Autosexual Behaviour in Primates:

Form, Phylogeny and Function

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STATEMENT OF ORIGINALITY

I, Matilda-jane Brindle, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

[redacted]

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ABSTRACT

Autosexual behaviour, or masturbation, occurs throughout the animal kingdom, but appears to be particularly prevalent in the primates. However, the fitness benefits of this solitary behaviour are unclear and its evolutionary significance has not yet been comprehensively studied, although various hypotheses have been proposed (Chapter 01). In this thesis, I conduct the first systematic, comparative study into this common sexual behaviour. I began by compiling and categorising the scattered published information on primate masturbation, for both females and males, supplementing this with questionnaire responses (Chapter 02). The resulting database consisted of nearly 400 sources, covering 105/281 species (37.4 %), 54/68 genera (79.4 %) and 18/19 (sub)families (94.7 %). I then investigated the natural history of masturbation across the primate order, highlighting the distribution and diverse forms the behaviour takes (Chapter 03). I found masturbation was present in females of 19/45 genera (42.2 %) and in males of 36/51 genera (70.6 %). The most targeted body parts were the genitals, most frequently stimulated by the hands and fingers, and masturbation occurred in wild-living as well as captive individuals, indicating this behaviour is not a pathological outcome of captivity. Next, I examined the evolutionary history of masturbation for the first time, using a Bayesian phylogenetic approach to reconstruct its ancestral state at eight key nodes (Chapter 04). Although the occurrence of this behaviour in early primate evolution was equivocal, masturbation was consistently present in the ancestor of all platyrrhines and catarrhines, and appears to have been retained at all subsequent nodes with varying probabilities. Finally, I employed Bayesian phylogenetic methods to test adaptive hypotheses about masturbation (Chapter 05). I found that masturbation in males tended to occur in species exhibiting a multi-male mating system, larger testes, and a higher pathogen load, while masturbation

in females tended to occur only in species with large testes. These findings support both the Postcopulatory Selection Hypothesis, in females and males, and the Pathogen Avoidance Hypothesis, in males. Together, the results of this research will help to increase our understanding of a very common, but little understood, behaviour (Chapter 06).

IMPACT STATEMENT

This project will substantially enhance our limited understanding of the distribution, form, evolution and function of autosexual behaviour, or masturbation: a common sexual behaviour that is present, not just in humans, but in other primates and across the wider animal kingdom.

Autosexual behaviour has not yet been systematically examined within a comparative framework, in either female or male primates, and this research therefore defines a novel area of study. The results presented here will provide a crucial starting point for future investigations on masturbation in other animals, highlighting key avenues of enquiry.

In terms of academic output, this thesis provides the material for several research papers, which are currently in preparation. I have also been awarded a Leakey Foundation Research Grant to conduct fieldwork that will further test some of the hypotheses presented here. I have given several invited talks on this research, for both academic and general audiences. This topic is inherently likely to attract non-academic interest, and thus provides an excellent opportunity for public engagement.

The findings of this study, that masturbation is ubiquitous throughout the primate order, practiced by captive and wild-living members of both sexes, and all age-groups, is a strong counter-argument to those who condemn human masturbation as ‘unnatural’ or wrong. Thus, the project will have broader implications related to societal health and wellbeing, in terms of helping to negate damaging attitudes towards a healthy sexual behaviour.

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CHAPTER 01

GENERAL INTRODUCTION

1.1 Introduction

This chapter first surveys autosexual behaviour across the animal kingdom (section 1.2) before briefly introducing the primate order (section 1.3). Next, I provide a brief cultural history of masturbation, exploring the major paradigms within which it has been conceptualised by humans (section 1.4). Following this, I describe the key analytical framework within which autosexuality will be examined (section 1.5), before examining previous attempts to understand masturbation (1.6). Finally, I describe the key aims of this thesis (section 1.7). This chapter provides the foundation for my examination of the form, phylogeny, and function of primate masturbation. Chapter 02 develops a clear, working definition of masturbation, before outlining the compilation of a large-scale, comparative database of masturbation across the primate order. Chapter 03 maps the presence and absence of primate masturbation, before reviewing its forms and context, while Chapter 04 examines the evolutionary history of masturbation. Finally, Chapter 05 examines potential adaptive functions of masturbation. A concluding discussion is provided in Chapter 06.

1.2 Masturbation across the animal kingdom

Masturbation is prevalent across the animal kingdom, in both females and males, appearing in a plethora of forms. Penguins (*Pygoscelis adeliae.;* Russell, Sladen, & Ainley, 2012), little auks (*Alle alle;* Jakubas & Wojczulanis-Jakubas, 2008), tortoises (*Geochelone sulcate*; Ritz et al., 2010), iguanas (*Amblyrhynchus cristatus;* Wikelski & Bäurle, 1996), elephants (*Loxodonta* *spp.;* Ellis, 1902; Ford & Beach, 1951; Jainudeen, Katongole, & Short, 1972), rats (*Rattus spp.;* Ford & Beach, 1951; Kihlström, 1966), ground squirrels (*Xerus inauris;* Waterman, 2010), porcupines (*Erethizon dorsatum;* Shadle, 1946), otters (*Lutra lutra;* Capber, 2007), dogs (*Canis lupus familiaris;* Ellis, 1902), cats (*Felis catus;* Ellis, 1902), lions (*Panthera leo;* Bagemihl, 1999), hyenas (*Crocuta Crocuta;* Bagemihl, 1999) bears (*Ursus arctos;* Ellis, 1902; Ishikawa et al., 2003), rhinoceroses (*Dicerorhinus sumatrensis*; Zahari et al., 2005), horses (*Equus caballus;* Ellis, 1902; McDonnell, 1991), zebra (*Equus quagga;* Bagemihl, 1999), deer (*Cervus elaphus;* Darling, 1937; Ellis, 1902; Ford & Beach, 1951), boars (*Sus scrofa;* Glossop, 1987), warthogs (*Phacochoerus spp.*; Ellis, 1902), goats (*Capra aegagrus hircus*; Ellis, 1902), sheep (*Ovis spp.;* Ellis, 1902), camels (*Camelus spp.;* Ellis, 1902; Tinson, Kuhad, Singh, & Al-Masri, 2000), dolphins (*Delphinus spp.;* Chen et al., 2001; McBride & Hebb, 1948), walruses (*Odobenus rosmarus;* McCord et al, 2016), and bats (*Desmodus rotundus;* Greenhall, 1965) – to name but a few – have all been observed to masturbate.

Masturbation may occur by hand, paw, foot, flipper, tail, or mouth. Where animals are unable to reach their genitals with prehensile appendages, masturbatory techniques may be more inventive. For example, many male ungulates and elephants stimulate the penis by 'bouncing' it upwards so that it slaps against the stomach (Figure 01.01; Bagemihl, 1999; McDonnell, 1991). Other animals may seek inanimate objects as stimulation devices. Many birds masturbate by mounting vegetation, rocks, or mounds of earth (Bagemihl, 1999), as exemplified by male Adélie penguins who may – in lieu of copulating with a female – "*assume the attitude and go through the motions characteristic of the sexual act, in some cases actually ejecting their semen on to the ground*" (Russell et al., 2012, pp. 392). In fact, the sexual behaviour of male Adélie penguins – which also includes necrophilia, sexual coercion, and sexual abuse of chicks – was considered so depraved by Dr Levick, who observed these "*hooligan cocks*" during the British Antarctic (Terra Nova) Expedition of 1910, that he wrote his observations in code, lamenting that "*there seems to be no crime too low for these Penguins*" (Russell et al., 2012, pp. 389).

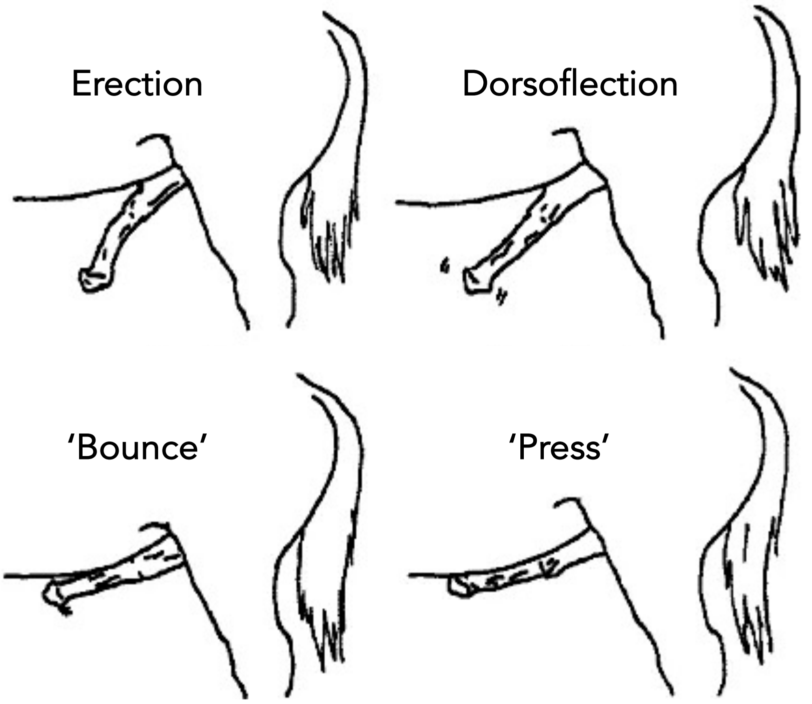

Figure 01.01. Characteristic masturbatory techniques in equids. Figure adapted from McDonnell (1991)

1.3 Why study primates?

Of all animals, however, the primates are perhaps the most commonly known to masturbate, and are even immortalised in the slang term 'spanking the monkey'. Primates constitute their own taxonomic order of mammals and range in size from around 60g in mouse lemurs (*Microcebus murinus*) to over

170 kg in male gorillas (*Gorilla gorilla*; Smith & Jungers, 1997). Primates arose 84–55 million years ago from small animals adapted to a life in trees (O'Leary et al., 2013; Pozzi et al., 2014). Primate morphology reflects this ancient arboreality, even in taxa such as baboons or humans, who have reverted to largely ground-dwelling lifestyles. Thus, despite numerous specializations, the need for safe grasping and navigation in trees is reflected in traits such as pentadactyly (hands and feet with five digits), flat nails, tactile pads at the terminal portion of digits, stereopsis (perception of depth and 3D-structure via binocularity, i.e. overlapping fields of vision), and, in many but not all primates, a tail. Non-human primates, therefore, have largely the same body parts at their disposal to use for masturbation as humans.

