Lucy Cooke

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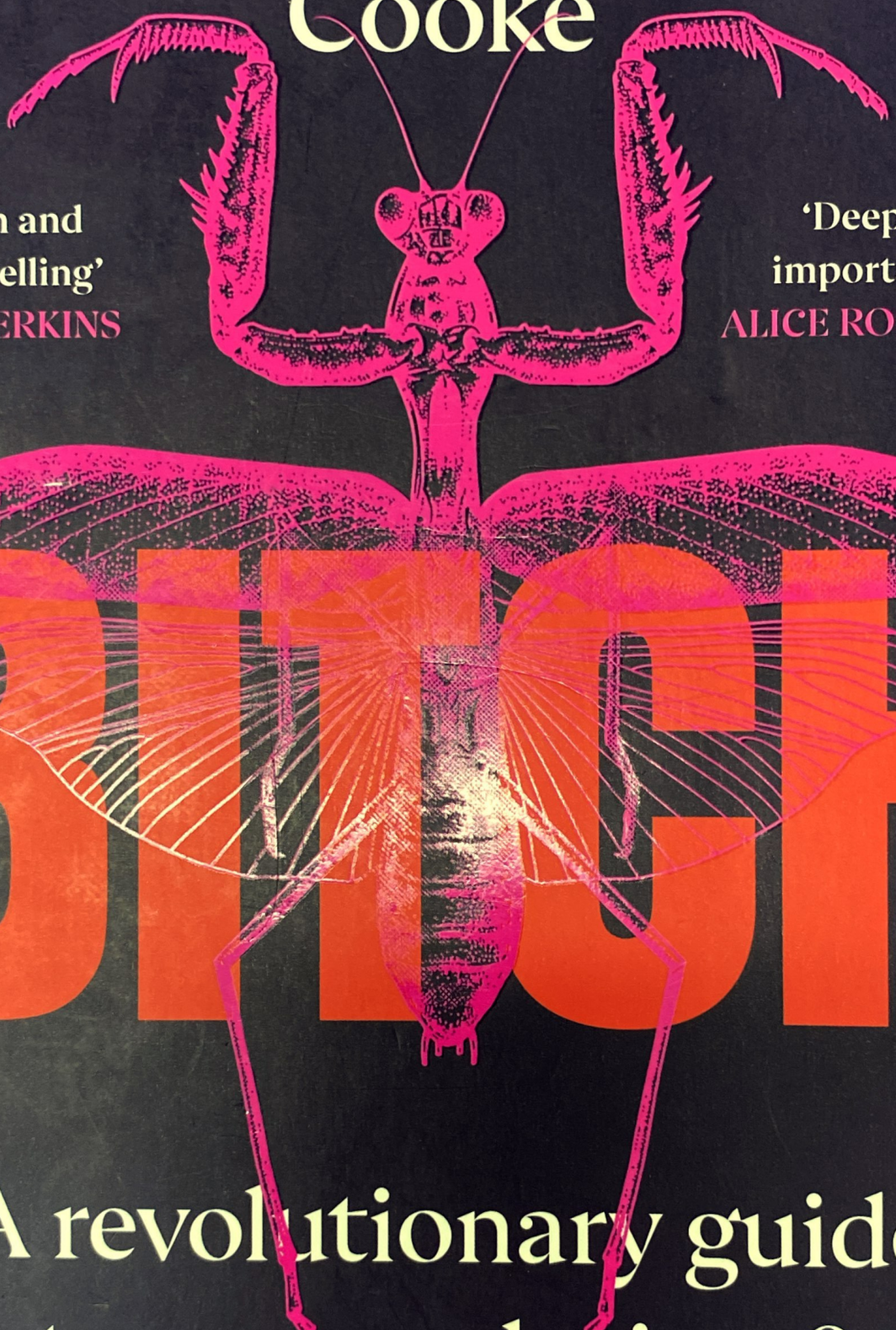

BITCH

A revolutionary guide to sex, evolution & the female animal

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A Revolutionary Guide to
Sex, Evolution and the Female Animal

LUCY COOKE

doubleday

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To all the bitches in my life
Thank you for the love and inspiration

AUTHOR'S NOTE ON LANGUAGE

Language evolves rapidly, and there is currently much conversation about the conflation of sex and gender terms. It is critical to use these terms appropriately and not to confuse them. Most scientists agree that non-human animals do not have gender. In this book, the terms female and male refer to an animal's biological sex. I do engage in anthropomorphizing, to an extent. Sometimes this is because these were the historical terms used. For example, I may refer to an animal's genitalia as being 'masculinized' or a brain being 'feminized' as this was the original scientific description. Such gendered terms needn't and shouldn't be used to describe animals' sex characteristics and behaviours in scholarly realms today. I also use gendered terms such as 'mother' and 'father' to describe animals, because these are the terms used by the scientists in question and most of my audience will understand what or who I refer to with these terms – for instance, 'mother' may mean the egg-producing parent of an individual animal. At other times, I have used anthropomorphic terms such as femme fatale, queen, lesbian, sister, lady and bitch for storytelling purposes, and readers needn't choose to replicate these labels in their academic work. I recognize that this anthropomorphizing can, unintentionally, have gendered implications. This book intends to demonstrate that sex is wildly variable and that gendered ideas based on assumptions of binary sex are nonsense. It is my sincerest hope that this intent has been clearly communicated.

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Lucy Cooke, far left, with (from left to right) Mary Jane West-Eberhard, Sarah Blaffer Hrdy and Jeanne Altmann

INTRODUCTION

Studying zoology made me feel like a sad misfit. Not because I loved spiders, enjoyed cutting up dead things I'd found by the side of the road or would gladly root around in animal faeces for clues as to what their owner had eaten. All my fellow students shared the same curious kinks, so there was no shame there. No, the source of my disquiet was my sex. Being female meant just one thing: I was a loser.

'The female is exploited, and the fundamental evolutionary basis for the exploitation is the fact that eggs are larger than sperms,' wrote my college tutor Richard Dawkins in his bestselling evolutionary bible, *The Selfish Gene*.

According to zoological law, we egg-makers had been betrayed by our bulky gametes. By investing our genetic legacy in a few nutrient-rich ova, rather than millions of mobile sperm, our forebears had pulled the short straw in the primeval lottery of life. Now we were doomed to play second fiddle to the sperm-shooters for all eternity; a feminine footnote to the macho main event.

I was taught that this apparently trivial disparity in our sex cells laid cast-iron biological foundations for sexual inequality. 'It is possible to interpret all other differences between the sexes as stemming from this one basic difference,' Dawkins told us. 'Female exploitation begins here.'

Male animals led swashbuckling lives of thrusting agency. They fought one another over leadership or possession of females. They shagged around indiscriminately, propelled by a biological imperative

to spread their seed far and wide. And they were socially dominant; where males led, females meekly followed. A female's role was as selfless mother, naturally; as such, maternal efforts were deemed all alike: we had zero competitive edge. Sex was a duty rather than a drive.

And as far as evolution was concerned it was males who drove the bus of change. We females could hop on for a ride thanks to shared DNA, as long as we promised to keep nice and quiet.

As an egg-making student of evolution, I couldn't see my reflection in this fifties sitcom of sex roles. Was I some kind of female aberration?

The answer, thankfully, is no.

A sexist mythology has been baked into biology, and it distorts the way we perceive female animals. In the natural world female form and role varies wildly to encompass a fascinating spectrum of anatomies and behaviours. Yes, the doting mother is among them, but so is the jacana bird that abandons her eggs and leaves them to a harem of cuckolded males to raise. Females can be faithful, but only 7 per cent of species are sexually monogamous, which leaves a lot of philandering females seeking sex with multiple partners. Not all animal societies are dominated by males by any means; alpha females have evolved across a variety of classes and their authority ranges from benevolent (bonobos) to brutal (bees). Females can compete with each other as viciously as males: topi antelope engage in fierce battles with huge horns for access to the best males, and meerkat matriarchs are the most murderous mammals on the planet, killing their competitors' babies and suppressing their reproduction. Then there are the femme fatales: cannibalistic female spiders that consume their lovers as post- or even pre-coital snacks and 'lesbian' lizards that have lost the need for males altogether and reproduce solely by cloning.

In the last few decades there has been a revolution in our understanding of what it means to be female. This book is about that revolution. In it, I will introduce you to a riotous cast of remarkable female animals, and the scientists that study them, who together

have redefined not just the female of the species, but the very forces that shape evolution.

To understand how we arrived at this cockeyed view of the natural world, we have to head back in time to Victorian England to meet my scientific idol: Charles Darwin. Darwin's theory of evolution by natural selection explained how the rich variety of life is descended from a common ancestor. Organisms that are more adapted to their environment are more likely to survive and pass on the genes that aided their success. This process causes species to change and diverge over time. Often misquoted as 'survival of the fittest' – a term coined by the philosopher Herbert Spencer and only incorporated by Darwin under duress into the fifth edition of *On the Origin of Species* (1869) – the idea is as brilliant as it is simple and justly hailed as one of the greatest intellectual breakthroughs of all time.

