exist is an empirical issue, one that (to this day) has not been thoroughly investigated because, in the attempt to create a bridge

Figure 9. Bateson (third from left) at a workshop on behavioural development at The Neurosciences Institute, Rockefeller University in 1985. Others present (left to right) are Ronald Oppenheim, Susan Oyama, Peter Marler, Josef Rauschecker, Antonio Garcia-Bellido (ForMemRS 1986), John Fentress and Colwyn Trevarthon. (Online version in colour.)

between the folk view and their theories, researchers have often assumed that the properties must somehow cluster. Bateson argued that these empirical questions must be answered before it can be decided whether the concept of innateness, or some successor term, has a useful role to play (51, 58).

The dichotomy of ‘innate’ and ‘acquired’ is a part of folk-biology, but these terms are also commonly used by biologists, psychologists and cognitive scientists in their disciplines. Bateson was forthright in arguing that they are wrong to do so. Instead of the conventional opposition between nature (genes) and nurture (environment), Bateson championed the interactionist perspective manifest in the writings of Lehrman and Gottlieb, in which development involves the continuous interplay of the organism with its environment, sometimes described as ‘developmental systems theory’ (Oyama 2000). Critical of dichotomies, Bateson emphasized how gene expression was commonly cued by the environment, and that learning was also dependent on the expression of genes (35, 54). Over-and-above his own writing, as a journal editor and through his authority with publishers Bateson was supportive of the work of the pioneers of developmental systems thinking, including Susan Oyama (figure 9), Paul Griffiths and Russell Gray. He also became increasingly critical of what he regarded to be inadequate forms of interactionism, which missed the dynamics that could induce qualitative as well as quantitative developmental transformations. These efforts helped to engender within the field a serious engagement with conceptual issues.

Bateson was respectfully critical of the reductionism implicit in Richard Dawkins' (FRS 2001) book *The Selfish Gene* (48), and the evolutionary psychology of the 1990s (36), maintaining that 'focusing on over-simplified causal factors in the name of clarity has caused great confusion' (54). He also questioned the widespread use of metaphors such as 'genetic program' or 'blueprint' (34, 39), as well as terms such as 'hardwiring', 'preprogramming' and 'developmental programming' (54), arguing that they were inconsistent with the dynamic, reciprocal nature of development and inheritance emerging from experimental studies. In addition, he was critical of those who too readily jumped to the conclusion that the semblance of design in a character implied adaptation (36, 39, 60).

However, Bateson was not shy to adopt more suitable metaphors and analogies. He suggested that: 'development is not like a fixed musical score that specifies exactly how the performance starts, proceeds and ends. It is more like a form of jazz in which musicians improvise and elaborate their musical ideas, building on what the others have just done' (39, p.157). He also regularly used the analogy of cooking or baking a cake to capture the irreducible interaction of internal and external components (35, p.9):

> The processes involved in behavioural and psychological development have certain metaphorical similarities to cooking. Both the raw ingredients and the manner in which they are combined are important. Timing also matters. In the cooking analogy, the raw ingredients represent the many genetic and environmental influences, while cooking represents the biological and psychological processes of development. Nobody expects to find all the separate ingredients represented as discrete, identifiable components in a soufflé. Similarly, nobody should expect to find a simple correspondence between a particular gene (or particular experience) and a particular aspect of an individual's behaviour or personality.

His writings emphasized how developing organisms both modify gene expression and modify developmental environments, generating feedback in the processes of ontogeny. These feedbacks invoke organism–environment relationships and nongenetic inheritance as causes of species-typical, invariant, phenotypes commonly seen as 'genetically determined' by evolutionary biologists, e.g. (35, 57).