Extant (living) primates can be divided into two major clades. The 'wet-nosed' primates (*strepsirrhines*) possess a rhinarium – a furless, moist skin surface surrounding the openings of the nostrils – which enhances the sense of smell and is often associated with a nocturnal lifestyle. Strepsirrhines include lorises and galagos in South Asia and Africa (e.g., slender lorises, slow lorises, bush babies) and the lemurs of Madagascar (e.g., aye-ayes, sifakas, indris, ring-tailed lemurs). 'Dry-nosed' primates (*haplorrhines*) lack a rhinarium and are mostly active during the day. They include three major clades: the small-bodied tarsiers of Southeast Asia, the monkeys of Eurasia and Africa (e.g., langurs, macaques, baboons, and apes), and the monkeys of the Americas (e.g. marmosets, tamarins, spider- and capuchin monkeys). The apes include two groups: the small apes of South Asia (gibbons, siamangs) and the big apes of Southeast Asia (orangutans) and Africa (gorillas, chimpanzees, bonobos – as well as humans, who have spread around the globe).

However, despite shared common characteristics, primates represent a 'generalised' order, given their often unspecialised morphology and flexible behaviour. Even members of the same species may show distinctly different habits. For these reasons, primates can be characterised as being specialised in non-specialisation.

Primates are agile animals, which allows for a variety of masturbatory forms via the differential use of body parts and techniques. Their extremities encompass considerable prehensility, reflecting the selection pressures of arboreality and their digits can be moved independently which, in taxa such as apes, involves an opposable thumb. Enabled by such morphological versatility, several primate species are tool users (Shumaker et al., 2011) – an ability that allows for even greater diversity in masturbatory techniques. In addition, most non-apes possess a tail. In some platyrrhines, this appendage possesses its own grasping ability.

Primates, closely followed by carnivores, are one of the most well-studied orders of the mammalian class, which itself has benefited from significant taxonomic bias in terms of research effort (Troudet et al., 2017). Indeed, primates and carnivores outnumber all other mammals in taxonomically defined studies (Verde Arregoitia, 2016), and comprise over half of all 'flagship' species for conservation campaigns (Smith et al., 2012). This taxonomic bias, albeit problematic in many ways, makes primates an ideal group to study, since it increases the potential data sources within which to find a relatively rare behaviour.

1.4 The major paradigms: a brief history

1.4.1 Masturbation in antiquity

References to masturbation are found throughout human history. A Neolithic clay figurine found in the Hagar Qim caves in Malta depicts a woman masturbating (Taylor, 1996). In Sumerian mythology, in order to fill the parched Euphrates and Tigris rivers with life-giving water, the youthful and virile deity, Enki "*stood up full of lust like an attacking bull, lifted his penis, ejaculated*" (Leick, 2003, p. 24). On an even grander scale, in Ancient Egyptian mythology, Atum created the universe by masturbating, triumphantly proclaiming "*I created my own every being. My fist became my spouse. I copulated with my hand*" (Alford, 2010; Chrystal, 2018, p. 165). While the annual flooding of the Nile River was believed to occur when the god Hapy masturbated (Elia, 1987). In a more depraved Ancient Egyptian myth, Set wrought revenge on his brother, Horus, by masturbating into a jar and pouring the semen over the lettuce growing in his garden, which Horus later ate (Elia, 1987).

Masturbation was a relatively unimportant topic to the Ancient Greeks and Romans, because it was not equated to any particular moral wrongdoing. In Ancient Greece, masturbation was considered a normal aspect of sexuality, if a little uncouth, as exemplified in an insulting diatribe by the Greek writer Lucian that states "*Surely […] you don't mean that notable Dion, that lusty, low-scrotumed, cuntish, and mastic-chewing youth who masturbates and gropes whenever he sees someone with a large penis and a long prepuce?*" (Chrystal, 2018, p. 165). Similarly, an aryballos flask depicts three satyrs – who, in Ancient Greek culture, symbolised lust and debauchery (Chrystal, 2018) – stimulating their large, erect penises with both hands (Figure 01.02; Richter, 1932). Terpekelos (whose name means "*shaft pleasure*") squats in the middle, flanked by Dophios ("*to knead oneself*") on the left, and Psolas ("*erect*") on the right (Laqueur, 2003, p. 96). Latin literature refers to masturbation more than Greek literature, although it was still a fairly rare topic, mainly providing material for jokes and ridicules, such as the quip regarding "*the girl from Gades*" who was "*so sexy she'd make a saint masturbate*" (Laqueur, 2003, p. 106).

Figure 01.02. Masturbating satyrs. Aryballos by Nearkos, The Metropolitan Museum of Art. Image from Archebuse, 2020.

1.4.2 The heinous sin of self-pollution

Given that ancient civilisations did not pay much attention to masturbation, and the act itself has not changed, why is it regarded as such a taboo topic in modern times? The answer to this question is often traced back to 18th century London, England, and the publication of an infamous book, *Onania; or, the Heinous Sin of Self-pollution, and all its Frightful Consequences. Both Sexes, Considered With Spiritual and Physical Advice for Those Who Have Already Injur'd Themselves by This Abominable Practice* (Anonymous, 1756). The shrewd author of *Onania* invented a new disease, and source of shame, and offered its cure for a hefty price (Laqueur, 2003). The concept of masturbation-induced ill-health caught on, spreading amongst physicians and into the public discourse. Doctors spoke of patients suffering all sorts of ailments, such as a young boy who, because of this "*preposterous entertainment*", had started to write in smaller and smaller handwriting, until he ended up nearly blind (Laqueur, 2003, p. 37). While masturbators became easily recognisable by their "*Pale, desiccated limbs, hollow chest, powerless, sunken head (…) dead white face (…) [and] eyelids falling powerlessly over [their] dying fading eyes*" (Laqueur, 2003, p.64; Figure 01.03).

In the 19th century, J. H. Kellogg advocated a diet of bland foods, including his eponymous cornflakes, to minimise sexual arousal lest it lead to masturbation (Money, 1995), "*a crime doubly abominable [in comparison to] the heinous sin of illicit commerce between the sexes*" (Laqueur, 2003, p. 47). Such was the strength of his abhorrence for masturbation that he advocated inserting silver wire under the foreskin, and using carbolic acid to burn off the clitoris, with the aim of causing enough pain to deter self-stimulation (Kontula & Haavio-Mannila, 2008). Anxiety surrounding the perils of 'self-abuse' continued well into the 20th century, even featuring prominently in the Boy

Scout's manual, which warned: "*should it become a habit it quickly destroys health and spirits; he becomes feeble in body and mind, and often ends up in a lunatic asylum*" (Baden-Powell, 1908, p. 197). While young women were cautioned that masturbation may send them, not only to an asylum, but "*to an early grave*" (Laqueur, 2003, p. 47).

Indeed, to a large extent, these anti-masturbation sentiments have been carried forward to the present day. Masturbation – even in private – is banned in most US prisons (Hughes, 2020; Kot, 2019), under threat of punishments ranging from charging detainees with indecent exposure to a spell in solitary confinement (Hughes, 2020). Such bans have been defended on various bases, some of which are more reasonable, for example that they help prevent hostile work environments for female prison guards, and others almost entirely nonsensical, for example that they reduce the transmission of sexually transmitted infections (Hughes, 2020). Indeed, these bans "*seem to be primarily motivated by sex-negativity and the desire to retributively punish incarcerated people*" (Hughes, 2020, p. 4).

In 1995 the surgeon general of the US, Jocelyn Elders, was fired by then President Bill Clinton for suggesting, tentatively, that masturbation should be discussed in sex education classes (Laqueur, 2003). On the one hand, the fact that Elders lost her job for this suggestion reflected the prevailing attitude that masturbation was a bad habit that should not be engaged with, for fear it might be seen as encouragement. On the other hand, the fact that Elders made the suggestion in the first place was a sign of a slow change that had been sweeping through society, towards a more sex-positive zeitgeist.

Figure 01.03. Typical 18th and 19th century depictions of masturbators. Image credit, top left: Tissot, S. A. D. 1836. *L'onanisme; ou dissertation physique sur les maladies produites par la masturbation*; top right: *male displaying the effects of onanism*, Wellcome collection; bottom: *the secret companion, a medical work on onanism (...) and on venereal and syphilitic diseases (...) followed by observations on marriage*, Wellcome collection.

1.4.3 Good vibrations

The middle of the 20th century saw the publication of the Kinsey reports: *Sexual Behaviour in the Human Male* (Kinsey et al., 1948) and *Sexual Behaviour in the Human Female* (Kinsey et al., 1953). These books were shocking when they were published: not only did they tackled taboo topics, such as masturbation, in a direct and scientific manner, but they challenged conventional beliefs about many aspects of sexuality. For example, it turned out that masturbation was not limited to those who were not educated enough to know better; in fact, the more educated people were, the more likely they were to have masturbated. Perhaps most importantly, they made clear that this 'heinous sin' was actually remarkably common (Laqueur, 2003).

Following the Kinsey reports – and at the height of the Free Love movement – Masters and Johnson published their book *Human Sexual Response* (1966). Where Kinsey's work was based on interviews and explored the occurrence of various behaviours within the population (e.g. the presence or absence of behaviours, and their frequency), Masters and Johnson's research was largely based on laboratory observations of masturbation and sexual intercourse, and aimed to understand the form, psychology and physiology of these behaviours. The outcome of their research was clear: self-stimulation was of vital importance to sexual pleasure (Laqueur, 2003).

By now, a counterculture had developed that embraced masturbation as a healthy aspect of human sexuality. Self-help books started to appear that advocated 'self-love' as an essential step along the path of self-knowledge, describing masturbation as "*the first, easiest, and most convenient way to experiment with your body*" (Boston Women's Health Book Collective, 1970, p. 13-14). At the same time, 'approachable' sex shops began to appear, such as Good Vibrations in San Francisco, one of the first such shops designed for women. The number of these shops has increased ever since (Daneback et al., 2011). Some embraced the fact that the taboos surrounding masturbation were beginning to break down, even celebrating it as an artform, such as the artist and feminist pornographer, Annie Sprinkle, whose films and art works celebrate the female body (Figure 01.04).

Figure 01.04. *Annie Sprinkle with Cigarette and Clitoris* (Sprinkle, 2001). Sprinkle is an artist, sex-educator, former sex-worker and feminist pornographer, with a PhD in human sexuality.