As ingenious as it is, natural selection cannot account for everything we find in nature. Darwin's evolutionary theory had some gaping holes in it, caused by elaborate traits like the stag's antlers or the peacock's tail. Such extravagances offer no benefit to the general process of being, and could even be considered a hindrance to everyday life. As such they could not have been sculpted by the utilitarian force of natural selection. Darwin recognized this, and for a long time it tortured him. He realized there must be another evolutionary mechanism at play, with a very different agenda. That, Darwin eventually realized, was the quest for sex – and so he named it *sexual* selection.

To Darwin this novel evolutionary force explained these flamboyant traits – their only purpose must be to win or attract the opposite sex. To mark their non-essential nature Darwin christened such indulgences 'secondary sexual characteristics', to separate them from 'primary sexual characteristics', like reproductive organs and genitals, which are instead quite indispensable for perpetuating life.

Just over a decade after he presented natural selection to the world, Darwin published his second great theoretical masterpiece: *The Descent of Man, and Selection in Relation to Sex* (1871). This hefty follow-up tome outlined his new theory of sexual selection, which accounted for the profound differences he observed between the sexes. If natural selection is the struggle for survival, sexual selection is essentially the struggle for mates. And as far as Darwin was concerned, this competition was largely the domain of males.

'The males of almost all animals have stronger passions than the females. Hence it is the males that fight together and sedulously display their charms before the females,' Darwin explains. 'The female, on the other hand, with the rarest of exceptions, is less eager than the male . . . she generally "requires to be courted"; she is coy.'

Thus, in Darwin's eyes, sexual dimorphism also extended to the behaviour of each sex. These sex roles were as predictable as physical characteristics. Males take the evolutionary lead by duking it out with 'weapons' or 'charms' specially evolved in order to take 'possession' of the female. Competition is such that males will vary wildly in their reproductive success and this sexual selection drives the evolution of winning traits. Females have less call for variation; their role is one of submission to and transmission of these male characteristics. Darwin wasn't sure why this disparity existed, but he suspected it could be traced back to the sex cells and the female being energetically drained by her maternal investment.

In addition to male competition, Darwin knew that the mechanics of sexual selection required an element of female choice. This was trickier to explain because it gave the fairer sex an uncomfortably active role in shaping the male – something which would not go down well in Victorian England and, as we shall discover in chapter two, ultimately made Darwin's theory of sexual selection distinctly unpalatable to the scientific patriarchy. So Darwin was at great pains to downplay this female power by stating that it is somehow achieved in a 'comparatively passive' and unthreatening fashion by females 'standing by as spectators' to the masculine battle of bravado.

Darwin's branding of the sexes as active (male) and passive (female) could not have been more effective if it had been devised by a multi-million-dollar marketing company with an unlimited budget. It subscribes to the kind of tidy dichotomy – like right or wrong, black or white, friend or foe – so relished by the human brain for feeling intuitively correct.

But Darwin was probably not the originator of this convenient sexual classification. He likely borrowed it from Aristotle, the father of zoology. In the fourth century BC the ancient Greek philosopher wrote the first ever animal almanacs: *On the Generation of Animals* was his treatise on reproduction. Darwin had certainly read this seminal academic work, which perhaps explains why there is a distinct whiff of familiarity in Aristotle's partitioning of the sex roles.

'In those animals that have . . . two sexes . . . the male stands for effective and active . . . and the female . . . for the passive.'

The stereotypes of female passivity and male vigour are as old as zoology itself. Such an endurance test of time suggests they've 'felt right' to generations of scientists, but that doesn't mean they are. One thing science in every domain has taught us is that our intuitions often lead us astray. The main problem with this neat binary classification is: it's wrong.

Try explaining the need to be passive to a dominant female spotted hyena, and she'll laugh in your face, after she's bitten it off. Female animals are just as promiscuous, competitive, aggressive, dominant and dynamic as males. They have equal right to drive the bus of change. It's just that Darwin, along with the coterie of gentlemen zoologists that helped inform his argument, couldn't, or perhaps wouldn't, see them that way. The greatest single leap forward in all of biology – perhaps all of science – was made by a group of Victorian men, in a mid-nineteenth-century milieu, and it smuggled with it certain assumptions about the nature of gender and sex.

It's fair to say that if Darwin was a contestant on *Mastermind*, his specialist subject would not be the opposite sex. Here was a

man that married his first cousin Emma, only after drawing up a list of nuptial pros and cons. This revealing romantic inventory, scribbled on the back of a letter to a friend, has, to Darwin's shame, been preserved, revealing his most intimate thoughts for all to judge in perpetuity.

In just two brief columns – 'Marry' and 'Not Marry' – Darwin thrashed out his inner connubial turmoil. His chief concerns were that he would miss out on the 'conversation of clever men at clubs' and might therefore succumb to 'fatness and idleness', or worse, 'banishment and degradation with indolent idle fool' (which is perhaps not the way Emma would have chosen to be described by her beloved fiancé). However, on the plus side, he would have 'someone to take care of the house' and a 'nice soft wife on a sofa' was 'better than a dog anyhow'. So Darwin bravely took the plunge.

One gets the feeling that, despite fathering ten children, Darwin was perhaps driven by cerebral rather than carnal urges. He may not have been terribly familiar with or even curious about the female sex. So the chances of him questioning evolution from the female perspective, as well as the male, were perhaps small, even before you consider the society into which he was born.

Even the most original and meticulous scientists are not immune to the influence of culture, and Darwin's androcentric reading of the sexes was no doubt shaped by the prevailing chauvinism of the era. Women in upper-class Victorian society had one main role in life: to marry, have children and perhaps assist with their husbands' interests and business. This was very much a supportive, domestic role since they were defined, physically and intellectually, as the 'weaker' sex. Women were, in all ways, subordinate to male authority, be that of fathers, husbands, brothers or even adult sons.

This social prejudice was conveniently substantiated by contemporary scientific thinking. The leading academic minds of the Victorian era considered the sexes to be radically different creatures – essentially polar opposites of one another. Females were believed to experience arrested development; they resembled the young of their species by being smaller, weaker and less colourful. Where male

energy goes into growth, female energy is required to nourish eggs and carry young. Because of males' generally larger physique, they were considered to be more complex and variable than females, as well as superior in mental capacity. Females were considered to be all of average intelligence, but males varied wildly to include levels of genius unseen in the opposite sex. Essentially, males were considered to be more *evolved* than females.

These sentiments were all incorporated by Darwin into *The Descent of Man, and Selection in Relation to Sex*, which, as the title suggests, used sexual and natural selection to explain human evolution and the sex differences upheld by Victorian society.

'The chief distinction in the intellectual powers of the two sexes is shewn by man's attaining to a higher eminence, in whatever he takes up, than can woman – whether requiring deep thought, reason or imagination, or merely the use of the senses and hands,' explained Darwin. 'Thus man has ultimately become superior to woman.'

Darwin's theory of sexual selection was incubated in misogyny, so it is little wonder that the female animal came out deformed; as marginalized and misunderstood as a Victorian housewife. What is perhaps more surprising, and damaging, is how tough it has been to wash this sexist stain out of science, and how far it has bled.

Darwin's genius has not helped. Because of his godlike reputation, biologists who followed in his wake have suffered from a chronic case of confirmation bias. They looked for evidence in support of the passive female prototype, and saw only what they wanted to see. When faced with anomalies, like the licentious promiscuity of the female lioness that enthusiastically mates scores of times a day during oestrus with multiple males, they studiously looked the other way. Or worse, as you will discover in chapter three, experimental results that didn't conform were manipulated with a statistical sleight of hand to conjure sideways support for 'the correct' scientific model.

A central tenet of science is the parsimonious principle, also known as Ockham's razor, which teaches scientists to trust in the

evidence and choose the simplest explanation for it, as it will probably be the best. Darwin's strict sex roles have forced an abandonment of this fundamental scientific process as researchers are compelled to dream up ever more tortuous excuses to explain away female behaviours that deviate from the standard stereotype.

Take the pinyon jay, *Gymnorhinus cyanocephalus*. These cobalt-blue members of the crow family live in noisy flocks of fifty to five hundred birds in the western states of North America. Highly intelligent creatures with such active social lives are likely to have some means of ordering their busy society – a dominance network – otherwise there would be chaos. The ornithologists John Marzluff and Russell Balda, who studied the jays for over twenty years and published an authoritative book on them in the 1990s, were interested in decoding the pinyon jay's social hierarchy. So they went in search of the 'alpha male'.

This took some ingenuity. It transpired that male pinyon jays are committed pacifists and rarely ever fight. So, the enterprising ornithologists built feeding stations loaded with tasty treats like greasy popcorn and mealworms to try to incite some kind of territorial war. But still the jays refused to engage in battle. The researchers were forced to base their scale of combat on some fairly subtle cues, like sideways glances. If the dominant male gave the submissive male what amounted to a dirty look then the submissive would leave the feeder. It wasn't exactly *Game of Thrones* stuff, but the researchers sat and diligently recorded around two and a half thousand of these 'aggressive' encounters nevertheless.

