PART I INTRODUCTION

1

Homosexual behaviour in animals: topics, hypotheses and research trajectories

PAUL L. VASEY AND VOLKER SOMMER

A paradox for Darwinian theory?

At first glance, homosexual behaviour seems to violate a basic 'law' of nature: that of procreation. The notion that organisms exist to reproduce themselves is a staple of pre-scientific worldviews, and evolutionary theory, from its very beginnings, has also elaborated upon this idea. In a strict Darwinian view, individuals should seek to maximize reproductive success; organisms are predicted to strive to maximize the number of viable offspring and with this the representation of their own genetic information passed down to future generations.

Sexual selection is the key theoretical framework for interpreting sexual behaviour from an evolutionary perspective. Darwin described sexual selection as a process of differential reproduction that occurs because males vary in their ability to acquire female mates (that is, reproductive partners). He identified two basic mechanisms that influence mate acquisition. Mate competition occurs intra-sexually among males for females and encompasses physical fights and threats as well as ritualized displays of courtship aimed at attracting discriminating females. Mate choice occurs inter-sexually, and typically involves females selecting the most attractive male competitor. More recently, sexual coercion has been proposed as an additional mate acquistion mechanism that males can employ if they are unsuccessful at competing for, or attracting, female reproductive partners (Smuts and Smuts, 1991).

Sex differences in patterns of mate acquisition were later explained by Trivers (1972) in terms of parental investment theory. In 'typical' species, females invest more into offspring than males, since they not only gestate and lactate, but also provide most of the post-parturition care to offspring. This difference limits

their potential reproductive rate, so that, at any one time, there will be fewer fertile females than reproductively active males in a population. Thus, males are, in theory, expected to compete intra-sexually for reproductive access to females, sexually coerce females if necessary, and copulate relatively indiscriminately. Females should discriminate among potential male mates in favour of those that contribute the most to offspring quality and survival. In 'atypical' species – such as sea-horses and various birds – the roles are reversed: males provide the bulk of parental investment and are choosy about the females with which they copulate, while females compete among themselves for male mates (Gywnne, 1991).

From the perspective of sexual selection and parental investment theories, one might be left with the impression that sex is synonymous with reproduction. Parental investment theory clearly predicts that individuals should choose and compete for sexual partners that confer the greatest reproductive advantage. As such, when given a choice, reproductive sex should be preferred over non-reproductive sex. It follows that opposite-sex mates should be preferred over same-sex sexual partners, and mate competition should occur intra-sexually.

In reality, many species engage in homosexual behaviours as well. However, animals which engage in sexual interactions with members of their own sex are obviously not in immediate pursuit of reproductive goals (that is, conception). Because homosexual behaviour appears to undermine reproduction, it seems appropriate to ask why animals engage in these behaviours at all.

Earlier studies of animal behaviour tended to dismiss occurrences of same-sex sexual behaviour as mere quirks or such instances were classified as pathological manifestations. The use of caged subjects was prevalent and meant that these interactions were invariably characterized as abnormal products of captivity, unlikely to be found in 'nature'. As early as the 1700s biologists such as George Edwards (1758–64) were speculating on the causes of such behavioural 'abnormalities'. He stated that 'three or four young [bantam] cocks remaining where they could have no communication with hens . . . each endeavoured to tread his fellow, though none of them seemed willing to be trodden. Reflections on this odd circumstance hinted to me, why the natural appetites, in some of our own species, are diverted into wrong channels' (p. xxi).

Research conducted throughout the 1890s purported that an absence of opposite-sex partners and artificial confinement could 'force' individuals to choose same-sex mates. It is interesting to note that the same researchers who reported such findings showed that pigeons (*Columbia livia*) will participate in same-sex sexual interactions even if they are housed in mixed-sex groups. Moreover, some researchers even demonstrated that certain same-sex pairs stopped their homosexual activity upon being isolated from their opposite-sex group

mates. For example, Whitman (1919) stated that 'a number of pairs of mature males were isolated; some of these were observed for several months, but no real matings resulted from any of these cases'. He then went on to conclude, however, that 'confinement will thus force matings which would not otherwise occur. Pairings between like sexes are secured in this manner'. Clearly, such an interpretation is more reflective of the opinions of the observer than an objective observation of the behavioural phenomenon under investigation.

It was not long before fieldworkers, confronted with evidence of homosexual behaviour in 'nature', were integrating this perspective into their lexicon and summarily dismissing such interactions as idiosyncratic pathological manifestations or worse (for example, Mute swans: Ritchie, 1926). Studies of domestic livestock that followed asserted that the 'artificial' effects of domestication produced homosexual behaviour. The economic benefits associated with livestock reproduction may have further promoted the view that homosexual behaviour is an undesirable 'problem' (for example, domestic chickens; Guhl, 1948).