In line with ever-increasing numbers of sex shops, the amount of sexual merchandise available on the internet has grown exponentially (Daneback et al., 2011), catering to all manner of tastes. A notorious (and now defunct) website even specialised in religious-themed sex toys, selling such products as a 'Baby Jesus Butt Plug' and a 'Diving Nun' dildo (Pearson, 2014; Figure 01.05), catering to those for whom the act of masturbation was not quite taboo enough.

Figure 01.05. 'Divine Interventions' sex toys. Clockwise from top left: Jackhammer Jesus, Buddha's Delight, the Diving Nun, and Baby Jesus Butt Plug. Images adapted from Pearson (2014).

Today, masturbation is largely accepted as a healthy element of human sexuality, albeit not by everyone. Websites such as OMGYes (www.omgyes.com) offer educational, instructional videos to those with (and without) vulvas that aim to teach its users how to masturbate (or touch sexual partners) in a more enjoyable way, and create better orgasms. Over 25 years since Jocelyn Elders was fired for voicing the suggestion, masturbation is finally starting to be discussed in sexual education classes (for example in workshops by The School of Sexuality Education; www.schoolofsexed.org).

Still, masturbation remains woefully understudied, particularly in non-human animals, and even more so within a comparative framework, as will be discussed in the following sections.

1.5 The analytical framework: proximate and ultimate causes

In his landmark paper, 'On aims and methods of ethology' (1963) Niko Tinbergen outlined four different types of problem that behavioural biologists tend to focus on: *causation* (i.e. 'mechanism'; how does the trait work?) *ontogeny* (how does the trait develop over the lifetime of an individual?), *evolution* (i.e. 'phylogeny'; what is the evolutionary history of the trait?), and *survival value* (i.e. 'adaptive significance'; what is the adaptive value of the trait?). Each of these levels of inquiry facilitates a different way of understanding a trait and, while the system was originally developed for behavioural analysis, it is a valuable heuristic for understanding most biological characteristics (Bateson & Laland, 2013). Tinbergen's four questions may be further grouped into *proximate* causes (*mechanism* and *ontogeny*) that relate to why and how an individual behaves a certain way during its lifetime, and *ultimate* causes (*phylogeny* and *adaptive significance*), that relate to how and why a population has evolved the behaviour.

The utility of this framework is best understood by examining its application to a given trait. One such example may be the baculum, an isolated bone found at the distal tip of the penis of many species of mammal (Stockley, 2012) that has been described as "*the most diverse of all bones*" (Patterson & Thaeler, 1982, p. 1). The *mechanism* of the baculum is to serve as a supportive staff, strengthening the penis and protecting the urethra, particularly during prolonged intromission (Brindle & Opie, 2016; Herdina et al., 2015). In terms of *ontogeny*, in bats – the order of mammals in which the bone has perhaps been most extensively studied – the cartilaginous distal tip of the baculum develops first, followed by the main 'rod', and finally the proximal tip (Smirnov & Tsytsulina, 2003). Ossification occurs throughout this process, starting at the central axis, and spreading outwards (Smirnov & Tsytsulina, 2003). Analyses of the evolutionary history (*phylogeny*) of the baculum indicate that it first evolved after placental and non-placental mammals diverged ~145 million years ago (mya), but before the most recent common ancestor of primates and carnivores evolved ~95 mya (Brindle & Opie, 2016). While the ancestral mammal did not have a baculum, ancestral primates and carnivores did (Brindle & Opie, 2016). Finally, research examining the *adaptive significance* of the baculum indicates that it is associated with high levels of postcopulatory selection in primates and carnivores, and likely facilitates the adoption of prolonged intromission as a reproductive strategy (Brindle & Opie, 2016).

This thesis will examine the *ultimate* function of autosexual behaviour across the primate order, focusing on Tinbergen's final two questions to examine both the evolutionary history and adaptive significance of masturbation.

1.6 Previous attempts to understand masturbation

At first glance, masturbation poses a problem to evolutionary theory. Natural selection favours genes, and thus phenotypes, that aid survival, while sexual selection proliferates genes that enhance reproduction. A scenario where masturbation aids survival is difficult to imagine and, by definition, it occurs to the exclusion of potential reproductive partners. Masturbation may also be energetically costly. For example, one ejaculatory emission constitutes up to 6.0 % of the daily basal metabolic rate of Japanese macaques (*Macaca fuscata*) (Thomsen et al., 2006). The physical act of masturbating and physiological correlates of orgasm may further add to these energetic costs. Not to mention the loss of time and attention that could otherwise be spent on other activities, such as the acquisition of food and mates, or vigilance against predators or towards conspecifics.

1.6.1 Non-adaptive hypotheses

Despite this evolutionary conundrum, there has been very little systematic or comparative research into masturbation, and hypotheses regarding its function are still nascent. Early attempts to understand masturbation in nonhuman primates characterised it as a pathological behaviour, or a consequence of captivity (e.g. Anonymous, 1756), as expressed by a past director of Hanover Zoo in Germany: *"In zoos, in addition to normal heterosexual sex relationships, one can occasionally observe homosexual and other abnormal sexual behaviour, most often masturbation*" (translated from Dittrich, 1968, p. 299). These suggestions, however, are contradicted by the presence of masturbation, and homosexuality for that matter, in healthy, wild populations (Sommer & Vasey, 2010). Nevertheless, masturbation may help to alleviate stress, either in captivity or the wild. It would be instructive to examine the social context of masturbation, for example whether there is an increase in masturbatory activity in periods of group tension (both in the wild and in captivity), or when individuals are housed in isolation (in captivity).

More recently, it has been hypothesised that masturbation is a byproduct of selection for neuroendocrinological mechanisms that facilitate sexual arousal, pleasure and performance (Dixson & Anderson, 2004). These mechanisms are particularly active in facilitating copulation in primates with multi-male multi-female mating systems, and it is posited that this is why masturbation is most common in these species. This **Sexual Outlet hypothesis** (Dixson & Anderson, 2004) also states that, in such species, masturbation should occur in response to a lack of mating opportunity, for instance in low-ranking males without access to females. But this cannot account for instances in which primates masturbate in the presence of willing partners, as sometimes happens, or when primates masturbate pre- or post-copulation. Importantly, however, the Sexual Outlet hypothesis need not be mutually exclusive with adaptive explanations. The immediate urge to masturbate (i.e. the *proximate mechanism*) may be driven by selection for high sexual arousal, but its *ultimate function* may still be adaptive.

1.6.2 Adaptive hypotheses

Theories regarding the adaptive function of masturbation fall broadly under two categories: mitigation of postcopulatory selection pressure and avoidance of pathogen infection.

The Postcopulatory Selection Hypothesis

Postcopulatory selection is a form of sexual selection that influences fertilisation success once mating is achieved (Brindle, 2018), and encompasses both sperm competition (competition between the sperm of different males for the fertilisation of a female) and cryptic female choice (a form of mate choice by which females differentially affect the chance that they are fertilised by a given male). In a sample of 52 primate species, male masturbation with ejaculation was more frequent in those with multi-male multi-female mating systems, in which mate competition is high (Thomsen et al., 2003). This correlation is supported by research showing that male masturbation, with or without ejaculation, was more likely in primates with relatively larger testes (a proxy for higher sperm competition; Dixson & Anderson, 2004). Further support for a postcopulatory function comes from a study of wild Japanese macaques on Yakushima island (Thomsen & Soltis, 2004). Here, males masturbate with and without ejaculation. Both forms are more common during the mating season, although ejaculation occurs exclusively within this period. On Yakushima, social status and masturbation rate are inversely related, such that lower ranking males masturbate more frequently. The increased rate during the mating season, and negative correlation with rank (and therefore mating opportunity) suggests a benefit to males facing high levels of male-male competition.

There are different ways in which masturbation could mitigate sexual selection pressure and affect reproductive outcomes through postcopulatory selection. For example, small male marine iguanas (*Amblyrhynchus cristatus*) are often separated from females during copulation by larger males. To combat this, small males have been observed to masturbate prior to copulating, subsequently storing the pre-prepared, viable ejaculate in a small pouch in their hemipene (Wikelski & Bäurle, 1996). In doing this, they can inseminate females much faster when they do manage to mate. Primates do not have specialised penile pouches in which to store ejaculate, but masturbation without ejaculation may still be beneficial by 'pre-arousing' males, so that they are able to ejaculate faster when mating. Similarly, it has been argued that, in low-ranking male Japanese macaques, enhancing sexual arousal via masturbation without ejaculation could increase the number of spermatozoa in the *cauda epididymis* and *vas deferens* before copulation (Thomsen & Soltis, 2004). Given that ejaculates of different males can mix in the female genital tract, an increased number of sperm cells will improve the chances of a given male becoming a sire. In both cases, masturbation without ejaculation acts to increase the probability of female fertilisation during subsequent copulation, by increasing the speed with which a female is inseminated, and potentially the number of sperm in the ejaculate, respectively.

Female masturbation may also influence reproductive outcomes, by increasing sexual arousal and thus facilitating cryptic choice (Brindle, 2018). While no study has directly addressed the function of female masturbation, various mechanisms may be at play.

For example, the vaginal transudate associated with female arousal helps filter out low-quality sperm, while helping to transfer higher-quality sperm towards the uterus (Suarez & Pacey, 2006). In addition, the circumvaginal contractions that occur during female orgasm may facilitate the journey of sperm through the uterine cavity, and associated secretions of prolactin are thought to capacitate sperm (Puts & Dawood, 2006; Suarez & Pacey, 2006). Finally, female arousal increases vaginal pH, bringing it closer to neutral, and thus creating a less hostile environment for sperm (Meston, 2000). Females that mate with numerous partners may therefore use masturbatory arousal and orgasm pre- or postcopulation, as a form of cryptic female choice.

The theories discussed above regarding the adaptive function of female and male masturbation can be grouped under the under the umbrella of **Sexual Arousal hypotheses**.