Investigations of mate choice and sexual selection

Bateson's investigations of imprinting in birds also drew him into studying the mate choice decisions of animals and to explore their evolutionary implications. Previously, Konrad Lorenz had shown that imprinting could affect the mate choice of birds, and suggested that 'sexual imprinting', as the process came to be known, functioned to enable adults to recognize their own species (Lorenz 1935). However, subsequent studies had found that a bird can show a sexual preference for members of its own species, even without relevant experience. Bateson concluded that a bird may have a predisposing bias for its own species and that sexual imprinting served to refine this bias. He proposed that sexual imprinting was required for recognition of close kin so that, by selecting mates that are slightly different, the animal could strike an optimal balance between inbreeding and outbreeding. Sexual imprinting enables the bird to avoid inbreeding and also avoid too much outbreeding, which is also disadvantageous. He went on to test the prediction that the strongest mating preference of a bird should be for

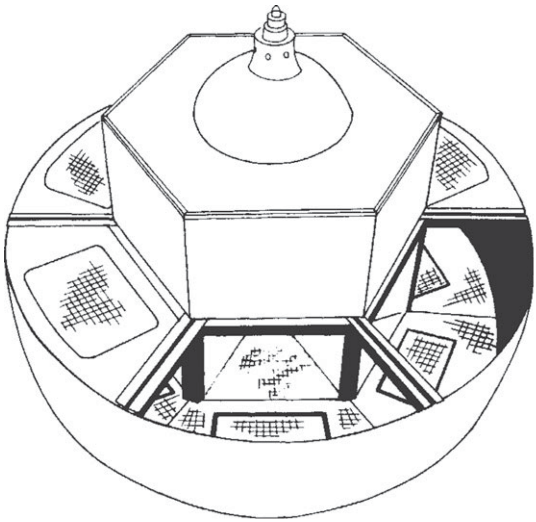

Figure 10. Apparatus used by Patrick Bateson to test courtship preferences in Japanese quail. Several stimulus birds are placed in the inner compartments behind one-way mirrors, with the focal bird in the outer region. Pressure sensitive pads record where the focal bird is standing, thereby allowing its preferred mate to be identified. Bateson called this ‘The Amsterdam Apparatus’, for obvious reasons. Figure reproduced from (19), reprinted by permission from *Nature*.

a mate a little different, but not too different, from the object on which it had been imprinted. Sure enough, Bateson found that male Japanese quail mate with slightly unfamiliar females in preference to females to which they were exposed in early life, or females with a very different plumage (14).

A few years later, Bateson was able to demonstrate with precision the level of optimal outbreeding exhibited by these birds. He found that Japanese quail of both sexes, having been reared with their siblings, subsequently prefer as mates a first cousin of the opposite sex (19) (figure 10), and that the nature of these preferences could be investigated through experimental manipulations of the birds’ plumage (27). Evidence that imprinting favours optimal outbreeding has subsequently been found in many other species (21, 22; Pusey & Wolf 1996), but Bateson’s study was the first to demonstrate this effect.

Bateson was later to point out that these findings offered a resolution to a paradox in the literature concerning the evolution of plumage traits. In imprinting species, the young are likely to inherit both the physical traits of their parents (through genetic inheritance) and, through sexual imprinting, a preference for those traits (e.g. a preference for their plumage). This observation led to the hypothesis that sexual imprinting provided a mechanism that could result in the rapid sexual selection of novel traits, even if such traits conferred no selective advantage. However, there was a problem with this idea. Imprinting would act as a barrier to the selection of new colour morphs if it meant that mutants would be rejected by the rest of the population that had learned preferences for established morphs. The paradox was that it was difficult to see how plumage trait characteristics could evolve in imprinting species, yet they manifestly did. According to ten Cate & Bateson (26), ‘the key to the understanding of the potential role of sexual imprinting in the evolution of conspicuous characteristics lies in the observed shift towards slightly novel partners'. They suggested that an asymmetrical preference for novel partners might provide a mechanism driving evolutionary change in the characteristics used in mate choice, arguing that the asymmetry may arise to offset the costs of inbreeding or as a consequence of a preference for more brightly coloured mates or mates with greater plumage contrast. Theoretical work subsequently confirmed the plausibility of this hypothesis (Laland 1994). Over-and-above his experimental work, in the early 1980s, Bateson's thinking gave impetus to the emerging field of sexual selection, to which he also contributed through organizing conferences and workshops, and editing the influential book, *Mate choice* (21).