Later research in the domain of behavioural endocrinology sought a causal link between the perinatal hormonal environment and adult homosexual behaviour in a variety of species, including rodents and primates. This work, too, may have inadvertently contributed to the perspective of animal homosexual behaviour as a disordered condition (for example, Phoenix *et al.*, 1959; Pomerantz *et al.*, 1986).

Nevertheless, more and more detailed studies of animals in their natural environments made it increasingly difficult to discount all sexual interactions in animals among members of the same sex as exceptions, as idiosyncrasies, or as pathologies. Slowly, but steadily, a quite different picture emerged. A recent encyclopaedic volume by Bruce Bagemihl (1999) on animal homosexual behaviour provides evidence that hundreds of mammals, birds, reptiles, amphibians, fishes, insects, spiders and other invertebrates engage in same-sex sexual activity. Clearly, what was once thought to be an aberration appears to be a behavioural pattern that is broadly, albeit unevenly, distributed across the animal kingdom (see also Dagg, 1984; Sommer, 1990; Vasey, 1995). Indeed, within a select number of species, homosexual activity is widespread and occurs at levels that approach or sometimes even surpass heterosexual activity.

A number of excellent reviews currently exist, which explore the hormonal and neural mechanisms underlying same-sex sexual behaviour (Adkins-Regan, 1988, 1998; Adkins-Regan *et al.*, 1997; Paredes and Baum, 1997). Important insights have been gained from such research. Nevertheless, it is difficult not to conclude that same-sex sexual behaviour is aberrant when viewed through the lens of this type of invasive experimental work. Many of the animal models used in such studies do not appear to spontaneously exhibit homosexual activity as

part of their species-typical behavioural repertoires. Instead, such behaviour has to be elicited experimentally, either by destroying areas of the brain or by exposing the subjects to abnormal levels of steroid hormones perinatally. For those researchers interested in spontaneously expressed same-sex sexual behaviour, the information gleaned from such studies may be limiting. Reflecting on this research emphasis, Adkins-Regan (1988) stated that more studies of same-sex sexual behaviour in intact, untreated animals are needed.

Nevertheless, to date, there has been a relative paucity of research on the evolutionary aspects of homosexual behaviour in intact, untreated animals. Moreover, locating the information that does exist has not always been an easy task, for it is often scattered throughout obscure journals, technical reports and unpublished dissertations, or as Bagemihl has noted 'buried even further under out-dated value judgments and cryptic terminology' (1999, p. 87). The current volume seeks to address this gap in our knowledge by exploring the extent to which homosexual behaviour in animals can be understood from an evolutionary perspective. Why does such behaviour persist when it appears to conflict with an individual's reproductive imperative and, as such, flout the expectations of a Darwinian world view?

An evolutionary perspective on the topic of animal homosexual behaviour was first articulated in a landmark paper by the ethologist Wolfgang Wickler (1967), who suggested that homosexual behaviour in animals served some adaptive social function. He proposed that same-sex mounting was a ritualized gesture that individuals used to communicate about their dominance relationships. Wickler saw mounting as an expression of dominance, while allowing oneself to be mounted expressed subordinate status *vis-à-vis* the mounter. He reasoned that same-sex mounting commonly occurred in response to incipient aggression because it reduced the chances of escalated fighting by reiterating the dominance status quo. Wickler termed such behaviours which were sexual in form, but which served some social function, 'socio-sexual'. The concept of socio-sexual behaviour is significant because – although Wickler never explicitly stated it as such – it suggested a possible adaptive basis for homosexual behaviour.

The adaptionist perspective was greatly stimulated by the emergence of sociobiology in the years preceding and following the publication of Edward O. Wilson's (1975) book *Sociobiology: The New Synthesis*. Sociobiology aims to understand the evolutionary forces that shape social behaviour in animals, including humans. This paradigm shift also resulted in an alternative view of homosexual behaviour. Namely, this type of behaviour was no longer seen as an abnormality, but rather, a product of evolutionary processes and explicable in adaptive terms. For example, Wilson (1975) suggested that homosexual behaviour might be maintained in the population because the actors, while foregoing direct reproduction,

would help their kin reproduce and in doing so reproduce indirectly any genes they shared with those kin (also see Weinrich, 1980; Ruse, 1981). The sociobiological perspective generated a number of adaptive hypotheses for homosexual behaviour, but was much less successful in establishing supporting evidence in either humans or animals (Wilson, 1975; Kirsch and Rodman, 1982; Ruse, 1988; Dickemann, 1993; Kirkpatrick, 2000). Despite this shortcoming, the wave of adaptationist thinking brought on with the emergence of sociobiology provided an important stimulus for ethologists to explore additional socio-sexual functions for homosexual behaviour in animals, and we describe some of these in greater detail below.