When they came to run the statistics they were further confused. Only fourteen of two hundred flock members qualified for a place in the dominance network and there was no linear hierarchy. Males reversed their dominance and subordinates 'aggressed' their superiors. Despite the puzzling results and general lack of macho hostility, the scientists still felt confident in declaring, 'There is little doubt that adult males are in aggressive control.'

The curious thing is, the researchers had seen jays behaving with significantly more antagonism than a few annoyed looks. They

documented birds in dramatic airborne battles where duelling pairs became locked in combat mid-air and 'flap vigorously as they fall to the ground' where they 'peck at each other with forceful stabs'. These encounters were 'the most aggressive behaviour observed during the year', but they were not included in any dominance network as the perpetrators weren't male. They were all female. The authors concluded that this 'testy' feminine behaviour must be hormonally driven. They proposed that a spring hormone surge had given these female jays 'the avian equivalent of PMS which we call PBS (pre-breeding syndrome)'!

There is no such thing as avian PBS. If Marzluff and Balda had had their minds open to the female birds' aggressive behaviour and used Ockham's razor to shave the fluff from their conjecture, they would have got close to figuring out the pinyon jay's complex social system. The clues that females are in fact highly competitive and play an instrumental role in the jay's hierarchy are all there in their meticulously recorded data, but they were blind to them. Instead they pushed forward dogmatically in search of 'the crowning of a new king', a coronation of their conviction which, of course, never happened.

There is no conspiracy here, just blinkered science. Marzluff and Balda illustrate how good scientists can suffer bad biases. The ornithological duo were faced with confounding novel behaviour, which they interpreted within a bogus framework. They are by no means alone in their honest error. Science, it transpires, is soaked in accidental sexism.

It hasn't helped that the academic establishment was, and in many areas still is, dominated by men who naturally view the animal kingdom from their standpoint; the questions asked to inspire research thus originated from a male perspective. Many simply weren't curious about females. Males were the main event and became the model organism – the default from which the female deviated, the standard by which the species was judged. Female animals, with their 'messy hormones', were the outliers, distracting tangents to the leading narrative, and didn't warrant the same level of scientific scrutiny. Their

bodies and behaviours were left unexamined. The resulting data gap then becomes a self-fulfilling prophecy. Females are seen as the invariant and inert sidekicks to male endeavour, because there's no data to sell them as anything otherwise.

The most dangerous thing about sexist bias is its boomerang nature. What started as chauvinist Victorian culture was incubated by a century of science and then spat back into society as political weaponry, rubber-stamped by Darwin. It gave a handful of, notably male, devotees of the new science of evolutionary psychology the ideological authority to claim that a host of grim male behaviours – from rape to compulsive skirt chasing to male supremacy – were 'only natural' for humans, because Darwin said so. They told women they had dysfunctional orgasms, that they could never break through the glass ceiling thanks to an innate lack of ambition, and should stick to mothering.

This turn of the century evolutionary psychobabble was gobbled up by a new breed of men's magazines, that shunted this sexist 'science' into the mainstream. In bestselling books and high-profile columns in the popular press, journalists like Robert Wright crowed that feminism was doomed because it refuses to acknowledge these scientific truths. From his ideological pedestal Wright penned imperious articles with titles like 'Feminists, Meet Mr Darwin' and awarded his critics 'a C in Evolutionary Biology 101', claiming that 'not a single well-known feminist has learned enough about modern Darwinism to pass judgement on it'.

But they had. The second wave of feminism had opened once-closed laboratory doors and women were walking the halls of top universities and studying Darwin for themselves. They were heading into the field and observing female animals with the same curiosity as male animals. They discovered sexually precocious female monkeys and, instead of ignoring them like their male predecessors had, they questioned why they might be behaving in this way. They developed standardized techniques for measuring behaviour that forced equal attention on *both* sexes. They harnessed new technologies to spy on female birds and reveal that far from being victims of male

sexual dominance, they were in fact running the show. And they repeated experiments that empirically underpinned Darwin's sexual stereotypes and discovered the results had been skewed.

It takes courage to challenge Darwin. He's more than just an iconic intellect; he's a national treasure in the UK. As one veteran professor pointed out to me, disagreeing with Darwin is tantamount to academic heresy and has led to a distinct conservatism in our homegrown evolutionary science. It is perhaps for this reason that the first seeds of rebellion came from the other side of the Atlantic, and a sprinkling of American scientists who ventured to originate alternative narratives about evolution, gender and sexuality.

You will meet these intellectual warriors in the pages of this book. I met some of them over lunch at a walnut farm in California where we discussed Darwin, orgasms and vultures, amongst other things. Sarah Blaffer Hrdy, Jeanne Altmann, Mary Jane West-Eberhard and Patricia Gowaty are the rabble-rousing matriarchs of modern Darwinism who dared to fight the scientific phallocracy with data and logic. They call themselves 'The Broads' and have met privately at Hrdy's home every year for the last thirty years to chew the evolutionary fat. I lucked out by landing an invitation to their annual cerebral jamboree. Although now semi-retired, these trailblazing professors still gather to support one another, discuss fresh ideas and generally keep the course of evolutionary biology evolving on an even path. They are feminists, yes, but they are clear that means they believe in the equal representation of both sexes, not the undeserved dominion of one.

Their science has enabled a new wave of biologists to look at the female of the species as fascinating in her own right; by examining female bodies and behaviour and asking questions about how selection works from the perspective of a daughter, sister, mother and competitor. These scientists have been willing to look beyond cultural norms and entertain unorthodox ideas about the fluidity of sex roles, overthrowing the machismo – inadvertent or otherwise – of evolutionary biology. Many are female, but, as you will discover,

this scientific mutiny is not a women-only space – all sexes and genders are playing a part. You will meet many male scientists in the pages of this book. The pioneering work of Frans de Waal, William Eberhard and David Crews, to name just a few, proves that you don't need to identify as female to be a feminist scientist. And fresh perspectives from the LGBTQ scientific community have been crucial in challenging zoology's heteronormative myopia and the binary dogma. Biologists like Anne Fausto-Sterling and Joan Roughgarden, amongst others, have drawn attention to the stunning variety of sexual expression in the animal kingdom, and diversity's fundamental role in driving evolution forward.

The result is not just a more fabulously rich and life-like portrait of the female animal, but also a wealth of surprising new insights into the tangled mechanics of evolution. These are exciting times for evolutionary biologists: sexual selection is in the throes of a major paradigm shift. Empirical revelations are turning accepted facts on their head and conceptual changes are sending long-held assumptions out of the window. Darwin wasn't all wrong on this score, by any means. Male competition and female choice *do* drive sexual selection, but they are just part of the evolutionary picture. Darwin was viewing the natural world through a Victorian pinhole camera. Understanding the female sex is giving us the widescreen version of life on earth, in full technicolour glory, and the story is all the more fascinating for it.

In *Bitch* I go on a global adventure to meet the animals and scientists that are helping to rewrite an outdated patriarchal view of evolution and redefine the female of the species.

I travel to the island of Madagascar to discover how female lemurs, our most distant primate cousins, came to dominate males physically and politically. In the snowy mountains of California I discover how a robot female sage grouse exploded Darwin's myth of the passive female. On the island of Hawaii I meet loved-up, long-term female albatross couples that have defied traditional sex roles and shacked up together to raise their chicks. And cruising along the Washington coast, I find kinship with a matriarchal killer

whale – the wise old leader of her hunting community, and one of only five known species, including humans, in which females go through menopause.

By exploring emerging tales from the fringes of femaleness I hope to paint a fresh, diverse portrait of the female animal, and to try to understand what, if anything, these revelations can inform us about our own species.

Since the time of Aesop, humans have looked to animals as illustrations and models of human behaviour. Many believe, somewhat misguidedly, that nature teaches human societies what is good and correct – the naturalistic fallacy. But survival is an unsentimental sport and animal behaviour encompasses female narratives that range from the fabulously empowered to the terrifyingly oppressed. Scientific discoveries about female animals can be used to fuel battles on both sides of the feminist fence; wielding animals as ideological weapons is a dangerous game. But understanding what it means to be a female animal can help counter lazy arguments and tired androcentric stereotypes; it can challenge our assumptions about what is natural, normal and even possible. If womanhood is going to be defined by one thing, rather than strict, outdated rules and expectations, it is its dynamic and varied nature.

The bitches in *Bitch* will demonstrate how being female is about being a fighter for survival and not just a passive sidekick. Darwin's theory of sexual selection drove a wedge between the sexes by focusing on our differences; but these differences are greater culturally than they are biologically. Animal characteristics – be they physical or behavioural – are both varied and plastic. They can bend according to a selection's whim, which makes sex traits fluid and malleable. Rather than predicting a female's qualities through the crystal ball of her sex, the environment, time and chance all play a significant role in shaping their form. As we shall discover in the first chapter, females and males are, in fact, far more alike than they are different. So much so, it can sometimes be hard knowing where to draw the line.