Interest in development and evolution

Bateson maintained a deep interest in evolutionary biology throughout his career, but was dissatisfied with the adequacy of traditional evolutionary explanations and pushed for change in conceptions of the structure of evolutionary theory, e.g. (25, 63, 64). His writings championed a view that eschewed gene-centrism and placed the organism centre-stage. This stance led some more conventional evolutionary biologists to view him as a maverick. Nonetheless, he was quick to recognize the evolutionary significance of imprinting, mate choice, sympatric speciation and developmental plasticity, which have subsequently become accepted into the mainstream. He also appreciated the evolutionary importance of epigenetic inheritance (Jablonka & Lamb 2005) and niche construction (Odling-Smee *et al.* 2003) before these ideas garnered increased attention.

A further indication of Bateson's prescience was his early use of neural networks to model imprinting, imitation and other forms of learning, and to explore their evolutionary implications, again well before these approaches became established (30, 40, 52). The imprinting model was inspired by Bateson and Horn's experiments, and its effectiveness and validity hung critically on the incorporation of known biologically relevant processes that the authors had observed in the chick brain. This commitment to the grounding of the model in hard empirical data was a departure from the often very abstract connectionist mainstream. The analysis provided compelling explanations for the existence of sensitive periods, the classification together of different cues, and how generalization could explain concept formation.

Behind the scenes, Bateson was indefatigable in organizing conferences and workshops designed to consolidate, synthesize and promote the work of progressive evolutionary thinkers, including Eva Jablonka, Richard Lewontin, Conrad Waddington FRS and Mary Jane West-Eberhard, and to support alternative ways of thinking, such as developmental systems theory (Oyama *et al.* 2001). He excelled in organizing productive meetings, where carefully chosen protagonists, commonly sporting quite different perspectives, would be brought to attractive locations. These meetings were often in Italy, in conjunction with the developmental biologist Bruno D'Udine, or evolutionary biologist Kevin Laland. Participants were encouraged to discuss complex issues, their conviviality enhanced by Bateson's astute leadership and fine catering. Together with Rose and D'Udine, Bateson took a memorable trip to the Galapagos, appropriately enough on a small research motor yacht, *The Beagle*. In recognition of past meetings, D'Udine had planned a celebratory festschrift for Bateson for 2017, which perforce became a memorial.

Bateson also played a leading organizational role in some major meetings on evolution. A century after William Bateson had organized the Darwin Centennial conference in Cambridge, Patrick Bateson chaired the huge Darwin Bicentennial conference in the same city in 2009. He was also co-organizer of a joint meeting of the Royal Society and British Academy in 2016, entitled *New trends in evolutionary biology: biological, philosophical and social science perspectives*. Through these efforts, combined with his own articles and books, Bateson helped to incubate ideas that are central to the emerging extended evolutionary synthesis (Laland *et al.* 2015).

Bateson summed up his views on development and evolution in the following passage (25):

> Many biologists (including myself) have unthinkingly accepted the Darwinian image of selection, with nature picking those organisms that fitted best into the environments in which they lived. The picture of an external hand doing all the work is so vivid that it is easy to treat organisms as if they were entirely passive in the evolutionary process. That is not, of course, to suggest that any biologist would deny that organisms, and animals especially, are active. But the notion of ‘selection pressure’ does subtly downplay the organisms’ part in the process of change ... When developmental issues are recoupled to questions about evolution, it becomes much easier to perceive how an organism’s behavior can initiate and direct lines of evolution. Developmental processes do not merely act as constraints, as much current thinking would seem to suggest (e.g. Maynard-Smith *et al.*, 1985), they can make certain types of evolutionary change more likely.