Early on in this project, we decided we would not attempt to cover all taxa in the animal kingdom. Bruce Bagemihl aimed for, and achieved, a much broader degree of comprehensiveness in his book, *Biological Exuberance: Animal Homosexuality and Natural Diversity* (1999). His compilation made it clear, however, that the evidence for homosexual behaviour in animals is overwhelmingly sketchy and anecdotal.

A number of reasons might account for the paucity of research on this topic. The most often-cited rationale as to why so little research is conducted in this area is that researchers are apprehensive about homophobic reactions (Wolfe, 1991; Bagemihl, 1999). Some researchers might fear being correctly, or mistakenly, labelled as gay or lesbian. Others imagine that their careers will be negatively impacted if their names become associated with this sort of subject matter. Linda Wolfe (1991, p. 130) reports that 'several (anonymous at their request) primatologists . . . have told me that they have observed both male and female homosexual behaviour during field studies. They seemed reluctant to publish their data, however . . . because they feared homophobic reactions ('my colleagues might think that I am gay').' She concludes: 'If anthropologists and primatologists are to gain a complete understanding of primate sexuality, they must cease to allow the folk model (with its accompanying homophobia) to guide what they see and report' (Wolfe, 1984, p. 130).

It is possible, however, that more theoretically motivated considerations dissuade the majority of researchers from ever undertaking research on homosexual behaviour in animals. If, for example, reproduction is the engine that drives evolution, then some investigators working on issues pertaining to the evolution of behaviour, particularly sexual behaviour, might reason that non-reproductive modes of sexuality, such as homosexual activity, are biologically irrelevant. Moreover, it is possible that scientists simply lack a theoretical framework for interpreting homosexual behaviour in animals and, as such, avoid studying the phenomenon because they 'don't know what it means' (Wolfe, 1984, p. 130).

Finally, the lack of research on this topic may be because, despite media hype and the claims of some researchers, relatively few species habitually engage in homosexual behaviour. One can hardly be expected to undertake a research project (let alone an entire research program that spans one's career) aimed at studying a particular behaviour if doing so necessitates observing the study species for hundreds of hours before a single instance of the behaviour is observed. No funding agency would support such work and no investigator would be able to sustain such a research agenda. Thus, most studies on homosexual behaviour are generated in conjunction with, or as a sideline to, research on other topics.

Here, we examine the extent to which prevailing evolutionary approaches to this subject are sufficient by concentrating on species that engage in homosexual activity on a routine basis. All of the current contributors were struck by the frequency of same-sex sexual interactions exhibited by their study species and were thus able to accumulate relatively large sets of data that lend themselves to quantitative analyses. The chapters contained in this volume are therefore unique in that they were written by a small group scientists who have enough data at hand so that they could test some of the current theories about the functions and evolutionary history of homosexual behaviour in animals.

The first half of the volume includes contributions about birds (Chapter 2, Kotrschal, Hemetsberger and Weiss: *geese*; Chapter 3, King: *flamingos*), cetaceans (Chapter 4, Mann: *bottle-nosed dolphins*), ungulates (Chapter 5, Vervaecke and Roden: *bison*; Chapter 6, Bartoš and Holečková: *deer*) and carnivores (Chapter 7, Yamane: *feral cats*). The second half focuses on primates such as Old World monkeys (Chapter 8, Vasey: *Japanese macaques*; Chapter 9, Kapsalis and Johnson: *rhesus macaques*; Chapter 10, Sommer, Schauer and Kyriazis: *langur monkeys*) and apes (Chapter 11, Yamagiwa: *mountain gorillas*; Chapter 12, Fruth and Hohmann: *bonobos*). The bias towards primates is due to the fact that homosexual behaviour has been reported more often in this order of mammals. At present, it is unclear whether this reflects a true phylogenetic difference in the frequency with which homosexual behaviour is expressed.