While these Sexual Arousal Hypotheses may explain some forms of masturbation, they do not account for masturbation with ejaculation, which is common in male primates. The potential function of this can be illustrated by male Japanese macaques, who can be characterised into two types: ‘guarders’ and ‘sneakers’. Guarders are high-ranking older males able to monopolise females, and sneakers are low- to middle-ranking younger males, who must mate opportunistically and surreptitiously (Thomsen, 2000). Guarders do not masturbate prior to copulation and have large volumes of ejaculate, however, many of their spermatozoa are dead or have low motility. By contrast, sneakers frequently masturbate to ejaculation prior to copulating and have smaller volumes of ejaculate, containing highly motile, live spermatozoa. Anecdotal evidence suggests that the strategy of the sneaker males is successful, given that, of nine infants subjected to paternity tests, six were sired by sneakers (Thomsen, 2000). These findings support the idea that masturbation with ejaculation serves an adaptive function. Thus, males under a high degree of postcopulatory selection pressure may improve sperm quality by shedding inferior sperm cells through masturbation-induced ejaculation (Baker & Bellis, 1993), henceforth referred to as the **Sperm Quality hypothesis**.

There are marked similarities between the Sexual Arousal and Sperm Quality hypotheses for males, in that both propose masturbation improves ejaculate quality. However, the affected parameter of ejaculate quality is different in each case. According to the former, masturbation without ejaculation may accelerate subsequent copulatory ejaculations and increase the number of sperm, while according to the latter, masturbation with ejaculation increases sperm quality.

The Pathogen Avoidance Hypothesis

Apart from reducing postcopulatory selection pressure, male masturbation has been postulated to reduce the risk of contracting sexually transmitted infections, by cleansing the reproductive tract after copulation (Waterman, 2010). Evidence for this **Pathogen Avoidance hypothesis** comes from research with polygynandrous Cape ground squirrels (*Xerus inauris*), which masturbate to ejaculation significantly more often after copulating than when they have not copulated. Masturbation rates increase in accordance with the number of females an individual has copulated with, as well as the number of mates these females have previously accepted (Waterman, 2010). The reason the males do not urinate instead might reflect adaptation to the arid desert environment: instead of losing water through urination, the genital tract can be cleansed with ejaculate, which may then be re-consumed to reduce moisture loss. Female masturbation may also influence pathogen outcomes if the secretion of vaginal transudate helps to cleanse the reproductive tract. However, patterns of female masturbation were not reported in Waterman's research on ground squirrels, and no other studies have explored this possibility.

A summary of the hypotheses and predictions discussed is provided in Table 01.01. Adaptive hypotheses (and predictions) regarding female masturbation are novel to this study.

Table 01.01. Hypotheses and predictions regarding the function of masturbation in female and male primates.

Functional significance	Hypothesis	Predictions	
Non-adaptive	Pathology (♀, ♂)	Masturbation is a pathological behaviour occurring only in unnatural living conditions such as captivity	Anonymous (1756); Dittrich (1968)
	Sexual outlet (♀, ♂)	Masturbation is more common in multimale-multifemale mating systems	Dixson & Anderson (2004)
		Masturbation is associated with lack of mating opportunity	
Adaptive	Sexual arousal (♀, ♂)	Masturbation is more common in multimale-multifemale mating systems	Wikelski & Bäurle (1996); Thomsen & Soltis (2004)
		Female masturbation occurs pre- or post-copulation. Male masturbation occurs pre-copulation.	
		Female orgasm may or may not occur. Male masturbation does not culminate in ejaculation	
	Sperm quality (♂)	Masturbation is more common in multimale-multifemale mating systems	Thomsen (2000)
		Male masturbation occurs pre-copulation	
		Male masturbation culminates in ejaculation	
	Pathogen avoidance (♀, ♂)	Masturbation is more common in multimale-multifemale mating systems	Waterman (2010)
		Masturbation occurs post-copulation	
		Female orgasm may or may not occur. Male masturbation culminates in ejaculation	

1.7 Aims of the current study

This thesis aims to investigate masturbation across the primate order and understand, not just *who* masturbates, but *how, where, when,* and *why* this very common, but little studied, behaviour occurs.

To address these aims, Chapter 02 introduces a working definition of masturbation, and collates the scattered published information about the distribution and diverse forms this behaviour takes across the primate order. This database is supplemented with questionnaire responses where there are notable 'gaps' for a given taxa. Using this database, Chapter 03 takes a descriptive approach, charting the presence and absence of masturbation across the primate order (*who* masturbates?), uncovering its natural history, and examining the different forms it takes (*how* do primates masturbate?), as well as the context in which it occurs (*where* does masturbation occur?). Chapter 04 reconstructs the evolutionary history of masturbation (*when* did masturbation evolve?), first testing for phylogenetic signal, before using Bayesian phylogenetic Markov chain Monte Carlo (MCMC) techniques to model ancestral states of masturbation occurrence at key nodes within the primate order. Finally, Chapter 05 tests adaptive hypotheses as to the potential function of masturbation (*why* do primates masturbate?; Table 01.01), employing Bayesian reversible-jump MCMC techniques and phylogenetic logistic regressions to test for coevolution between masturbation and different socioecological and environmental variables.

1.8 Chapter summary

Chapter 01 introduced the topic of masturbation across the animal kingdom and why primates, in particular, are an ideal group in which to study this relatively rare behaviour. I provided a brief cultural history of masturbation from antiquity to the modern day, before discussing previous attempts to study masturbation in the animal kingdom within a scientific framework. Finally, I outlined the aims of the current study.

CHAPTER 02

DATABASE: WHAT AND WHO?

2.1 Abstract

Autosexual behaviour, or masturbation, occurs widely across the animal kingdom, and appears to be particularly prevalent in the primates. Despite this, its potential evolutionary significance has not been comprehensively studied, although various adaptive functions have been proposed. In order to facilitate the first systematic, comparative research into this common sexual behaviour, it was necessary to devise an operational definition of masturbation equally applicable to human and nonhuman animals. Accordingly, I define masturbation as the self-stimulation of the ano-genital or breast region, carried out with an individual's own body parts or external tools. Employing this definition, I compiled and categorised the scattered published information about its distribution and forms across the entire primate order, in both females and males. Where there were notable 'gaps' in the database, i.e. missing or scant information for a given taxa, information was supplemented with questionnaire responses. The resulting database consists of nearly 400 sources, and covers 105 of 281 species (37.4 %), 54 of 68 genera (79.4 %) and 18 of 19 (sub) families (94.7 %). Together, these data will help to increase our understanding of a very common, but little understood, behaviour.

2.2 Introduction

Masturbation occurs in many vertebrate animals, but seems to be especially common in the primates. However, due to the paucity of research into this phenomenon, there is no consensus on the definition of masturbation, nor has there been a systematic study of patterns of masturbation in any group of animals. After briefly outlining what is missing from previous attempts to understand masturbation (section 2.2.1), the purpose of this chapter is to develop a clear definition of masturbation (section 2.3) and to describe the compilation of comparative primate data used in this PhD thesis (section 2.4). This chapter provides an essential starting point for my analysis of the basic forms and patterns of masturbation (Chapter 03), the reconstruction of its evolutionary history (Chapter 04), and exploration of its potential functional significance with respect to sexual selection and pathogen load (Chapter 05) across primates.

2.2.1 What is missing?

It is surprising that so little is known about the evolution and potential functions of masturbation, given how widespread it is. While single-species studies are a helpful starting point, they cannot elucidate the evolutionary history of masturbation, and only provide a narrow view of its potential functions. Similarly, it is crucial that both females and males are studied. While it may be tempting to focus on males, in whom masturbation is often more conspicuous, this approach is, at best, reductive, and at worst, misleading. Research on the importance of female choice in reproduction is, rightly, gaining more and more traction. Unsurprisingly, this has led to a shift from the perspective that females are the passive beneficiaries of competition between males, to a recognition of the active role they play. Yet there remains a woeful lack of data regarding female sexual behaviour and anatomy. Collecting such data is the first step towards attaining a balanced understanding of reproductive behaviour.

In order to uncover the evolutionary history and potential functions of masturbation, it is vital to take a comparative perspective. Primates are an ideal group in which to test macroevolutionary questions. They are highly diverse, both behaviourally and ecologically, and are relatively well studied. But most importantly for this study, masturbation appears to be prevalent throughout the order.

2.3 What? Definitions of masturbation

2.3.1 Historical interpretations and the challenge of cross-taxa definitions

The word *masturbation* entered the English lexicon nearly 250 years ago in around 1785, having previously been described euphemistically in such terms as 'solitary pleasure' or 'youthful passion' (Elia, 1987). Its origin can be traced back to Ancient Rome where the words *masturbor* and *masturbator* were first used, albeit very rarely (Laqueur, 2003). There is no broad consensus as to the etymology of *masturbor* and its derivatives, but many believe that it may be a composite of the Latin *manus* (hand) and *stuprare* (to defile) (Laqueur, 2003), suggesting the act was considered somewhat less than savoury.

Moral judgements aside, this etymology suggests a manual undertaking; an assumption prevalent in historical writings on the subject. According to *De figuris Veneris* (The Manual of Classic Erotology) – an anthology of classical and medieval literature on various erotic topics – to masturbate means "*to excite the member by friction with the hand until sperm comes spirting out of it… this may be done by one's own hand or by borrowing someone else's. If by one's own, it is generally the left hand that is employed, hence the impression, 'left-hand whore'*" (Forberg, 1884, pp. 200). The author hastens to add that there were, of course, also those who employed their right hand, as exemplified by a quote from Pacificus Maximus, an Italian noble who bemoaned,

> *"What shall I do? I am so stiff – I'm bursting, and I could easily fill three or four large bottles. It is long since my member has known a vulva, long since it has stirred the entrails of a man. It is stiff day and night, and will never relax – night and day it lifts its head. No youth, no girl will listen to my prayer, no help – my right hand must then do the service!"* (Forberg, 1884, pp. 201).

