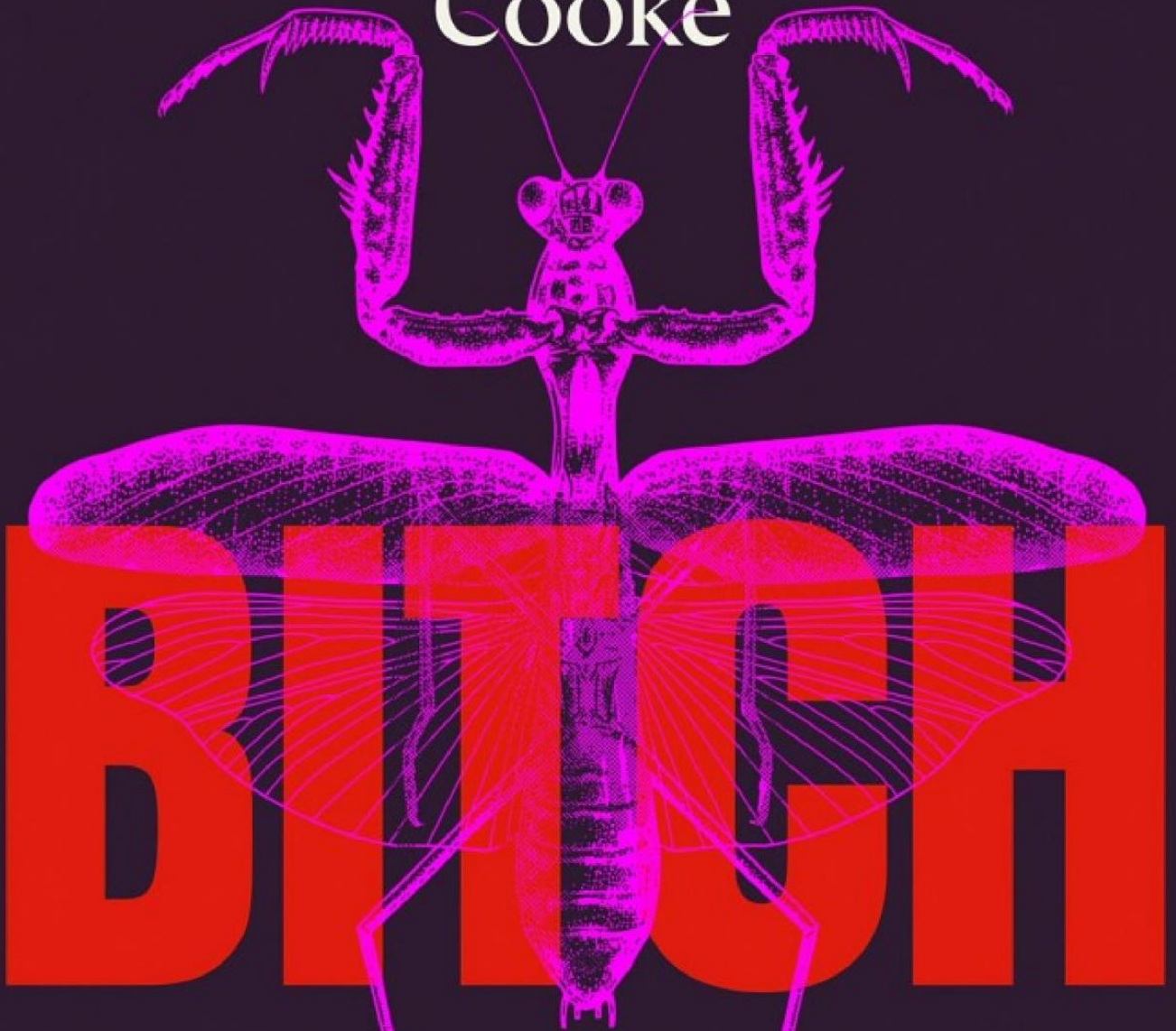


Lucy
Cooke



A revolutionary guide
to sex, evolution &
the female animal

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About the Author

Lucy Cooke is an award-winning broadcaster and documentary filmmaker with a Masters in Zoology from the University of Oxford, where she was tutored by Richard Dawkins. She has presented prime-time series for BBC, ITV and National Geographic and is a regular on Radio 4, hosting her own *Power of ...* series along with regular spots on *The Infinite Monkey Cage* and *Sue Perkins: Nature Table*. Lucy has written for the *Sunday Times*, *Telegraph*, *Mail on Sunday*, *New York Times* and *Wall Street Journal*. She is the author of two previous books, *A Little Book of Sloth*, which was a *New York Times* bestseller, and *The Unexpected Truth about Animals*, which was shortlisted for the Royal Society Insight Investment Science Book Prize and has been translated into seventeen languages.

Also by Lucy Cooke

The Power of Sloth
The Unexpected Truth About Animals

*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.



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*.¹

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.² '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.³

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.⁴ 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.⁵ 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.⁶

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.⁷ 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.^{8, 9}

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.’¹⁰

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'.¹¹ 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.¹² 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.¹³

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.'¹⁴

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'.¹⁵

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.'¹⁶

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)'¹⁷

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.¹⁸

There is no conspiracy here, just blinkered science.¹⁹ 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.²⁰ 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.²¹ 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.²²

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’.²³

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.¹

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.² And she sports an extra 'thumb'.³ 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.⁴

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.⁵

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.⁶ 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.⁷

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^{fn1},⁸ to giant African elephants, 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.⁹ 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.¹⁰

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'.¹¹ 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.¹²

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.^{fn2, 14, 15} 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.^{fn3, 16}

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,

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.²²

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'.²³ 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.

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