CHAPTER ONE

The anarchy of sex: what is a female?

Let's start by heading underground to meet a highly secretive female: enemy number one of the landscape gardener and greedy consumer of worms. I'm talking about the mole, *Talpa europaea*.

Most of you will be familiar with the mole's handiwork, if not the beast itself. Their conical piles of freshly turned dirt can disrupt a smoothly manicured lawn like a chronic case of acne – the ultimate pain in the grass.

Back in the 1970s my father would be driven to distraction by molehills invading his precious turf. Much to my dismay, he'd set barbaric-looking metal traps to catch their creators. Once a mole was ensnared, I would insist he hand their lifeless bodies over to me so I could stroke their oh-so-velvety silver-black fur and marvel at their strangeness – their minute beady eyes (which despite popular mythology are poorly sighted but not totally blind) and comically oversized pink front paws – before giving them a proper burial. Back into the earth, where they belong.

The female mole is indeed a wondrous creature. A solo operator who makes her living by hunting worms using a network of tunnels that act as her own form of animal trap. When a worm pushes through her subway ceiling, she quickly sniffs it out using a long pink snout that can actually smell in stereo – each nostril acts independently, allowing her brain to accurately compute the direction of dinner in the pitch black. Her quarry, once caught, isn't killed

immediately; instead, the mole paralyses it with her venomous saliva so it can be stored alive in a specially constructed larder without turning to rot. As many as four hundred and seventy wrigglers have been recorded in one lucky mole's pantry, which is helpful as she needs to consume over half her body weight in worms a day.

Life underground is tough. Burrowing earth is exhausting work and there's comparatively little oxygen to breathe. To survive this hostile environment evolution has equipped the mole with some cunning specializations. Her blood sports a modified form of haemoglobin that increases her affinity for oxygen and tolerance of toxic waste gases. And she sports an extra 'thumb'. Just like in the panda, a bone from her wrist has shot off on its own evolutionary path and formed a useful new digit for shifting extra earth. But perhaps most impressive of all are the female mole's balls.

The mole sow's gonads are described as 'ovotestes'. These internal reproductive organs consist of ovarian tissue at one end and testicular tissue at the other. The ovary side produces eggs and expands during the short breeding season. But, once the job of reproduction is done, this egg-making tissue shrinks and the testicular tissue expands until it is actually larger than the ovarian.

The female mole's testicular tissue is full of Leydig cells that make testosterone, but not sperm. This sex steroid hormone is commonly associated with males: beefing up muscles and fuelling aggression. It does both in the female mole, giving her the evolutionary edge underground: extra digging power and added hostility for defending her pups and worm larder.

It also gives her genitalia that are indistinguishable from the male's: an enlarged clitoris variously described as a 'phallus' or 'penile clitoris' and a vagina that seals up outside of breeding.

The female mole forces us to confront age-old assumptions about what distinguishes the sexes. For the majority of the year, on a genital, gonadal and hormonal level, the mole sow could easily be mistaken for a boar. So, how do we know she's a female?

This is a book about non-human animals, so it is important to begin by separating sex and gender. Most biologists agree that

animals don't have gender. This social, psychological and cultural construct is considered the preserve of humans. When biologists talk about females they are referring only to their sex, but what does that mean?

In the beginning, reproduction was simple. The earliest life forms simply split, fused, budded bits off or cloned themselves in order to multiply. Then along came sex, which complicated matters somewhat. Now individuals needed to combine sex cells – gametes – in order to proliferate. Across the animal kingdom these come in just two sizes: big and small. This basic gametal dichotomy provides the standard biological definition of sex: females produce large, nutrient-rich eggs and males make small mobile sperm.

So far, so binary. Or is it?

Well, no. Sex is a complicated business. As you will discover in this first chapter, the ancient network of genes and sex hormones that interact to determine and differentiate the sexes have the ability to create a mixture of gametes, gonads, genitals, bodies and behaviour that disregards binary expectations. All of which makes marshalling sex into two neat deterministic buckets far from straightforward.

Starting at the most superficial level, many would consider genitals an easy indicator of sex. But the female mole's 'phallus' blows that notion clean out of the water. She's no freak. Dozens of female animals, from tiny cave-dwelling barklice* to giant African elephants,

* Two distinct genera of barklice, *Neotrogla* in South America and *Afrotrogla* in southern Africa, have evolved fully erectable 'penises' in females and 'vaginas' in males. Females of these cave-dwelling insects are the more promiscuous and aggressive sex. They are about the size of a flea and use their tiny, spiny penis to anchor on to the male during sex. This can last for 40–70 hours, during which time a capsule of sperm travels from the male to the female. Given the geographical distance between these two barklice populations, it would appear that the female's sexual tackle evolved on two independent occasions and not from a single shared ancestor.

sport ambiguous sexual anatomy that's commonly described in phallic terms.

The first time I saw a female spider monkey in the Amazon I assumed it was a male because of its dangling sexual appendage, the ostentatious size of which seemed to me frankly hazardous as it cavorted about the canopy. The primatologists I was with politely corrected me. Male spider monkeys are the sex with no apparent penis, since they keep theirs tucked away inside. Females on the other hand have a very obvious pendulous clitoris, known in biological circles as a 'pseudo-penis'. Such androcentric terminology grates somewhat, especially when you consider that the female spider monkey's 'fake' phallus is in fact longer than the male's 'real' phallus.

The strangest example is perhaps the fossa. Madagascar's greatest predator is the largest member of the mongoose family and looks a bit like a puma with a shrunken head. Its scientific name, *Cryptoprocta ferox*, translates as 'ferocious, hidden anus'. That taxonomists chose to highlight the fossa's anus as cryptic is somewhat unconventional, when it's the rest of her privates that are so mysterious.

When a female fossa is born she has a small clitoris and vulva, as might be expected. Then, at around seven months of age, something odd starts to happen. The fossa's clitoris enlarges, grows an internal bone and acquires spines to become a facsimile of the male's penis. It even exudes yellow liquid on its underside, like an adult male's. The female fossa sports her penile clitoris for a year or two, until she becomes reproductively active, when it magically disappears. Authors of a scientific paper on fossa genitalia postulated that this might protect the adolescent female from the unwanted attention of sexually pushy males or aggressively territorial female fossas.

The female fossa's transitory flirtation with a lookalike penis might, of course, serve no function at all. Not all traits do. Much like the redundant human appendix, it could simply be a relic from the fossa's evolutionary past that was sufficiently benign to

avoid being selected against. Or be a side effect of another trait that evolution has selected for. Deciphering the ultimate evolutionary cause of a novel characteristic is a speculative sport. But decades of study into a close relative of the fossa has provided valuable evidence for the mechanics underlying such 'masculinized' genitalia. These insights have challenged a long-standing scientific prejudice concerning the 'passive' nature of female sexual development and gendered stereotypes of the hormones involved.

The genitals of the spotted hyena, *Crocuta crocuta*, have been causing a stir since the time of Aristotle. Ancient naturalists believed the hyena to be a hermaphrodite on account of the female's pudenda, which are the most sexually ambiguous of any known mammal's. Not only does the female spotted hyena have an eight-inch clitoris that's shaped and positioned exactly like the male's penis but she also gets erections. Both female and male spotted hyenas display and inspect one another's sexual tumescence during 'greeting ceremonies'. Crowning all this female virility is what appears to be a prominent pair of furry testicles.

This scrotum is in fact false: the hyena's labia have fused and filled with fatty tissue and merely resemble male gonads. This means that the female spotted hyena is the only mammal with no external vaginal opening at all. Instead she must urinate, copulate and even give birth through her curious multi-tasking clitoris – hence the antiquated hermaphrodite rumour. In more recent years, scientists have noted that males and females are so similar that they can be differentiated only by 'palpation of the scrotum' – something of a last resort, one assumes, when sexing an animal famous for its bone-crunching bite.

The female spotted hyena's sexual transgression doesn't stop at her genitals. Scientists have also been fascinated by her similarly 'masculinized' body and behaviour. Females can be up to 10 per cent heavier than males in the wild (20 per cent in captivity). This

is unusual, as amongst mammals males are generally larger in size.* In the rest of the animal kingdom, and thus the majority of animals, sexual size dimorphism is however generally the reverse. Fatter, more fecund females produce more eggs, so amongst most invertebrates and many fish, amphibians and reptiles it is the females that often outsize the males.†

Female spotted hyenas are also more aggressive than males. These highly intelligent, social carnivores live in matrilineal clans of up to eighty individuals governed by an alpha female. Males tend to be the sex that disperses from the natal matriline and, as such, the lowest rung of hyena society: submissive outcasts begging for acceptance, food and sex. Females are considered dominant in most situations, engage in rough play and vigorous scent-marking as well as leading the territorial defence – all behaviours more commonly associated with the opposite sex.