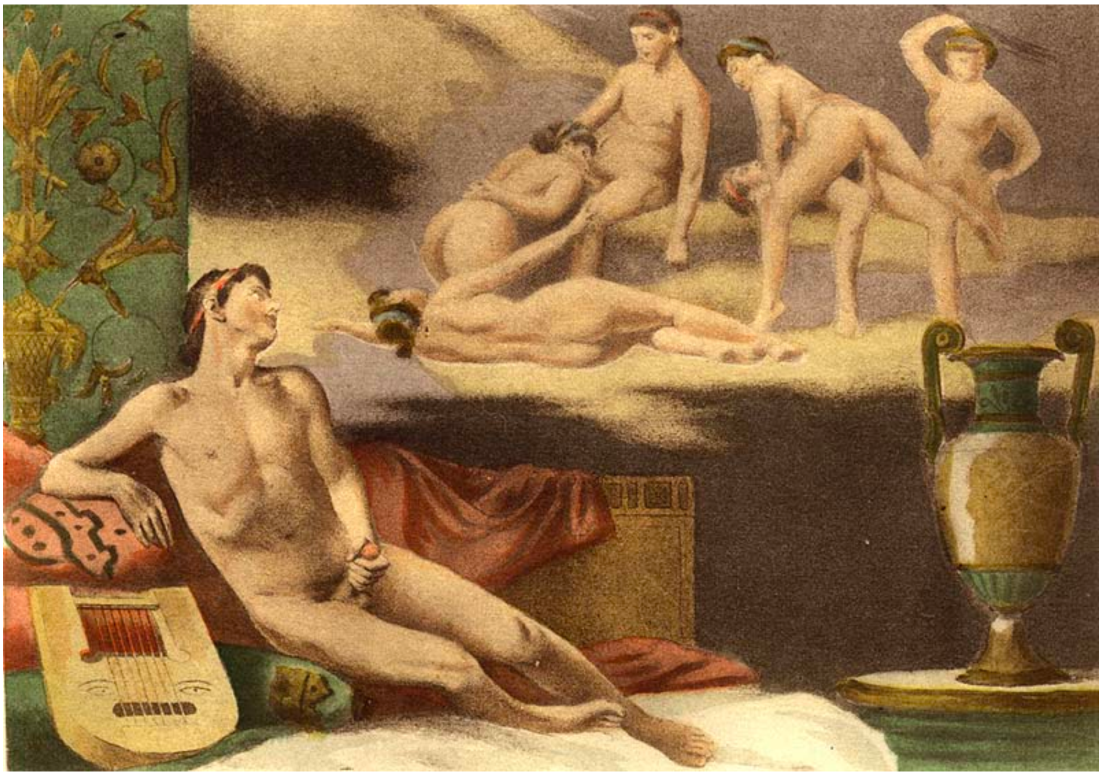

Figure 02.01. Plate XI from De figuris Veneris, by Édouard-Henri Avril. A male is portrayed masturbating, with his left hand, whilst sexually fantasising

By contemporary standards, this definition of masturbation is rather narrow. Not only does it dictate that it must be carried out by hand, but it implies that it is the preserve of those in possession of a penis, while ignoring other body parts that may also be stimulated. For example, men and women with spinal cord injuries describe hypersensitive skin surrounding their injury, which is painful to an accidental touch, but can produce orgasmic sensations if stimulated in the right way (Komisaruk & Whipple, 2005). Another woman with a spinal cord injury reached orgasm in the laboratory, with an associated increase in heart rate and blood pressure, when applying a vibrator to the junction between her neck and shoulder (Sipski et al., 1993). Several studies document the experiences of women who have orgasms from stimulation of the mouth, anus, breasts or nipples (Komisaruk & Whipple, 2005). Indeed, manipulation of the breasts or nipples is reported to cause or enhance sexual arousal in 82% of women (Levin & Meston, 2006).

A less-restrictive definition is provided in Kinsey et al.'s (1948) classic, *Sexual Behavior in the Human Male*, where masturbation is defined as "*any sort of self stimulation that brings erotic arousal*" (p. 497). Crucially, the authors distinguish between 'deliberate' and 'accidental' stimulation, the latter referring to tactile stimulation that is not designed to bring sexual satisfaction: "*Rubbing or scratching one's body, even one's genitalia, is not masturbation when it serves some other function than that of effecting erotic arousal*" (p. 498). The definition of 'any sort of self-stimulation' is certainly broad enough to encompass the wide spectrum of ways in which humans may masturbate, but visual observation of nonhuman animals cannot reliably ascertain cognitive processes, such as intentionality, or subjective feelings, such as 'erotic arousal'. The picture is especially complicated when attempting to collect data from literature that does not directly address the behaviour of interest, as is the case for the vast majority of studies in the database. Establishing that a behaviour is masturbatory is more difficult still, because it often goes unnamed or is described euphemistically.

Another complication for the definition of masturbation in non-human primates is that many species of strepsirrhine and playtrrhine scent-mark and orally or manually groom their genitals (Nunn & Altizer, 2004). For example, ano-genital rubbing forms part of the scent-marking repertoire of small-eared bush babies (*Otolemur garnettii*) (Watson, Ward, Davis, & Stavisky, 1999). Similarly, a female tufted capuchin monkey (*Cebus apella*) was observed stroking her vaginal area with a stick tool that had been dipped in honey (Westergaard & Fragaszy, 1987). Whilst this sounds like it could constitute masturbation, in fact, the female was using the tool to groom wounds sustained in fights with other group members. Although there is no indication that either of these forms of self-stimulation bring 'erotic arousal', it would be rash to exclude the possibility. In all likelihood, it is unlikely that behavioural observers will ever be able to confidently parse apart behaviours such as masturbation on a substrate from scent-marking on a substrate. It is therefore necessary to provide an operational definition that can be inferred from behavioural observations alone.

Ford and Beach (1951) provide a description that does not require the inference of internal states, where masturbation is "*any sort of bodily stimulation that results in excitation of the genitals*" (pp. 153). However, even an erect penis is not necessarily indicative of sexual excitement; it may, for example, be a reflexive response to a full bladder (Sachs, 1995). Female arousal is difficult to discern for the opposite reason, as its physiological correlates are often inconspicuous. This means that cases of female masturbation may be subject to type II errors (i.e. they may be masturbating, but without visible excitation of the genitalia), and male masturbation may be subject to type I errors (i.e. they may be touching their erect penis, but they are not masturbating). In addition, self-stimulation may be purely cognitive, as exemplified by the French artist Jean Cocteau, who, as a party trick, was allegedly able to ejaculate without touching his genitals (Gatewood, 2010). Similarly, arousal and orgasm can occur spontaneously during sleep in both men and women (Komisaruk & Whipple, 2011).

For their study on masturbation in Japanese macaques, Thomsen and Soltis (2004) describe masturbation as "*rhythmic manual rubbing of the erect penis for ≥ 5 sec*" (p. 1035). While this certainly makes masturbation easy to identify, it is too restrictive for the purpose of the present work: it is not relevant for most female primates and does not necessarily reflect the diverse suite of behaviours that may be considered to be masturbatory.

It is therefore necessary to construct a definition appropriate for female and male, human and nonhuman, primates. It must take into account morphological and phenotypic differences between primates, as well as the fact that it is not always possible to ascertain the cognitive processes or subjective experiences of an individual. The definition must also be robust to use in a comprehensive literature search of the observations of hundreds of different researchers over the past century, each with their own opinion as to what does or does not constitute masturbation, and potentially a reluctance to describe it when they see it.

2.3.2 Working definition

I define masturbation as *the self-stimulation of the ano-genital or breast region carried out with an individual's own body parts or external tools.* This operational definition treats internal motivations as a black box, albeit without ascribing to the radical behaviourist stance that mental causes are absent. Importantly, I exclude those cases of self-stimulation identified as typical non-sexual behaviours by the reporting author(s). That is, if an individual is specifically described as 'scratching' or 'grooming' themselves, out of the context of a description of masturbation, this is taken at face value.

2.3.3 The boundaries of masturbation

Euphemistic reports

Even with this definition, given the astounding variety of different autosexual behaviours across the primates, it is useful to consider behavioural vignettes in which it is difficult to state whether it has or has not occurred, in order to delineate the 'boundaries' of masturbation.

Historical – and to some extent, prevailing – negative attitudes towards masturbation have instilled reticence to report observations. What are more difficult to navigate, however, are misleading or euphemistic reports. For example, Collias & Southwick (1952, pp.149) provide a detailed account of what they unambiguously identify as 'autoerotic behaviour' in a male mantled howler monkey (*Alouatta palliata*) during which "*regular scrotal contractions* [were] *accompanied by extrusion and lifting of the penis bringing it up against the fur of the legs (…) every few seconds (…) occasionally the scrotum was rubbed against the heel of the foot or branch with the terminal portions of the tail*". However, instead of going on to report what was most likely the subsequent ejaculation of the male, the authors observe that "*Finally the male scratched vigorously with the hand in the region of the genitals and a stream of fluid, apparently urine, emerged, and within about fifteen minutes the scrotal pulsations ceased*". It is unclear why the authors do not label this as ejaculation, given that it has all the hallmarks.

In instances such as this, where language is clearly used euphemistically, cases were interpreted according to the most likely true scenario. For example, on this occasion, masturbation would be recorded as occurring with ejaculation, with a note that the authors have labelled it otherwise.

Auto- versus allosexual behaviour

It is not controversial to state that an individual who uses some sort of tool for their own sexual gratification is masturbating. There are a huge wealth of sex toys available to humans and, as will be discussed in more detail in subsequent chapters, nonhuman primates are often ingenious in manufacturing and using masturbatory tools. However, what is less clear is whether other animals may be used as tools. A quick search of online video sharing or social media platforms reveals a plethora of videos showing various primates using other animals – often rather unfortunate frogs – for their own sexual gratification (see Figure 02.02, for example). It would not be unfair to argue that these individuals are using frogs to masturbate with.

A similar case, this time involving animals within the same taxonomic Class (Mammalia), comes from recent observations of female and male Japanese macaques sexually soliciting and/or mounting sika deer (*Cervus nippon*), and performing pelvis thrusts against their backs (Gunst et al. 2017; Pelé, et al., 2017; Figure 02.03). The deer do not actively participate in this behaviour and the macaques appear to be using them simply as instruments for their own sexual satisfaction, similar to the way in which primates have been observed to utilise frogs. However, the fact that they mount the deer in a similar way to how they would mount a copulatory partner makes it look less like masturbation and more like an inter-species sexual act. Indeed, the behaviour is referred to as 'reproductive interference' in the literature, rather than masturbation (Gunst et al., 2017; Pelé et al., 2017).

Figure 02.02. A young long-tailed macaque (*Macaca fascicularis*) attempting to pry open the mouth of an Asian common toad (*Duttaphrynus melanostictus*) in order to insert his penis. Stills taken from YouTube footage (Animal Post, 2019).

What, then, about individuals of the same species? Forberg's (1884) definition of masturbation stipulates that it may be done "*by one's own hand or by borrowing someone else's*". If the 'other' is considered simply to be a tool, then one could make the argument that this is masturbation. But by following that argument to its logical conclusion, any sexual behaviour between two or more individuals could then be considered masturbatory if those involved considered the 'other' participant(s) to be tools for their own sexual gratification.