This quote eloquently captures the significance that Bateson attributed to developmental processes in evolution. These views grew out of his own experimental work. Bateson’s filial imprinting studies had taught him that birds (and animals in general) played an active role in their own development: ‘far from waiting around passively to be stimulated, they had a hunger for learning’ (54). His studies of sexual imprinting convinced him that the choices of individual animals could have important evolutionary consequences, such as eliciting sexual selection (25, 26). His investigations of play in cats had established his early recognition of the adaptive significance of parental effects (34, 57, 64), while his experimental work demonstrating transgenerational effects of impaired maternal care in mice (53) had left him sensitive to epigenetic inheritance.

A key focus of Bateson’s many books and papers on this topic is the active role of organisms in their own development and evolution. Bateson repeatedly stressed diverse means by which an organism’s behaviour can influence the subsequent course of evolution (25, 57, 63, 64). These included the active choices of animals, which extended beyond mate choice and sexual selection, and applied equally to habitat and resource choice, as emphasized by Waddington (1959). Also important was the observation that organisms actively change their environments, both through active modification of conditions and through migration and dispersal (Odling-Smee *et al.* 2003). A third mechanism was the adaptability of organisms, which stemmed from developmental plasticity and learning (Baldwin 1896; West-Eberhard 2003). Adaptability allowed organisms to adjust to novel or stressful environments and thereby survive, in the process setting the scene for selection on genetic variation that stabilized adaptive phenotypes.

While the fact that animals make choices, modify selective environments and exhibit developmental plasticity is not in itself contentious, in Bateson’s view the evolutionary ramifications of these commonplace observations were not fully appreciated. To the end he believed that subtle forms of genetic determinism still pervaded evolutionary theory (64).

He himself strongly rejected the view that all evolutionarily significant aspects of animal behaviour, and developmental plasticity more generally, were genetically determined, and instead regarded the genetic influence on phenotypes as much more diffuse and limited. As a consequence, for Bateson and his developmental systems perspective (39), an animal's behaviour patterns and decisions were perceived to introduce novelty and impose direction on adaptive evolution. He conceived that the manner in which organisms developed summed up across individuals in a population, and over time, to influence evolutionary dynamics. Evolution can be shaped by heritable variation revealed through behaviour, which in turn is dependent on reciprocal interactions between organism and environment during development (63).

Investigations of developmental plasticity

For Bateson, developmental plasticity evolved because it is adaptive, promoting Darwinian fitness by enhancing survival and reproductive success. This stance underpinned his views of both evolution and development. He maintained that adaptive plasticity, mediated in part by epigenetic processes, gives an advantage in environments that change over several generations (57). He also envisioned that plasticity exploited environmental cues, often transduced by the mother, in a manner that allowed organisms to maximize their fitness, both by making the best of present conditions and through preparing descendants for the future environment.

Through an influential series of articles (46,55,59,62) and a book, *Plasticity, robustness, development and evolution* (57), most of them co-authored with paediatrician Peter Gluckman FRS, Bateson helped bring to prominence the view that an understanding of development could shed important light on health and disease. Thanks in part to this work, it is now widely recognized that changes in maternal or infant nutrition can produce heritable effects on the risk of chronic disease, that the mismatch between evolved physiological capabilities and contemporary environments can lead to ill health, and that stressors during critical developmental periods can affect growth, tissue differentiation and physiological functioning for life. More generally, Bateson and Gluckman's work contributed importantly to the now widespread recognition that understanding the underlying mechanisms of plasticity is clinically important.

As always, Bateson's conceptual work was informed by experimentation. In collaboration with Frances Champagne, James Curley and Barry Keverne FRS, Bateson's epigenetic research with mice showed how early life experiences (here social enrichment during postnatal development) could induce effects on mothers' emotional and reproductive behaviour, which could be epigenetically inherited for multiple generations (53, 56). This work established how diverse resources were passed from parent to offspring (parental effects), including transgenerational epigenetic inheritance, which function to fine-tune offspring characteristics to future environmental states anticipated by parents or more distant ancestors. In this way, parents confer on descendants a 'predictive adaptive response' that would be advantageous to offspring providing that the environment they experienced matches that anticipated by parents (57).