The radical gender-bending life of the female spotted hyena was originally assumed to be the result of an excess of testosterone circulating in her blood. Androgens, the group of sex steroid

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* There are other female mammals that also buck the size trend. The most extreme mammalian case is a South American bat, *Ametrida centurio*, whose males are so much smaller they were originally classified as a separate species. This 'reversed' size dimorphism may be linked with an aerial lifestyle as it is also common in birds – the rationale being that competing males need to be agile rather than strong, and thus evolve to be smaller in size than females. At the other end of the scale, many species of baleen whale have bigger females than males, including the blue whale. One female specimen taken off the coast of the island of South Georgia was almost 30 metres long and weighed in at 173 tonnes – three times the length of a double-decker bus and over thirteen times its weight. Which means that the largest animal to have ever lived was, in fact, female.

† The deep-sea angler fish *Ceratias holboelli* has taken this to an extreme. Males may be more than sixty times shorter and half a million times lighter – essentially little more than swimming sacs of sperm. Once the male has sniffed out a female from her leaking pheromones in the pitch-black depths, he will latch on to her with his mouth, physically fusing with her body for the rest of his life – the evolutionary embodiment of a clingy sexual freeloader. The female is thereafter in control of the male's entire existence, including when he ejaculates his sperm. The Danish fisherman who discovered this intimate set-up in 1925 declared that 'so perfect and complete is the union of husband and wife that one may almost be sure that their genital glands ripen simultaneously'. And they say romance is dead.

hormones that includes testosterone, have been unambiguously branded as male: andro meaning 'man' and gen a 'thing that produces or causes'. So the obvious assumption was that these big, belligerent female hyenas, much like the mole we met earlier, must be swilling with the stuff. But much to everyone's surprise, the circulating levels of testosterone in adult female spotted hyenas do not rival those in males.

So where was all this virilization coming from? The bitches' pseudo-penises pointed to a different timing for testosterone's influence, namely during fetal development.

The standard paradigm for sexual differentiation was developed in the 1940s and '50s by a French embryologist named Alfred Jost, following a series of pioneering, if barbarous, experiments on rabbit fetuses at various stages of development in their mother's womb.

Mammal embryos, whether they're female or male, all start off with a unisex kit of parts: an assortment of ducts, tubes and protogonadal tissue with the potential to develop into either ovaries or testes. The developing fetus is thus considered sexually 'neutral' until this primordial sexual medley starts its journey down the ovarian or testicular path.

Jost's experiments on developing rabbits didn't figure out what triggers the initial differentiation (more on that later), but he did establish that testosterone plays a primary role in driving the fetal gonad towards becoming testes and the subsequent development of male genitalia.

Jost discovered that if he removed the male embryonic gonads early in development, the fetus failed to grow a penis and scrotum and developed a vagina and clitoris instead. Removing the developing ovaries of a fetal female, on the other hand, did not obviously impact her sexual development. Oviducts, uterus, cervix and vagina all developed in an apparently automatic fashion without the need of her embryonic ovaries or their hormones to direct them. In contrast, just 'a crystal of androgen could counteract the absence of testicles' and ensure the development of male

sexual characteristics, heralding this sex steroid to be the dynamic elixir of maleness.

By a process of elimination over dozens of experiments Jost established that high concentrations of testosterone in the male fetus, produced by the developing testicular cells, actively pushed an embryo down the path of male sexual development. In contrast, the creation of a female was seen as a passive process – the 'default' result of an absence of gonadal testosterone.

Jost's theory slotted in nicely with the widespread notion, popularized by Darwin, that females were generally passive and males active. The theory was embellished by others and labelled the Organizational Concept – the universally accepted model for sexual differentiation not just of bodies, but behaviour too. It placed male gonads and androgens in the starring role – the saviours of the sexual paradigm and chief architects of all things male.

Testes and their testosterone-pumping powers became the engine driving the demarcation of not just the embryonic gonads and genitals, but also the fetal neuroendocrine system and developing brain. This then programmed sexual differences in bodies and behaviour that could be activated by sex steroid hormones in later life. Thus testosterone became the executive director of sexual dimorphism; responsible for characteristics ranging from the hefty horns on the stag to the bull elephant's raging musth and the male walrus's fearsome size and temper.

Jost's findings revolutionized the ongoing debates in endocrinology on the hormonal origins of masculinity and femininity. At a conference in 1969, Jost explained: 'Becoming a male is a prolonged, uneasy and risky adventure; it is a kind of struggle against inherent trends toward femaleness.'

The masculine journey was seen as a heroic quest worthy of investigation. In contrast, the now-famous French embryologist referred to females simply as the 'neutral' or 'anhormonal' sex type. Ovaries and oestrogen were considered irrelevant to our story: inert and insignificant. Our sexual development was unreactive and

scientifically trivial. Females basically 'just happened' because we lacked the embryonic balls to be male.

This prejudice has been remarkably enduring and damaging. The legacy of the Organizational Concept is an understudied female system and an unyielding binary view of sexual differentiation, as promoted by the all-powerful developmental male-wash of testosterone. But then along came the spotted hyena with her big phallic clitoris to suggest there's trouble in the paradigm.

Testosterone is indeed a potent hormone. If delivered at the right time, it has the power to reverse the gonadal sex of female fish, amphibians and reptiles. In mammals, it can't force a full sexual U-turn but marinating a female fetus in androgens radically alters the formation of her genitals. Experiments in the 1980s created female rhesus monkeys with a penis and scrotum 'indistinguishable from that of males' by exposing them to testosterone at key stages during their gestation.

Sure enough, when tested, female spotted hyenas revealed rocketing levels of testosterone during their pregnancy. But, with no testes in sight, what could be the source of this 'male' hormone, and how does the developing female fetus manage to survive its omnipotence yet still develop a functioning reproductive system?

The answers lie in how testosterone is synthesized. All of the sex hormones – oestrogen, progesterone and testosterone – originate as cholesterol. This steroid is converted by the action of enzymes to progesterone, a hormone commonly associated with pregnancy and the precursor to androgens, which are, in turn, the precursors to oestrogens. These 'male' and 'female' sex hormones can convert from one to the other and are present in both sexes.

'There's no such thing as a "male" hormone or a "female" hormone. It's a common misconception. We all have the same hormones,' Christine Drea revealed to me over Skype. 'All that differs between males and females are the relative amounts of enzymes that convert the sex steroids from one to another and the distribution and sensitivity of hormone receptors.'

Drea is a professor at Duke University and knows more than

most about the hormonal politics of female sexual differentiation. She's devoted her career to studying a suite of so-called 'masculinized' females, including the spotted hyena along with meerkats and ring-tailed lemurs.

Drea is part of the team that established the source of the pregnant hyena's testosterone. It comes from a lesser-known androgen called androstenedione, or A4, that's actually produced by the pregnant female's ovaries. This form of androgen is known as a precursor hormone, as it converts to either testosterone or oestrogen following the action of enzymes in the placenta.

In most pregnant mammals carrying daughters, A4 is preferentially transformed into oestrogen, but in the spotted hyena it transforms to testosterone instead. This 'male' hormone then exerts its influence on the developing genitals and brain of the female fetus, transforming both her pudenda and her post-natal behaviour.

Historically, A4 aroused little interest as a sex hormone; it was dismissed as 'inactive' for not binding to known androgen receptors. But receptors are now being located that suggest it does have direct action and, more crucially, its effects may differ depending on the sex of the fetus.

'There's a growing body of literature suggesting that hormones can have sexually differentiated effects in different animals. It's all about amount, duration and timing,' Drea articulated.

Drea's work clearly demonstrates that making a female is far from a 'passive' process, and one in which androgens can play an active role. 'Testosterone is not a "male" hormone. It is just a hormone that is more obviously expressed in males than females,' she reiterated.

It's clear to Drea that the female hyena's sexual development must also be under dynamic genetic control to resist the overpowering effects of an excess of androgens and still create a functional, if eccentric, reproductive system. But how is still much of a mystery. The functional genetic steps of how to actually make

female reproductive organs are still poorly understood when compared to the male.

This bias in our understanding comes from Jost's famous but flawed theory of sex differentiation, which only ever explained how you differentiate a male and never questioned how the female is created. The idea that any development process could be 'passive' is clearly quite ludicrous – ovaries require just as much active assembly as do testes. Yet for fifty years the 'default' female system went unstudied.

'Sexual differentiation isn't about describing how you get females and males. It's only about describing how you get males. For decades people were happy not to have an explanation of how you get the female form and just saying, "Well, it's passive," ' Drea asserted.

A foundational publication on mammalian sexual development from 2007 referred to the development of the ovary as 'Terra Incognita'. The prevailing view that ovarian development is the 'default' state had, it claimed, led to 'a widespread understanding that no active genetic steps need to be taken to specify or create an ovary or female genitalia'. Which, the authors wryly note, is 'a rather amazing situation given the importance of this organ for proper female development and reproduction'.

Things are improving. The unknown land of ovarian development has now been partially explored, but its genetic map is far emptier than the one that exists for testes. The chauvinistic hangover of the Organizational Concept has focused the genetic quest for sexual determination firmly on the male; at its core was the hunt to find the elusive testis-determining factor, the genetic trigger that instructs those neutral fetal gonadal cells to rouse themselves out of their sexually indifferent slumber and transform into testes (and start pumping out testosterone).