Figure 02.03. A male Japanese macaque (*Macaca fuscata*) mounting and thrusting on a sika deer (*Cervus nippon*). Figure adapted from Pelé et al., (2017).

Of course, this makes use of the classic 'slippery slope' argument, and in reality few people would argue that sexual acts involving others of the same or closely-related species would constitute masturbation; however, it is difficult to discern where to draw the line. For this reason, the criteria for what constitutes masturbation will exclude the use of animate living beings as tools (i.e. other animals can not be used for masturbation, but plants and fungi can). This establishes a distinction between auto- and allosexual behaviour, where 'auto' is derived from the Greek *autos*, meaning 'self' or 'same', and 'allo' from the Greek *allos*, meaning 'other' or 'different'.

2.4 Who? The database

To curate the database, I followed three broad steps, which were: (i) to systematically search for, collate and classify all available primary literature relating to masturbation in the primate order; (ii) to establish where there were 'gaps' in the database, i.e. where little or no information was available for a species or genus; and (iii) to design and send out questionnaires targeted towards individuals with significant experience with these taxa and incorporate this information into the database. I then classified all information, ready for analysis.

2.4.1 Taxonomy and phylogeny

The International Union for the Conservation of Nature Species Survival Commission (IUCN SSC) Primate Specialist Group currently recognise 522 species of primate, with a total of 709 species and subspecies overall (IUCN SSC Primate Specialist Group, 2021). However, new species are frequently described and taxonomic classifications are subject to constant revision (e.g. Rowe & Myers, 2017). For the purpose of these analyses, I adopt the same taxonomy as that used by the 10kTrees (v3) phylogenies (Arnold et al., 2010). These phylogenies are inferred via Bayesian phylogenetic methods, utilising genetic data available from GenBank, a database of publicly available DNA sequences (Benson et al., 2013). All primate species listed in GenBank at the time these phylogenies were inferred are included. If there were no data for a given primate species on GenBank, it was not included (Arnold et al., 2010). The taxonomic nomenclature used within the phylogenies, and throughout this thesis, thus mirrors that used within the GenBank database. While these phylogenies only include 301 species and subspecies, they facilitate analyses that incorporate phylogenetic uncertainty.

Two of the species in the phylogenies are extinct (*Archaeolemur majori* and *Homo neanderthalensis*) and were therefore excluded from the database, leaving 299 extant species in the phylogenies. The phylogenies also include several subspecies. It was rare that data were acquired to this level, and I therefore extrapolated any information I did acquire for a subspecies to the species level. When conducting analyses, I nominated a single subspecies as a proxy for the entire species. For example, *Pan troglogytes troglodytes* (central chimpanzees) became the representative of *P. troglodytes*, and thus also represents *P. troglodytes schweinfurthii* (Eastern chimpanzees), *P. troglodytes troglodytes*, *P. troglodytes ellioti* (Nigeria-Cameroon chimpanzees), and *P. troglodytes verus* (Western chimpanzees). I was therefore left with 272 species to which I assigned data.

Data for species outside of the 10k Trees phylogenies were still collected *ad libitum*, and, where possible, reconciled with the database. This was often the case when the taxonomic nomenclature used in reports was outdated, for example, reports under the name of *Presbytis entellus* were entered as *Semnopithecus entellus.* In other instances, the phylogenies did not reflect the most up-to-date, or accepted, taxonomic classification or nomenclature. In these cases, reports were entered under the names within the phylogenies, to maximise data available for analysis. For example, reports under the name of *Cebuella pygmaea* (pygmy marmosets) were entered as *Callithrix pygmaea*, regardless of the fact that *Cebuella pygmaea* is well established.

Where species were truly not present within the phylogenies, reports were collected and entered into the database, but were not used in phylogenetic analyses, which are reliant on the 10kTrees phylogenies. Similarly, reports at the genus-level, or those that referred to hybrid species, were included in the database, but were not used for analyses.

2.4.2 Data assembly and classification

Data assembly

The database builds upon preliminary compilations by two UCL MSc students, E. Jones (2005) and C. Frearson (2005). These sources were re-read in full for this study, to confirm the original coding of these preliminary compilations and to identify any additional information available could be extracted and added to the database. This appraisal step was important to ensure the data followed the definition of masturbation employed in the present work. For example, potential cases of scent-marking were removed from the database, as were instances in which other individuals were involved (which here would be defined as allosexual behaviour).

An additional literature search was then conducted to cover the period of time since the original data were collected, as well as ensuring there was no further information available for those species with little or no data. The primary literature searched consisted of peer-reviewed scientific papers and books, as well as popular science books written by experts. The literature search was executed using a web-based search engine (Google Scholar) and targeted publications pertaining to primates included within the 10kTrees phylogenies (by genus and common name), for example, a search for squirrel monkeys would include the search terms “Saimiri” and “squirrel monkey” alongside the following keywords: “masturbat*”, “autosexual”, “autoerotic”, and “genital stimulation”.

By comparison to other comparative studies, in which the traits of interest (such as body size) are usually recorded fairly conspicuously, collating data on masturbation was especially challenging. The vast majority of sources identified were not directly about masturbation, or even sexual behaviour. This, combined with the pervasive attitude – even amongst many scientists – that masturbation is an unseemly or crass topic, meant that observations were often mentioned euphemistically, or in passing. All additional sources identified were therefore read in full, because screening sources in other ways (for instance, by whether the search terms appeared in the abstract) was not usually informative. Only studies that confirmed either the occurrence or non-occurrence of masturbation for an individual, or individuals, of a given species were included in the database.

Questionnaires were employed as a means of supplementing primary literature. Particular care was taken to solicit information from primatologists and others who had extensive experience with taxa for which published literature provided little or no information about masturbation. Questionnaires were circulated and responses received during three periods (1992, V. Sommer and A. Parish, n = 44 respondents; 1997-1998, R. Thomsen, n = 55 respondents; 2018-2021, M. Brindle and V. Sommer, n = 51 respondents; Appendix I - IV). The questionnaires compiled and circulated during this project (M. Brindle and V. Sommer, 2018 – 2021) were constructed to reflect the research questions of the present work, rather than following the format of previous questionnaires.

Figure 02.04 provides an overview of the database construction and appraisal process.

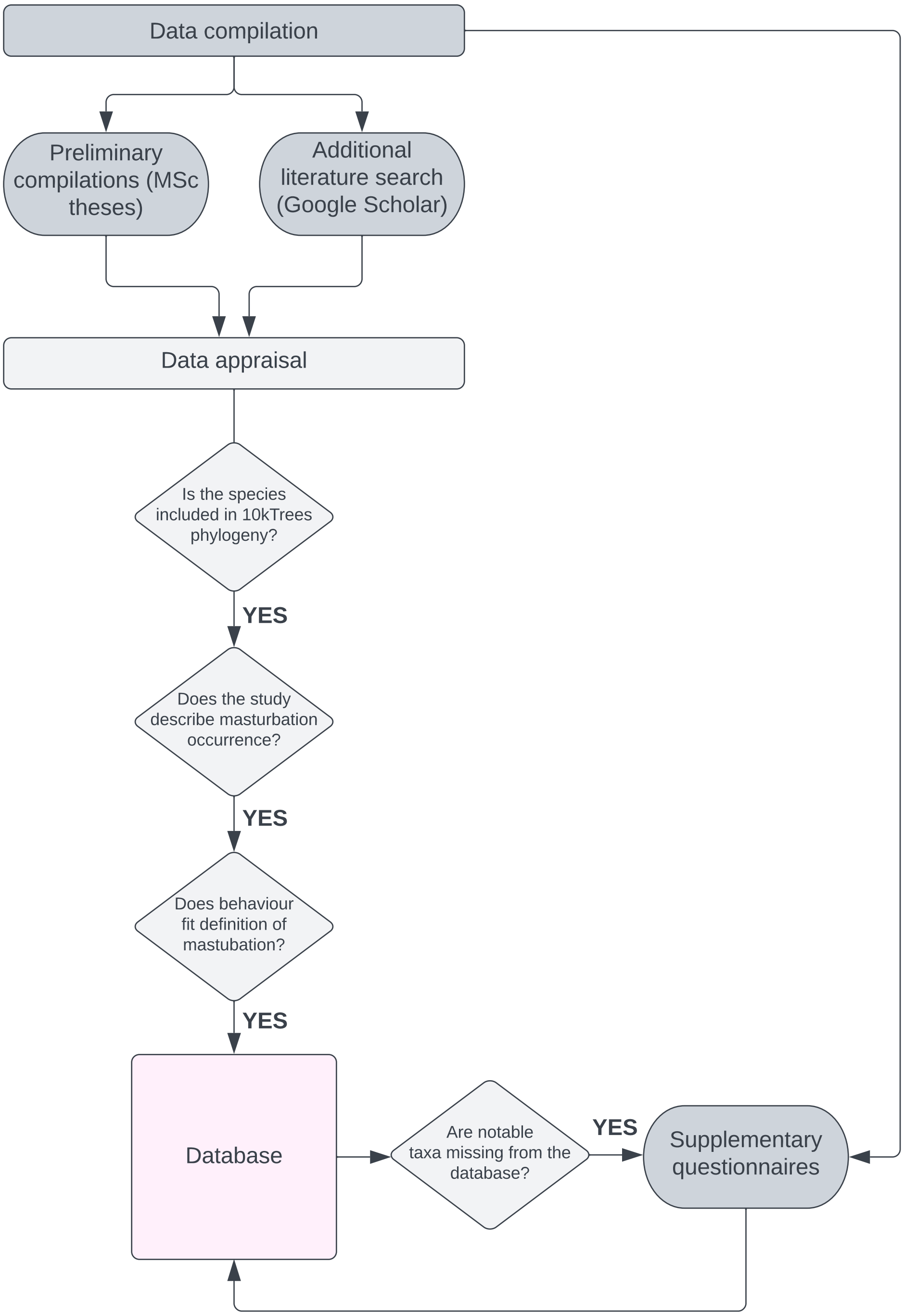

Figure 02.04. Flow chart of the data compilation and appraisal process.