Bateson also took issue with the dichotomy of plasticity and robustness. He emphasized how plasticity is frequently governed by robust rules (such as associative learning) and ontogenetic selective processes (such as regulated cell death in the brain), while species-typical characteristics are often maintained through active and regulatory plastic responses rather than insensitivity or constraint, with transgenerational constancy often resulting from environmentally sensitive epigenetic or behavioural forms of inheritance (57). He also stressed how the inheritance of species-typical phenotypes (like within-population differences) requires reference to the recurrence of nongenetic causes of development throughout the lifetime of an animal (60).

Interest in animal welfare

Patrick Bateson maintained a longstanding interest in issues to do with animal welfare, and played a leading role in many debates on these matters. As president of the Association for the Study of Animal Behaviour in the late 1970s, he established an ethics committee, which produced guidelines for animal behaviour researchers still deployed today. He helped to devise a balanced approach to animal experimentation designed to protect animals used in experiments while at the same time maximizing scientific and medical benefits (23, 29, 43, 47). He defended the moral arguments mounted for using animals in order to understand the fundamental problems of biology and thereby help to alleviate the suffering of humans (and other animals), but at the same time strove to minimize the distress experienced by experimental animals. These ideas subsequently became enshrined in British law (54).

One practical solution that Bateson provided was in the form of a decision cube specifying whether a scientific research project should be allowed to proceed. What became known as ‘the Bateson cube’ required three independent assessments to be made: concerning the maximum suffering that the animals are likely to endure in the course of the project; the overall scientific importance of the project; and the likelihood of medical benefit. Only if the three assessments fell into the acceptable region of the cube should the work be conducted (23).

Bateson showed courage and leadership in tackling one of the most contentious animal welfare issues in the UK—hunting with dogs. In 1995, he was commissioned by the National Trust to examine whether red deer hunted with hounds experienced undue suffering. The research project carefully recorded and analysed a wide variety of physiological data, obtaining an index of the deers’ distress through measuring lactate, sugar levels and cortisol in blood and muscle samples drawn from the hunted animals. The published study (32, 33, 37) concluded that hunting with hounds caused excessive suffering to the deer, and could not be condoned on welfare grounds. On the strength of this report, the National Trust banned hunting on their land. The media coverage of this study was huge, and Bateson was vilified by hunting enthusiasts. However, other scientific analyses supported Bateson’s conclusions. He later sought to help mediate in other controversies, including genetically modified plants and dog breeding.

Administrative roles

Bateson held some of the most exalted positions in British science. He was biological secretary and vice-president of the Royal Society (1998–2003), provost of King’s College, Cambridge (1988–2003), director of the sub-department of animal behaviour, University of Cambridge (1976–1988), head of the Department of Zoology, University of Cambridge (1994–1996), and president of the Zoological Society of London (2004–2014). He chaired or sat on numerous national committees, including the Council of the Association for the Study of Animal Behaviour (1965–1985), the Biological Sciences Committee of the Scientific Research Council (1979–1982), the Council of the Royal Society (1998–2003) and the Scientific Committee of the Institute of Zoology, London (1985–1989). He was also a trustee of the Institute for Public Policy Research (1988–1995) and the Council for Science and Society (1989–1991).

As biological secretary of the Royal Society, Bateson instituted procedures designed to enhance the fairness of the decision-making process for the nomination of new Fellows, worked towards making the society more responsive to public concerns, contributed to initiatives designed to raise the profile of the Royal Society as an independent source of authoritative information about science, and regularly gave evidence to select committees of the House of Lords. As provost of King's College, Cambridge, he took overall responsibility for the running of the college, sat on 'interminable committees' (54), as well as many national bodies such as the Museums and Galleries Commission (1995–2000), and participated in the high-profile events that took place in the chapel, including the famous Nine Lessons and Carols service on Christmas Eve, broadcast every year to over 100 million people around the world. Patrick and Dusha Bateson hosted many famous people at the college, including the Queen, Princess Margaret, Mikhail Gorbachev, Salman Rushdie and the Dalai Lama.