The genetic recipe that actually determines the sexes is, however, positively byzantine in nature and features an ancient cast of surprisingly androgynous genes.

CHAOTIC CHROMOSOMES

You might think the ultimate answer to what makes a female animal is a pair of XX chromosomes. We're all taught in school, after all, how this anomalous pair of sex chromosomes defines the sexes, with males being XY and females XX. But sex is never that simple.

The XY sex-determination system is best known because it occurs in mammals, along with some other vertebrates and insects. In this system females have two copies of the same sex chromosome (XX), whereas males have two kinds of sex chromosomes (XY). The first misconception is that the letters X and Y refer to the shape of the chromosomes. All chromosomes are sausage-shaped and their resemblance, when paired, is entirely coincidental.

The very first X chromosome was discovered in 1891 by Hermann Henking, a young German zoologist who noticed something curious while inspecting the testicles of a fire wasp (which, to add further confusion, is a bug not a wasp). Chromosomes inhabit cells as matching pairs, but Henking noticed that in all the specimens he studied there was one chromosome that didn't appear to have a matching partner and remained aloof. He named it X – the mathematical symbol for unsolved – after its mysterious nature. Henking made no association between this now iconic, yet enigmatic, strand of DNA and sex determination, which is a shame as it could have made him quite famous. Instead, a year later, he abandoned his cytology studies and moved on to a career in fisheries, which was more financially rewarding but offered significantly less opportunity for scientific fame.

The Y chromosome was eventually discovered lurking in the reproductive organs of a mealworm some fourteen years later, in 1905, by the American Nettie Stevens – a pioneering female geneticist. Stevens recognized its key role in sex determination, but also received little fame for her epic breakthrough. The same chromosome was also discovered, more or less simultaneously, by a male

scientist called Edmund Wilson, who sucked up most of the fame. It was eventually named Y to continue the alphabet system that Henking had started. But thanks to its peculiar stunted size, it also resembles the letter that provides its name when paired with the longer X.

Compared to the X, the Y is essentially a runt of a chromosome: stunted and with significantly less genetic material. When it comes to chromosomes, however, it's not size that matters, it's what you code with it. And the Y is indeed home to a very significant sex-determining gene called SRY (standing for Sex-determining Region of the Y).

In the 1980s Peter Goodfellow's lab in London finally unmasked this unassuming piece of genetic code as the elusive testis-determining factor in humans. His team discovered that the switching on of SRY proved to be the crucial first genetic step in triggering the neutral fetal gonad sex cells to develop into testes and start pumping out testosterone. In its absence, the unisex primordial kit matures at a more leisurely pace into embryonic ovaries.

This time there was much fanfare. The master switch for mammalian sex determination had finally been revealed and the 'essence of maleness' located. SRY was the missing trigger for the cascade of genes that code for testes development – the male sex-determining pathway.

I spoke to Jennifer Marshall Graves, the distinguished Australian professor of evolutionary genetics who was part of the international cohort of scientists hunting for this crucial male sex-determining gene. Her work on marsupial chromosomes prompted the search to switch direction to a fresh section of the Y, where the SRY gene was eventually located. Graves explained why their triumph at solving the puzzle of sex was, in fact, short-lived.

'We thought it was going to be the Holy Grail,' she confessed over Zoom from her home in Melbourne. 'When my student found the SRY gene we thought it would all be really simple. A kind of switch. But sex determination turns out to be much more complicated than we thought.'

The way sex is taught, you'd be forgiven for assuming the genes for creating testes inhabit the Y and the genes for ovaries reside on the X. That would be helpful. But evolution has done nothing to make the work of geneticists easy.

The entire process of sex organ determination involves an orchestra of around sixty genes working in concert. These sex-determining genes don't all exist on the sex chromosomes, let alone sit in a disciplined and gendered fashion on either the X or the Y. They are, in reality, scattered haphazardly throughout the genome.

SRY is like their conductor. If this crucial testes-determining trigger is present it instructs these sex-determining genes to start playing in the key of T for testes. If SRY is absent they'll play in the key of O for ovary. For a long time geneticists assumed these must be two entirely separate linear pathways, one for males (triggered by SRY's presence) and the other for females (triggered by SRY's absence). But the idea that evolution would produce such a tidy binary solution for sex proved to be woefully naive.

This is where sex becomes fabulously complicated. Aside from SRY, this orchestra of sixty sex-determining genes is basically the same in males and females. These genes have the ability to create either ovaries or testes, but exactly which gonad they actually produce depends on a complex network of inter-gene negotiation.

This kind of blew my mind. But Graves patiently spelt it out. 'A lot of these genes are not a "testes" gene or an "ovary" gene. They're kind of "both" genes and it depends on how many there are and which way they're driving the biochemical reactions. We're finding out all the time that some of these genes have more than one function at more than one stage.'

What's more, the two pathways – to either testes or ovaries – are neither linear nor separate. They're enmeshed. For example, some genes along the male path are needed to promote the development of the gonad in the direction of testes, whilst others are required to suppress the gonad heading in the direction of ovaries.

'It is overly simplistic to say that there's a single pathway that makes a testis, because there's also one that doesn't make an ovary

at the same time. It's a whole contradictory mess of reactions, because there are so many genes that are intermediate – inhibiting one pathway and strengthening the other. So, these two sex "pathways" are intimately linked,' Graves explained.

In an effort to clarify this complexity, Graves sent me an animation of a crazy machine with dozens of interconnected ratchets and cogs all whirring around with little blue balls pinging in between them, and occasionally being squashed and recreated. The passage of the blue balls through this jumbled mess is her idea of how these purportedly neat binary sex-determination pathways really work.

This interconnected chaos of androgynous genes explains the plasticity of sex. Subtle tweaks in the expression of any of the interwoven cogs will produce novel variations – the grit that drives evolution forward and allows animals to adapt and exploit challenging new environments.

The female mole we met at the start of this chapter provides a handy illustration. A global consortium of scientists recently sequenced the entire genome of the Iberian mole, *Talpa occidentalis*. They compared the code with other mammals and found no differences in the protein products of the genes involved in sex determination. They did however discover mutations that altered the *regulation* of two of the sex-determination genes. These enabled a gene that's vital for developing testes to remain switched on in the female, as opposed to being inhibited. This accounts for the swollen section of testicular tissue in the sow's ovaries. In addition, another gene that codes for an enzyme involved in the production of androgens had two extra copies, increasing the female mole's testosterone output and allowing her to exploit the benefits of 'adaptive intersexuality'.

There is further variation still. SRY, the genetic trigger for this orchestra of sixty sex-determination genes, is not the universal master switch for sex across the animal kingdom, or even amongst all mammals for that matter.

Enter the platypus. This egg-laying mammal from Australia

specializes in being contrary, and its sex chromosomes are no different. Graves was part of the team that discovered how the platypus has five pairs of sex chromosomes. Females are XXXXXXXXXX and males XXXXXYYYYY. Despite this extravagance of Y chromosomes there is no sign of the SRY master switch on any of them.

'It was a shock,' Graves recalled.

The platypus is an ancient mammal whose group, the monotremes, diverged from humans some 166 million years ago. Its quirky sex chromosomes provided Graves with valuable insights into the evolution of sex chromosomes, and the shaky future of the Y.

The orchestra of sex-determining genes in the platypus, it transpires, is basically the same as it is in other mammals. Graves has discovered that these sixty or so genes are, in fact, remarkably conserved across all vertebrates. Birds, reptiles, amphibians and fish all have more or less the same set of genes as mammals for creating a testis or an ovary. What differs, however, is the master switch that kicks off the pathways. In the platypus this turned out to be one of the genes that's in the orchestra and has stepped up to the front to trigger the whole sex-determination process.

'SRY is just one way of kicking off the pathway, but you can do it by really almost any one of these sex-determining genes,' Graves explained, blowing my mind just a little bit more. 'That is the weirdest thing about sex. There are so many ways of doing it and they look to be quite different, but they're actually not. They all have to do with this pathway of sixty genes. So, the pathways are similar. But it's a completely different trigger.'

The platypus genome also revealed something else to Graves: the Y chromosome is losing genetic material. This runt of a chromosome is actually shrinking. Graves looked at how the platypus Y was different to the human Y and calculated how much genetic material had been lost in the time since our species diverged. This enabled her to estimate how long it might be before the human Y chromosome disappeared completely.

'It turned out the human Y was losing about ten genes per

million years, and there's only forty-five genes left. So it doesn't take Einstein to figure out at that rate we're going to lose the entire Y chromosome in four and a half million years.'

Certain high-profile geneticists, notably men, found the news that their 'male' chromosome was on a withering path to extinction rather hard to swallow.

'I thought it was hilarious. But David Page [eminent professor of genetics at MIT who contests Graves's prediction] did not think it was hilarious. He was apparently attacked by feminists saying, "Hey, you're all washed up!" To this day there is still that sort of crinkly animosity about the whole idea. And his desperate attempt to save the Y chromosome and show how terribly stable it is. Whereas I think, what does it matter?'