Data classification

Species with a single confirming scientific report were considered to be masturbatory. Thus, reports of masturbation presence overrode those of masturbation absence, regardless of the number of times absence was reported, i.e. if ten people said a species did not masturbate, but one individual confirmed they had, this species would be classed as masturbatory. Conversely, a species was not simply classified as non-masturbatory if there were a lack of reports on the behaviour, because behavioural studies of many primate species are limited, and masturbation may be rare, so anecdotal incidences are unlikely to be published. Attempts were made to mitigate this problem by seeking questionnaire responses from researchers with long-term experience with taxa for which there is a dearth of publications. Consequently, a species was only rated as non-masturbatory if a publication or questionnaire respondent explicitly stated that the behaviour was not observed. Of course, this approach leaves open the possibility that the behaviour is present, but has not been observed, in species classed as non-masturbatory. It is therefore advised that 'absence' data are approached with a degree of caution, when interpreting results.

Information was extracted from each source regarding a range of aspects of autosexual behaviour. First, I examined the **forms** of behaviour. Form refers to 'how' masturbation occurs, and was split into five categories: stimulated body parts, stimulation devices, techniques, associated traits, and temporal context. Second, I examined the **context** of the behaviour reported. Context refers to 'where' masturbation occurs, and in which individuals, and was split into two categories: living environment and individual phenotype.

Information was classified according to the descriptors provided in the original source to avoid bias, and because the full range of behaviours that occur was not known. Where information was not available for a given variable, it was left out of the database. For example, if a source described masturbation in a species, but did not specify which sex- or age-class it was observed in, these variables would be left blank.

In certain cases, variables were not comparable across, or relevant to, all species in the dataset. For example, the importance and rigidity of dominance hierarchies varies across sexes and species, while other species adopt a more egalitarian system. By the same token, the way in which certain variables were recorded was often not commensurable. For instance, masturbation occurrence was sometimes defined descriptively (i.e. as ‘frequent’, ‘occasional’, ‘rare’, or similar), and sometimes recorded as a rate per day, week, month, or year. Depending on a researcher’s experience with different species of primates, rates and descriptive terms can easily be interpreted differently. For example, a researcher with extensive experience with macaques may interpret two observations of masturbation per month as ‘rare’, while a researcher who has worked with callitrichids may class this as ‘frequent’. I therefore adopted a cautious approach, following the form of the source when extracting data, rather than attempting to interpret the information myself. While this reduces the amount of information available for analysis, it removes the risk of biasing the results according to my own assumptions.

If functional explanations for masturbation were proffered by the authors of a report, these were included in the database, as well as any additional comments or observations regarding a particular case. Where there was more than one source for a given species, each source was treated separately. Sources that referenced several species, or males and females of the same species, were included multiple times.

In order to maximise the use of a source, reports were generally treated as documentation of species-level observations, rather than as descriptions of individuals. For example, the general statement that "*a type of behavior that is tentatively classified as masturbation was seen in adult males and females, and in juveniles*" (Altmann, 1959, p. 325) would be included in the database once for females and once for males of the species, in this case the mantled howler monkey.

Similarly, observations regarding a single individual would be included once in the database. Such as the following statement, describing masturbation in Koko the female lowland gorilla (*Gorilla gorilla*) "*We find that another form of self-stimulation, masturbation with toys, appears an average of 6 days after menses*" (Patterson et al., 1991, p. 187).

An exception to this was when individuals were clearly discussed separately within a source, as was sometimes the case in papers specifically discussing masturbation. In these instances, each individual was included as a separate case. For example, one paper specified:

> "*The third male was a [Hylobates agilis agilis] (northern agile gibbon) who rubbed his penis up and down over the dorsal aspect of his foot or on the chain link enclosure. The fourth male H. a. agilis was observed to masturbate twice when his sexual partner terminated copulation prior to his ejaculation. Following her retreat, he sat on the branch they*

> *had been copulating on and rubbed his penis against the branch by moving his pelvis back and forth. He was not observed to ejaculate.”* (Mootnick & Baker, 1994, p. 348)

Each source therefore usually only occurs in the database a single time for each sex and/or species described within it, regardless of the number of individuals discussed, with the exception of a few papers, in which observations of separate individuals are clearly differentiated. Each of these entries constitutes a separate ‘report’.

Each variable within a report may also include multiple or overlapping factors, for example, a single report might detail that an individual or group have been observed to masturbate in captivity and in the wild.

2.4.3 Patterns of data availability and coverage

On the basis of the approach outlines above, I was able to collect data on primate masturbation from almost 400 sources, including 246 publications and 150 questionnaire responses and personal communications from colleagues. This generated a total of 569 separate reports.

Table 02.01 provides an overview of the proportion of taxa covered by the reports in this database. I was able to obtain information for 105/281 species (37.4 %), 54/68 genera (79.4 %) and 18/19 (sub)families (94.7 %). On this basis, the proportion of species of the major radiations covered by the database are: lemurs 19.7 % (13/66), lorises and galagos 33.3 % (7/21), tarsiers 20.0 % (1/5), South and Central American monkeys 42.6% % (28/68), African and Eurasian monkeys 40.4 % (40/99), and apes 68.2 % (15/22).

Table 02.01. Proportion of genera covered by my database on the presence and absence of masturbation across the primate order. See following pages.

Semiorder	Infraorder	(Sub)family	Genus	Common name	Sources (n)	Species per genus (n)	Species covered (%)
Strepsirrhini	**Lemuriformes**	**Lemuridae**	Eulemur	True lemurs	4	6	50
			Hapalemur	Gentle lemurs	0	3	0
			Lemur	Ring-tailed lemur	2	1	100
			Varecia	Variegated lemurs	0	2	0
		Indriidae	Avahi	Woolly lemurs	1	5	20
			Indri	Indri	1	1	100
			Propithecus	Sifakas	1	6	17
		Cheirogaleidae	Allocebus	Hairy-eared dwarf lemur	0	1	0
			Cheirogaleus	Dwarf lemurs	1	3	33
			Microcebus	Mouse lemurs	7	17	18
			Mirza	Coquerel's dwarf lemurs	0	2	0
			Phaner	Fork-crowned lemur	0	1	0
		Lepilemuridae	Lepilemur	Sportive lemurs	2	17	12
		Daubentoniidae	Daubentonia	Aye-aye	0	1	0
	Lorisiformes	**Lorisidae**	Arctocebus	Angwantibos	0	2	0
			Loris	Slender lorises	1	2	50
			Nycticebus	Slow lorises	2	5	40
			Perodicticus	Potto	0	1	0
		Galagidae	Euoticus	Needle-claw bushbaby	0	1	0
			Galago	Bushbabies	3	6	33
			Galagoides	Dwarf galagos	1	2	50
			Otolemur	Greater galagos	1	2	50
	Tarsiiformes	**Tarsiidae**	Tarsius	Tarsiers	1	5	20
Haplorrhini	**Platyrrhini**	**Pitheciinae**	Cacajao	Uakaris	2	2	100
			Chiropotes	Bearded saki	1	1	100
			Pithecia	Sakis	0	2	0
		Callicebinae	Callicebus	Titi monkeys	3	6	33
		Alouattinae	Alouatta	Howler monkeys	7	7	29
		Atelinae	Ateles	Spider monkeys	4	5	60

Semiorder	Infraorder	(Sub)family	Genus	Common name	Sources (n)	Species per genus (n)	Species covered (%)
			Brachyteles	Muriqui	2	1	100
			Lagothrix	Wooly monkey	1	1	100
		Aotidae	Aotus	Owl monkeys	2	8	25
		Cebidae	Cebus	Capuchin monkeys	10	5	80
			Saimiri	Squirrel monkeys	8	4	25
			Sapajus	Robust capuchin monkey	1	1	100
		Callitrichidae	Callimico	Goeldi's monkey	1	1	100
			Callithrix	Marmosets	9	10	20
			Leontopithecus	Golden lion tamarins	2	3	67
			Saguinus	Tamarins	12	11	36
	Catarrhini	**Cercopithecinae**	Allenopithecus	Allen's swamp monkey	0	1	0
			Cercocebus	Terrestrial mangabeys	4	3	67
			Cercopithecus	Guenons	4	18	17
			Chlorocebus	Vervets	7	4	75
			Erythrocebus	Patas monkey	1	1	100
			Lophocebus	Arboreal mangabeys	1	2	50
			Macaca	Macaques	158	22	55
			Mandrillus	Mandrill, drill	9	2	100
			Miopithecus	Talapoin	6	1	100
			Papio	Baboons	27	5	80
			Rungwecebus	Kipunji	0	1	0
			Theropithecus	Gelada baboon	1	1	100
		Colobinae	Colobus	Black and white colobuses	0	5	0
			Nasalis	Proboscis monkey	2	1	100
			Piliocolobus	Red colobuses	5	9	22
			Presbytis	Langurs	0	2	0
			Procolobus	Olive colobus	1	1	100
			Pygathrix	Douc langurs	2	2	100
			Rhinopithecus	Snub-nosed langurs	1	4	25
			Semnopithecus	Hanuman langur	4	1	100
			Trachypithecus	Lutongs	3	13	15

Semiorder	Infraorder	(Sub)family	Genus	Common name	Sources (n)	Species per genus (n)	Species covered (%)
		Hylobatidae	Hoolock	Hoolock gibbons	2	2	100
			Hylobates	Dwarf gibbons	7	6	67
			Nomascus	Crested gibbons	2	5	20
			Symphalangus	Siamang	1	1	100
		Homininae	Pongo	Orangutans	9	2	100
			Gorilla	Gorillas	17	3	67
			Homo	Human	2	1	100
			Pan	Chimpanzee, Bonobo	41	2	100

This table also shows that the number of sources for a given genera varies greatly, ranging between one and 158. Taxa with the most sources confirming absence or presence of masturbation were: *Macaca mulatta* (n = 72), *Pan troglodytes* (n = 35), *Macaca fuscata* (n = 31), *Macaca arctoides* (stump-tailed macaque; n = 17), *Gorilla gorilla* (n = 15), *Papio ursinus* (chacma baboon; n = 10), *Callithrix jacchus* (common marmoset; n = 8), and *Saimiri sciureus* (common squirrel monkey; n = 8). Entries for *Homo sapiens* (humans) would outnumber those of other primates, had input not been restricted to two classic sources (Kinsey et al., 1948, 1953).

Looking more closely at those cases where data were available, Table 02.02 provides a summary of each report in the database, including information on sex and environment. The majority of the reports are for males (67.0 %, 381/569), although females are also well represented (28.6 %, 163/569). With respect to environment, there are more data on primates in a captive setting (65.9 %, 375/569) than from those in the wild (31.6 %, 180/569). This table also records the presence and absence of masturbation in each case, which will be analysed in the next chapter.