Because we are committed to a broad comparative perspective on the topic of homosexual activity, this volume also includes a chapter on the human 'animal' (Chapter 13, Werner). It is our conviction that evolutionary treatises should not be 'homocentric' in that they either focus on humans, while excluding a comparison with other animals, or that they focus on animals, while excluding our species, *Homo sapiens*. Such boundaries, when maintained for reasons of orthodoxy and dogmatism, are meaningless and counterproductive to scientific understanding – a point which we will reiterate below. Of course, humans are unique

and the behaviour of humans does, therefore, require unique explanations – but so does the behaviour of bottlenose dolphins and bisons. Darwinian theory, unlike anthropocentric philosophies, recognizes the need to identify the unique characteristics of a taxon, while not ignoring the many similarities with other organisms that are likely to exist.

Finally, we include a brief discussion of recommendations for future research trajectories in a field that is clearly still in its infancy (Chapter 14, Vasey).

Even a strictly scientific treatment of the topic is likely to become an issue of moral and political debate. It would be disingenuous to suggest that this research has no sociopolitical implications for humans because animals are often used as a gauge for measuring what constitutes 'natural' versus 'unnatural' behaviour worthy of legal protection or persecution (Boswell, 1980; Weinrich, 1980; Haraway, 1989; Sommer, 1990; Travis and Yeager, 1991). We therefore dose the volume with a brief essay on how comparisons of human homosexuality and animal homosexual behaviour have been used and abused throughout the centuries (Chapter 15, Sommer).

Defining 'homosexual behaviour' in animals

Any useful discussion of homosexual behaviour in animals requires an explicit statement concerning what counts as 'sexual behaviour'. For the purposes of this volume, an ethological definition of sexual behaviour is needed that can be easily operationalized. As such, sexual behaviour is defined as including courtship displays (or sexual solicitations), mounting, and any interaction involving genital contact between one individual and another. Although stimulation of the genitals or other erogenous zones can result in orgasm, orgasmic response is not a necessary criterion for labeling a behaviour as sexual, nor is penetration.

Other definitions of sexual behaviour are much broader than the one we employ in this paper. For example, Bagemihl (1999) characterizes sexual behaviour in terms of five sweeping categories that include courtship, affection, interactions involving mounting and genital contact, pair bonding and parenting activities. Our concern with such an approach is that by casting the net too widely, there is a risk of including social interactions under the rubric of sexual behaviour. This, in turn, could result in interactions with particular social partners being labeled as sexual behaviour. This is not to say that relationships such as pair living, or affectionate behaviours such as kissing, cannot be sexual. However, labeling them as such typically occurs because they exist in close temporal association with courtship displays, mounting or genital contact. In the absence of such sexual markers, the sexual or social character of a particular behaviour

is often open for debate. Clearly, this conservative definition of sexual behaviour risks excluding potential examples of sexual activity and some researchers will find it decidedly narrow. Nevertheless, a much stronger case can be made that those behaviours that are consistent with the definition we present here are, indeed, sexual.

The subjectivity involved in defining *homo*sexual behaviour according to context, function and motivation has been repeatedly called into question and criticized as ignoring the multifaceted nature of these interactions (Hanby, 1974; Reinhardt *et al.*, 1986; Srivastava *et al.*, 1991). For the purposes of this volume then, homosexual behaviour refers to courtship displays, mounting and/or genital contact and stimulation between same-sex individuals. Thus, homosexual behaviour or activity refers to discrete acts or interactions. As such, this term does not imply some sort of life-long pattern of homosexual activity or exclusivity, nor does it denote any particular form of enduring sexual relationship, monogamous or otherwise.

It deserves to be stressed that homosexual behaviour is not and should not, be taken as synonymous with sexual orientation, sexual orientation identity, sexual partner preference or categories of sexual beings.

- *Sexual orientation* (for example, heterosexuality, homosexuality, bisexuality, autosexuality, asexuality) refers to an individual's overall pattern of sexual attraction and arousal (or lack thereof) during some defined time period (for example, adolescence, adulthood, the previous year). Typically, this pattern is characterized by multiple parameters, including sexual solicitations, actual sexual contact and genital blood flow. In humans, sexual fantasy is often used to characterize sexual orientation as well, but researchers studying animals have no means by which to assess sexual fantasy in their subjects, assuming that such a phenomenon exists.
- *Sexual orientation identity* refers to the sexual orientation that an individual considers themselves to have (Cass, 1983/84). This may or may not dovetail with the various parameters that characterize an individual's sexual orientation. With the exception of the great apes, evidence for self-recognition in animals is weak (Tomasello and Call, 1997). As such, there is no reason to expect that animals would develop personal identities based on some introspective sense of sexual orientation.
- *Sexual partner preference* refers to an individual's predilection for sexual partners of one sex, or the other, or both, when given a choice (Vasey, 2002).