Graves is confident her gloomy prophecy won't spell the end of mankind. She's certain that the human male would simply evolve a fresh genetic trigger for his gonads. Other mammals have already done so. A spiny rat from Japan (*Tokudaia osimensis*) and a Transcaucasian mole vole (*Ellobius lutescens*) are just two species of mammal known to have completely lost their Y chromosomes, yet hung on to their testicles. Both males and females have a solitary X chromosome and sexual development is triggered by an entirely different, and as yet unidentified, master sex-determining gene.

Fresh chromosomal oddities are turning up all the time amongst obscure little brown rodents. In South America there are nine species of vole from the genus *Akodon* in which a quarter of females are XY, not XX. Their Y chromosome is complete with SRY, yet they still develop ovaries and produce viable eggs, suggesting they must have an entirely new master switch gene that can suppress the bossy SRY.

These peculiar rodents with their perverse sex chromosomes appear to be an evolutionary botch job. And Graves agrees: they basically are.

'If you or I were designing a creature, we would never come up with something that stupid,' she explained. 'But that's what

evolution came up with. And the only way you can explain it is that it evolved from another system and it had advantages. Even if we don't know what those advantages are.'

Now in her eighties, Graves has spent her career investigating the evolutionary genetics of sex in an astonishing array of animals, and still fizzes with enthusiasm for her subject. She's now 'sliding back the evolutionary scale' and studying ancient creatures like the lancelet, *Amphioxus* – a primitive fish with no backbone – and even nematode worms. And, to her amazement, she keeps finding the same old genes cropping up in similar sex-determining pathways, albeit with different triggers. 'These genes have been hanging around for a long time. They've been doing something about sex, not necessarily the same thing, but they're there. I find that quite hair-raising,' she professed, her eyes glinting.

Sex is a master at reinventing itself. It has to be. It is essential in order for sexually reproducing species to persist, after all. This anarchy of common genes may have once been more logical and linear, hundreds of millions of years ago at the start of sex. But eons of evolutionary time have left their mark, creating an extraordinary array of apparently nonsensical, yet somehow functional, botched systems in this ever-evolving sex-defining chaos.

'Nothing makes sense, except in the light of evolution,' Graves offered, wisely, quoting the infamous words of Theodosius Dobzhansky, father of Physiological Ecology. 'You have to get over the idea that this was meant to be. Nothing is meant to be. We're all being buffeted by the forces of evolution all the time.'

The confusion of sex chromosomes seen in mammals is just the tip of the iceberg when it comes to the bewildering diversity of systems that exist in nature. For a start, not all sex determination follows the genetic XY system. Birds, a number of reptiles, and butterflies have much the same sex-determining genes, but on different sex chromosomes – a big Z and a withered W. In this system the reverse pattern is the norm – females are ZW and males are ZZ. In this

alternative ZW system the master switch gene may be highly conserved, as SRY is in the majority of mammals, or vary between closely related groups.

In some reptiles, fish and amphibians, sexual differentiation might not be triggered by a master sex-determining gene at all but instead stimulated by an external factor. Turtles, for instance, haul themselves out of the sea to bury their eggs in the sand on tropical beaches. Eggs incubating above 87.8 degrees Fahrenheit will activate genes to create ovaries, whereas those below 81.86 will make testes. Temperatures that fluctuate between the two extremes produce a mixture of male and female baby turtles.

Heat is just one of several known external sex-determination stimuli. Exposure to sunlight, parasitic infections, pH levels, salinity, water quality, nutrition, oxygen pressure, population density and social circumstance – how many of the opposite sex are in your neighbourhood – can all influence an animal's sexual fate.

In some animals sex determination can be controlled by any, or indeed many, of the above. Which means sex can get very confusing indeed if, for example, you are a frog.

Nicolas Rodrigues might just have the best job in the world. He spends spring in the Swiss Alps hanging about high-altitude ponds surrounded by snow-capped mountains and verdant pastures scattered with wild flowers and the occasional goat herd – an idyll straight out of *Heidi*. This evolutionary biologist's job is to catch frogs: tiny baby common frogs, *Rana temporaria*, that have just metamorphosed and are graduating from their pond nursery to an adult life on land. Sometimes he has to wait for days and just drink in the view until, all of a sudden, an army of the little hoppers emerges en masse and it's time to get busy with his net.

If he ever needs an assistant, I'm his woman. I spent some of the happiest days of my childhood catching common frogs in a pond a few fields from my parents' house. Like Rodrigues, I was fascinated by the cute little metamorphs bouncing out of the pond. To me they

represented the pioneering evolutionary explorers that forged the great leap from water to land some 400 million years ago. Inside the bodies of these emerging froglets an almighty upheaval of tissue and organ reconfiguration means they must switch to obtaining their oxygen by breathing air through budding lungs, rather than filtering it out of water using gills. Many would emerge still clutching a souvenir of their aquatic youth in the form of the unabsorbed tip of tadpole tail, suggesting to me they might also be exiting the pond with their vital air sacs a touch undercooked.

It turns out these adolescent amphibians were more liminal than I could have imagined. Around half of the froglets I caught would also have been in the throes of another major organ change – their ovaries would be switching to testes as they transitioned from life as an aquatic female tadpole to that of a terrestrial male frog.

Sexual differentiation isn't exactly a watertight process if you're a common frog. In fact, according to Rodrigues, it's more than a bit 'leaky'. He's part of a team that has discovered the master switch for these frogs to develop testes rather than ovaries is sometimes genetic, sometimes environmental, sometimes a bit of both. It all depends on where the frogs are from.

The common frog is widespread throughout Europe, from Spain to Norway. These familiar little brown amphibians are all the same species but according to Rodrigues they fall into three different 'sex races' depending on their mode of sex determination.

Common frogs from the northernmost parts of their range have the familiar XY genetic sex determination and develop as one would expect – XY individuals grow testes and XX develop ovaries.

The frogs I caught as a kid were in the southern range and their sex is a little more fluid. All tadpoles are XX and develop as females. But as they emerge from the pond, around half of these genetic females reverse their sexual development. Their ovaries transform into testes and they become XX males.

Switching sex might seem like a big deal, but frogs do it without batting an eyelid (or rather, I should say 'eyelids', since they are in possession of three for each eye). The underlying mechanism isn't

fully understood but is thought to be temperature-related. In the laboratory, frogs have been encouraged to change sex from male to female by exposure to chemicals that mimic oestrogen. These are found in herbicides like Atrazine, popular with lawn-growers in the USA whose liberal use of them forces male frogs to switch sex and become female.

The frogs in the middle range are intermediates in every way. Some males have their sex governed by temperature and start out with ovaries; others are triggered by sex-determining genes. As a result, some frogs are regular XY males and XX females but Rodrigues has also documented XY females and XX males. Externally these frogs appear to be either male or female, but their gonads tell a different story. Some have a blend of ovarian and testicular tissue, which makes marshalling their sex into one of two neat buckets all but impossible.

'There is a continuum between male and female at the gonadal level and at the genetic level, but if you go to a random pond and catch a random frog it will still look like either a male or female,' Rodrigues told me.

It would be easy to dismiss this sexual mishmash as the glitches of an imperfect, less-evolved system of sex determination. Many scientists have. But that's a primitive, mammal-centric viewpoint. This extraordinary plasticity is now understood to persist in a range of reptiles, fish and amphibians. It's persevered for hundreds of millions of years across diverse species, which suggests there must be some evolutionary benefit.

A recent study on central bearded dragons (*Pogona vitticeps*), an Australian desert reptile with an impressive spiky neck, gave clues to this benefit. Researchers discovered that the combination of environmentally triggered sex reversal and genetic sex determination has the power to create two distinct types of female.

Most bearded dragons have genetic sex determination – females develop from ZW sex chromosomes, and males from ZZ. But this genetic sex-determination system can be overridden by excessive heat. If during development a clutch of ZZ male eggs gets baked by too

much Australian sun, the high temperature overrides their chromosomal sex and ZZ males switch sex to female.

These sex-changed ZZ females have a unique constellation of male-like and female-like physical and personality traits. They lay twice as many eggs, yet their behaviour is more in line with male dragons – they're bolder, more active and their temperature is higher. This novel variation allows genetic or sex-reversed female dragons to respond differently to a more diverse range of environmental pressures, giving them an evolutionary advantage.

The researchers behind the study noted that although the dragons' gonads may be female, their behaviour and morphology are more masculine, leading them to propose that these sex-reversed super-charged dragons should perhaps be considered a separate third sex – one which could offer the species distinct fitness advantages. Rather than being seen as 'an aberration', this hotchpotch of sex-determination systems and the resulting sex-reversed females could, in fact, be a powerful driver of evolutionary change.