Achievements and recognition

Patrick Bateson published well over 300 scientific articles in leading journals, a number that does not do justice to his contribution, both because he tended not to put his name on his students' papers and because he wrote and edited numerous hugely influential books, many of which have run to multiple editions. In particular, his book *Measuring behaviour: an introductory guide* with Paul Martin (24), now in its third edition, has been universally regarded as the definitive methodological introduction for students of animal behaviour for decades, while *The domestic cat*, with D. C. Turner (38), is highly successful and also in its third edition. Other edited volumes, notably *Growing points in ethology* (12), and *Mate choice* (21), had an impact and shaped thinking in these fields. Together with Peter Klopfer, he also edited the influential *Perspectives in ethology* series for 20 years (10 editions), and was editor of *Animal Behaviour* for five years. Bateson's contribution to science was recognized with many honours, notably his election to Fellowship of the Royal Society in 1983, a knighthood in 2003 in recognition of outstanding contributions to behavioural research and British science more generally, the Scientific Medal of the Zoological Society of London in 1976, the Association for the Study of Animal Behaviour Medal in 2001, the prestigious Frink Medal of the Zoological Society of London in 2014 and the Distinguished Animal Behaviorist Award of the Animal Behavior Society in 2015. He was also the recipient of several honorary degrees.

Personal qualities

Bateson was a man of deep liberal principles and moral concerns, and his compassion for and tolerance of others marked him out. His views of religion reflected a wider respect for pluralism of perspective. While he did not believe in God, he viewed science and religion as 'non-overlapping magisteria', and regarded scientists who believed that science had disposed of religion 'as wrong-headed as creationists' (42).

While always scrupulous in his language, Bateson wasn't afraid to take a publicly committed stand even when he knew it was likely to be controversial. One example has already been provided—his accepting the commission to investigate the suffering of deer hunted with hounds, despite the obvious contention such research was likely to generate. However, issues of animal welfare had always been important to Bateson.

A second issue was Bateson's support for calls for nuclear disarmament, following the example of Robert Hinde, who had been an active peace campaigner over the years, and was chair of the British section of the Pugwash Conferences on Science and World Affairs, through which scientists provided scientific advice to governments. It was the arrival of American cruise missiles in the UK in 1977 that triggered Bateson's active engagement with this cause. A small group of colleagues at the sub-department of animal behaviour, including Bateson, Hinde and Nick Humphrey, held seminars, gave public lectures, debated with politicians and organized 'teach-ins' promoting the Campaign for Nuclear Disarmament (CND). In 1983, Bateson and Hinde led a high-powered group of Cambridge academics to publish an edited book about nuclear weapons, entitled *Defended to death* (Prins 1983).

Equally contentious was Bateson's signing a letter in *The Guardian* in 2002 calling for a moratorium on European funding for research in Israel until that nation abided by UN resolutions and opened peace negotiations with the Palestinians, and he remained supportive of the Palestinian cause subsequently. However, this did not stop him collaborating generously with Israeli colleagues throughout his career.

Within academia, Bateson showed courage, integrity and leadership in standing up against overly simplistic adaptationism and gene-centric accounts, and in pushing for a richer understanding of development and evolution, even if it was not always popular for him to do so at the time. In many of these respects, his stance has been vindicated—for instance, he long argued that plasticity plays important roles in evolution, a position that is now beginning to be accepted within evolutionary and behavioural biology. Another admirable personal quality was Bateson's receptiveness to new ideas and theory, as witnessed by his embracing widened views of inheritance (Jablonka & Lamb 2005) (57), novel conceptual frameworks (e.g. 'developmental systems theory'; Oyama *et al.* 2001) or novel theoretical approaches, 'neural net modelling' (30). A further example is provided by his collaboration with Kevin Laland to update the contemporary understanding of Tinbergen's four questions (60). Bateson was a progressive thinker, in his element devising new conceptual theory, always connecting ideas and searching for the big picture, and with great faith in the power of science to progress and provide answers.