These sex-reversed dragons, with their mixture of female gonads and male behaviours, also throw a spanner in the Organizational Concept. Their 'male-like' brain appears to be driven by their inherent genetic make-up, rather than the cascade of hormonal changes initiated by sex determination. They are not alone. In the last few decades, research into other sexually ambiguous animals has challenged this universal paradigm of sexual differentiation and begun to reveal the extraordinary complexity of sex and its expression in gonads, bodies and brains across the animal kingdom.

In 2008, a retired high school teacher named Robert Motz was staring out the window into his backyard when he spotted a rather curious bird. One side of the bird's body was covered in striking scarlet feathers and topped off with a dramatic red crest, while the other side was a dowdy buff brown. It looked as if two half birds had been glued together down the middle, and, in a way, they had.

The bird was a gynandromorph – an exceptional intersex that's split straight down the centre line. The showy red side was a male cardinal bird complete with solitary internal testicle, whereas the brown side had an ovary instead. This bilateral condition is rare but has been documented in a number of birds, butterflies, insects and crustaceans – animals all with the ZW sex-determination system. They're particularly spectacular in sexually dimorphic species like the cardinal, and arise when fertilized twin embryos fuse very early during development – between the 2-cell and 64-cell stage – to form a chimera with ZW sex chromosomes (female) on one side and ZZ (male) on the other.

These 'half-siders' offer a unique opportunity to test the authority of gonadal sex hormones in shaping brains and behaviour. Gynandromorphs may be made up of two sexes, but they share just one bloodstream, which means they're bathed in the same hormonal milieu. Is the solitary testis and its brawny androgens the supreme driver of sexual fate for the chimera's entire brain, as the Organizational Concept predicts, or could the 'passive' feminine side somehow prevail?

One of the first 'half-siders' to fall into scientific hands was discovered in a physician's poultry yard in Canada in the 1920s. Dr Schaef noticed one of his chickens looked like a hen from one side and a rooster from the other. This funky chicken's behaviour was equally confused: the cock tried to mate with the hens but also laid eggs.

Unfortunately, before the bird's brain and behaviour could be fully scrutinized the good doctor took the unconventional move of killing this valuable anomaly and roasting it for supper. Schaef donated the bones and eviscerated gonads to an anatomist friend who noted in great detail how the skeleton on one side of the bird was bigger and more cock-like, but how the chicken's ovaries, although functional, contained some testicular tissue. She imagined the mixture arose from a conflict of male and female hormones produced by the dual sex organs, but could presume no more on account of most of her study subject having been eaten by Dr Schaef.

Almost a century later Arthur Arnold, a research professor at the University of California, Los Angeles, got his hands on a zebra finch gynandromorph. He chose not to eat it, but instead eagerly examined the bird's brain. Zebra finch are songbirds, but only the males sing, so their neural circuitry is more developed than females'. This zebra finch had been observed singing, so Arnold assumed it would have a uniform 'male' brain. When he dissected the bird, however, he discovered the female side of the brain a little more masculinized than normal, but crucially the bird's song circuit had only developed on the gynandromorph's male side.

'It blew me away,' Arnold told *Scientific American* at the time. The gynandromorph's semi-female brain cast doubt on the omnipotence of gonadal steroids to differentiate sexual dimorphism in birds. In other words, this bilateral intersex bird kicked the Organizational Concept in the nuts. Here was evidence that androgens were not the exclusive force sculpting the sexuality of a bird's body, brain and behaviour. Instead the sex chromosomes, exerting their identity inside neural cells, must be playing a crucial role.

Gynandromorphs can also develop as sexual mosaics, with ZZ and ZW cells intermingled throughout the body rather than being organized as a neat bilateral hermaphrodite. A later study of three such gynandromorph chickens found that cells throughout the birds' bodies followed their own sets of genetic instructions, and were not necessarily dominated by the sex hormones to which they were exposed. So, with birds at least, the genetic sexual identity of individual cells plays a significant role in driving sexual dimorphisms in the body and brain.

'Sex is not a unitary phenomenon,' David Crews explained to me over the phone. The recently retired professor of zoology and psychology at the University of Texas should know. Crews spent forty years unpicking the mechanisms behind sexual determination and differentiation in an eclectic cast of wild animals. He's decoded the exact genes involved in gonad development in turtles,

encouraged whiptail lizards to switch sex, and monitored how incubation temperature affects not just the sex but also the sex appeal of leopard geckos.

According to Crews there are five types of sex: chromosomal, gonadal, hormonal, morphological and behavioural. They don't necessarily all agree with one another or even remain fixed for life. They are cumulative and emergent in nature, and can be influenced by genes or hormones, as well as the environment or even an animal's life experience. This plasticity allows for the huge variety in sex and sexual expression that we see both within and between species.

'Variation is the fabric of evolution. If you don't have variation you can't have an evolving system. So it's important that we have variation in sexual characteristics.'

Crews is a self-confessed free thinker whose fresh perspective comes from studying wild reptiles, birds and fish as opposed to laboratory-bred mice – the standard animal archetype for studies of sexual development. These unconventional model organisms, he tells me, are 'real' rather than simply 'realistic' – their natural instincts have not been blunted by decades of inbreeding. Their sexual development is triggered by an array of factors – genetics, temperature or environment – giving him the opportunity to look beyond the standard lab mouse model and travel back in evolutionary time to study the systems that existed before mammalian sexual development, yet formed its basis.

Crews blames the Organizational Concept for promoting a rigid deterministic view of sex, which focuses on the differences between the sexes, reinforcing the binary concept and ignoring the glorious diversity of sexual characteristics found in nature.

'It's offensive,' he spat down the phone from his home near Austin during one of our many long and fascinating chats. The standard paradigm has, in his opinion, had its day. It is mammal-centric, overly simplistic and underplays the role of oestrogen as an organizing and activating sex hormone. 'Females are just as differentiated [active] as males. I've tried to make this point several times. My

conclusion has been that the female is the ancestral sex. I think there's a lot of evidence for that.'

Crews has focused his career on studying the diversity itself and how it is actually controlled by the same mechanisms. Studying what is conserved in all this botched chaos is the key to discovering what is fundamental. This approach has enabled Crews to develop an alternative evolutionary perspective for thinking about sexual differentiation. One which is grounded in the very origin of sex.

'There is little doubt that the first creatures reproduced by cloning,' he told me. 'The earliest reproductive organism had to be able to lay eggs and that's a female.'

Crews' research estimates that 600–800 million years ago the only creatures in existence were these cloning egg-layers. Males did not arrive on the evolutionary scene until the dawn of sex, when gametes diverged in size, which Crews reckons was around 250–350 million years later. With this divergence came the need for complementary behaviours to facilitate the union of these different-sized gametes; individuals must locate one another, become sexually attracted and reproduce. So sexual dimorphisms evolved that were activated by androgens.

'Maleness evolved as an adaptation to femaleness,' Crews continued. 'When males came along what they did was to facilitate reproduction in the female. To stimulate and coordinate the neuroendocrinological processes that underlie the shedding of gametes. Males are behavioural facilitators.'

If males are the derived sex, that evolved out of the original female, it is logical to assume they must contain evolutionary traces of egg-makers. And, it turns out, they do. Crews discovered active relics of ancient femininity in the very seat of masculinity: the testes.

'We published the first photomicrographs showing that the testis is loaded with oestrogen receptors,' he told me. Oestrogen, the primary 'female' sex steroid hormone, turns out to play a fundamental role in the development of male testes and sperm.

Crews collaborated with Joe Thornton, a professor of genetics at the University of Chicago, to do some molecular time travel and

resurrect the ancestral receptor for oestrogen from an ancient mollusc. Thornton's work on this, and other primitive animals like lampreys, has subsequently shown that the oestrogen receptor is the oldest transcription factor (a protein whose job is to turn genes on or off) in vertebrates – far older than previously thought, with an origin between 600 million and 1.2 billion years ago. The genes for androgen receptors did not evolve for a further 350 million years.

'Oestrogen has to be the original steroid hormone because the ancestral animals only produced eggs, and eggs produce oestrogen,' Crews explained. 'The oestrogen receptor is important in virtually every tissue of the body. I can't think of any tissue in the body that doesn't have an oestrogen receptor.'

The Organizational Concept may have focused on the omnipotence of testosterone, but oestrogen is proving to be equally powerful. It has even been demonstrated to have the same organizing effects as testosterone in early development, with the ability, as we have seen, to cause sex reversal in frogs. Crews has also reversed the sex of developing female lizards using oestrogen blockers. Oestrogen clearly plays a fundamental role organizing both female and male sexual development but also activating sexual behaviours later in life. Not only is the 'female' sex hormone required to make testis and sperm, it is also understood to stimulate male copulatory behaviour in some species.

'The "female" sex steroid has a critical role even in males, because males were originally females,' Crews expounded.

So, in the gospel according to Crews: Eve wasn't created out of Adam's rib, it was the other way round. In the beginning there was female, and she gave rise to male. From this alternative evolutionary perspective, the ultimate answer to *what is a female* is: she's the ancestral sex. Relics of this primal egg-layer exist within all of us. Which puts a fresh spin on males getting in touch with their feminine side.