The steady stream of leadership roles that Bateson undertook is testament to the reputation he acquired as a man who took his duties, passions and goals seriously. An approachable and affectionate scientist, Bateson insisted on being called Pat by everyone. He was open-minded, a good listener, curious about science, dedicated to his students and collaborators, and made time for anyone who wanted to discuss their research. While provost of King's College Cambridge, Bateson pointedly invited all new undergraduates in small groups to have lunch or supper with him and his wife at the provost's lodge, a characteristic effort to make everyone feel welcome, and testament to his inclusiveness and approachability. While highly valued as a supervisor, Bateson typically declined to put his name on his PhD students' papers, in an effort to ensure the students reaped full credit for their work. His final book, *Behaviour, development*

Figure 11. Patrick Bateson birding in the Shetlands with daughters Melissa and Anna. Pat is introducing Melissa to ground nesting birds. (Online version in colour.)

and evolution (64), Bateson made available to students as a not-for-profit, free-to-download publication.

A loyal colleague, mentor and friend, Bateson was widely prized for his enthusiasm and kindness. Despite the many accolades and achievements, he never showed a hint of pomposity, and always expressed criticism respectfully. Some of Bateson's contemporaries suggested that, as a leader, he could occasionally be indecisive, and that his academic writing sometimes had a vague quality. To the extent that there is any basis to these suggestions, they almost certainly reflect Bateson's agreeableness and the continuous efforts he made to not offend or upset others. It is tempting to conclude that Bateson's friendliness and approachability helped to shape attitudes in the field of animal behaviour. In an autobiographical piece he wrote: 'I think that ethologists have been lucky as much of the competition that disfigures many other areas of science has been unusual in ours' (54).

Bateson also had a good sense of fun. On one occasion, in 1999, he and a small group of friends had the idea at a dinner party that the best place to view an impending solar eclipse would be above the clouds. Bateson chartered a small plane to do so.

Bateson's diplomacy, charm and judgement were manifest in his 15-year tenure as provost of King's College, Cambridge. All guests at the provost's lodge, whether graduate students or international dignitaries, would be warmly welcomed and introduced to their feline collection. Bateson was also devoted to the college gardens, which flourished during his time as provost. Indeed, he continued to sit on the garden committee until his death. He is remembered by the members of the college with both great affection and appreciation for his many contributions to the institution.

A committed family man, Bateson took enormous pride in the academic achievements of his daughters, both of whom graduated from New College Oxford (the sister college to King's College, Cambridge) with first class degrees. Indeed, Melissa was awarded the Gibbs

Figure 12. Picture of shelduck by Patrick Bateson, painted in 1955 when on holiday bird watching on the Northumbrian coast. (Online version in colour.)

prize for the top first in zoology, following on from her father winning the equivalent prize at Cambridge. He enjoyed long walks in the countryside, birdwatching (figure 11), water colour painting (figure 12), usually landscapes, and listening to opera.

After retiring, Patrick and Dusha moved to a charming old house in Suffolk that had belonged to Dusha's parents. He battled with a serious heart condition from 2014. Nonetheless, the pair continued their sociable ways, with the house and its gardens playing host to numerous guests, cats and chickens. At the Service of Thanksgiving, held in King's College Chapel on 18 November 2017, Bateson's younger daughter, Anna, gave an address that finished with the following quote from her father: 'Every year of my life has been the best year'. Neither age nor illness could diminish Patrick Bateson's enthusiasm for life and scientific enquiry.

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