Table 02.02. Overview of available data on masturbation presence and absence across the primate order. See following pages.

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
Strepsirrhini	**Lemuriformes**	**Archaeolemur**	*Archaeolemur majori*										
		Lemuridae	*Eulemur coronatus*		X		X			X	X		Kappeler (1992)
			Eulemur coronatus	X			X			X	X		Kappeler (1992)
			Eulemur fulvus albifrons										
			Eulemur fulvus albocollaris										
			Eulemur fulvus collaris										
			Eulemur fulvus fulvus		X		X		X		X		Ganzhorn (1992)
			Eulemur fulvus mayottensis										
			Eulemur fulvus rufus		X		X			X	X		Kappeler (1992)
			Eulemur fulvus rufus	X			X			X	X		Kappeler (1992)
			Eulemur fulvus sanfordi										
			Eulemur macaco flavifrons										
			Eulemur macaco macaco										
			Eulemur mongoz		X			X		X	X		Peckre (2018)
			Eulemur mongoz	X				X		X	X		Peckre (2018)
			Eulemur rubriventer										
			Eulemur rufifrons		X			X	X		X		Peckre et al. (2018)
			Eulemur rufifrons	X				X		X	X		Peckre et al. (2018)
			Hapalemur aureus										
			Hapalemur griseus										
			Hapalemur griseus alaotrensis										
			Hapalemur griseus griseus										
			Hapalemur griseus meridionalis										
			Hapalemur griseus occidentalis										
			Hapalemur simus										
			Lemur catta		X		X		X		X		Fichtel (2018)
			Lemur catta	X			X			X	X		Fichtel (2018)
			Lemur catta	X			X			X	X		Kappeler (1992)
			Lemur catta		X		X			X	X		Kappeler (1992)
			Varecia rubra										
			Varecia variegata variegata										
		Indriidae	*Avahi cleesei*										
			Avahi laniger										
			Avahi meridionalis		X			X		X	X		Campera (2021)
			Avahi meridionalis	X				X		X	X		Campera (2021)
			Avahi occidentalis										
			Avahi unicolor										
			Indri indri		X			X		X	X		Torti (2018)
			Indri indri	X				X		X	X		Torti (2018)
			Propithecus coquereli										
			Propithecus deckenii										
			Propithecus diadema										
			Propithecus edwardsi										
			Propithecus tattersalli										
			Propithecus verreauxi		X			X		X	X		Rudolph & Fichtel (2018)
			Propithecus verreauxi	X				X		X	X		Rudolph & Fichtel (2018)
		Cheirogaleidae	*Allocebus trichotis*										

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Cheirogaleus crossleyi										
			Cheirogaleus major										
			Cheirogaleus medius		X		X			X	X		Nieschalk (1992)
			Cheirogaleus medius	X			X			X	X		Nieschalk (1992)
			Microcebus berthae		X			X	X		X		Henke-von der Malsburg (2018)
			Microcebus berthae	X				X		X	X		Henke-von der Malsburg (2018)
			Microcebus bongolavensis										
			Microcebus danfossi										
			Microcebus griseorufus										
			Microcebus jollyae										
			Microcebus lehilahytsara										
			Microcebus lokobensis										
			Microcebus macarthurii										
			Microcebus mamiratra										
			Microcebus mittermeieri										
			Microcebus murinus		X		X		X		X		Radespiel (2018)
			Microcebus murinus	X			X			X	X		Radespiel (2018)
			Microcebus murinus		X		X			X	X		Thomsen (1998)
			Microcebus murinus		X		X		X		X		Zimmerman (1992)
			Microcebus murinus		X		X			X	X		Wrogemann (1998)
			Microcebus murinus		X			X		X	X		Henke-von der Malsburg (2018)
			Microcebus murinus	X				X		X	X		Henke-von der Malsburg (2018)
			Microcebus myoxinus										
			Microcebus ravelobensis										
			Microcebus rufus		X		X			X	X		Wrogemann (1998)
			Microcebus sambiranensis										
			Microcebus simmonsi										
			Microcebus tavaratra										
			Mirza coquereli										
			Mirza zaza										
			Phaner furcifer										
			Phaner furcifer pallescens										
		Lepilemuridae	*Lepilemur aeeclis*										
			Lepilemur ankaranensis										
			Lepilemur dorsalis										
			Lepilemur edwardsi										
			Lepilemur fleuretae		X			X		X	X		Campera (2021)
			Lepilemur fleuretae	X				X		X	X		Campera (2021)
			Lepilemur hubbardorum										
			Lepilemur leucopus										
			Lepilemur manasamody										
			Lepilemur microdon										
			Lepilemur mitsinjoensis										
			Lepilemur mustelinus										
			Lepilemur otto										
			Lepilemur randrianasoli										
			Lepilemur ruficaudatus										

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Lepilemur sahamalazensis		X			X		X	X		Mandle (2021)
			Lepilemur sahamalazensis	X				X		X	X		Mandle (2021)
			Lepilemur seali										
			Lepilemur septentrionalis										
		Daubentoniidae	*Daubentonia madagascariensis*										
	Lorisiformes	**Lorisidae**	*Arctocebus aureus*										
			Arctocebus calabarensis										
			Loris lydekkerianus										
			Loris tardigradus		X		X			X	X		Nieschalk (1992)
			Loris tardigradus	X			X			X	X		Nieschalk (1992)
			Nycticebus bengalensis										
			Nycticebus coucang		X		X		X		X		Zimmerman (1992)
			Nycticebus javanicus		X		X	X		X	X		Maynard & Nekaris (2018)
			Nycticebus javanicus	X			X	X		X	X		Maynard & Nekaris (2018)
			Nycticebus menagensis										
			Nycticebus pygmaeus										
			Perodicticus potto										
		Galagidae	*Euoticus elegantulus*										
			Galago alleni										
			Galago gallarum										
			Galago granti										
			Galago matschiei										
			Galago moholi		X			X		X	X		Bearder (1997)
			Galago moholi		X		X			X	X		Bearder (1997)
			Galago senegalensis		X		X		X		X		Zimmerman (1992)
			Galago senegalensis		X			X		X	X		Bettridge & Ellison (2018)
			Galago senegalensis	X				X		X	X		Bettridge & Ellison (2018)
			Galagoides demidoff							X		X	Voland (1978)
			Galagoides zanzibaricus										
			Otolemur crassicaudatus		X		X			X	X		Bearder (1997)
			Otolemur crassicaudatus		X			X		X	X		Bearder (1997)
			Otolemur garnettii										
Haplorrhini	**Tarsiiformes**	**Tarsiidae**	*Tarsius bancanus*										
			Tarsius dentatus										
			Tarsius lariang										
			Tarsius syrichta										
			Tarsius tarsier		X		X			X	X		Hidayatik (2018)
			Tarsius tarsier	X			X			X	X		Hidayatik (2018)
			Tarsius sp.		X					X	X		Sajuthi (2018)
			Tarsius sp.	X						X	X		Sajuthi (2018)
	Platyrrhini	**Pitheciinae**	*Cacajao calvus*		X			X		X	X		Bowler (2018)
			Cacajao calvus	X				X		X	X		Bowler (2018)
			Cacajao melanocephalus		X		X	X	X			X	Bezerra et al. (2011)
			Chiropotes satanas	X				X	X		X		Norconk (1992)
			Chiropotes satanas		X			X	X		X		Norconk (1992)
			Pithecia irrorata										
			Pithecia pithecia										

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
		Callicebinae	*Callicebus donacophilus*										
			Callicebus hoffmannsi										
			Callicebus moloch		X		X			X	X		Anzenberger (2021)
			Callicebus moloch	X			X			X	X		Anzenberger (2021)
			Callicebus personatus										
			Callicebus torquatus										
			Plecturocebus cupreus		X			X		X	X		Heymann (1997)
			Plecturocebus cupreus		X			X		X	X		Dolotovskaya & Heymann (2021)
			Plecturocebus cupreus	X				X		X	X		Dolotovskaya & Heymann (2021)
		Alouattinae	*Alouatta belzebul*										
			Alouatta caraya										
			Alouatta guariba										
			Alouatta palliata		X			X	X			X	Altmann (1959)
			Alouatta palliata	X				X	X			X	Altmann (1959)
			Alouatta palliata		X			X	X			X	Carrera-Sanchez (1994)
			Alouatta palliata		X			X	X			X	Collias & Southwick (1952)
			Alouatta palliata	X				X	X			X	Collias & Southwick (1952)
			Alouatta palliata		X			X		X	X		Moorman (1992)
			Alouatta palliata	X				X		X	X		Moorman (1992)
			Alouatta palliata		X			X	X		X		Whitehead (1992)
			Alouatta palliata	X				X	X		X		Whitehead (1992)
			Alouatta palliata		X			X		X	X		McKinney (2018)
			Alouatta palliata	X				X		X	X		McKinney (2018)
			Alouatta pigra										
			Alouatta sara		X		X			X	X		Brindle (2018)
			Alouatta sara	X			X			X	X		Brindle (2018)
			Alouatta seniculus										
		Atelinae	*Ateles belzebuth*		X		X			X	X		Jaffe (2018)
			Ateles belzebuth	X			X		X		X		Jaffe (2018)
			Ateles fusciceps										
			Ateles geoffroyi	X				X	X			X	Campbell (2004)
			Ateles geoffroyi	X				X	X		X		Davis & Tórrez-Herrera (2018)
			Ateles paniscus										
			Ateles chamek	X			X		X		X		Brindle (2018)
			Brachyteles arachnoides		X			X	X		X		Strier (1997)
			Brachyteles arachnoides		X			X		X	X		Strier (1992)
			Brachyteles arachnoides	X				X		X	X		Strier (1992)
			Lagothrix lagotricha		X		X		X		X		Jaffe (2018)
			Lagothrix lagotricha	X			X			X	X		Jaffe (2018)
		Aotidae	*Aotus azarai*		X			X		X	X		Huck (2018)
			Aotus azarai	X				X		X	X		Huck (2018)
			Aotus azarai boliviensis										
			Aotus brumbacki										
			Aotus infulatus										
			Aotus lemurinus		X		X			X	X		Dixson (2021)
			Aotus lemurinus	X			X			X	X		Dixson (2021)
			Aotus lemurinus griseimembra										

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Aotus nancymaae										
			Aotus nigriceps										
			Aotus trivirgatus										
			Aotus vociferans										
		Cebidae	*Cebus albifrons*		X			X	X			X	Fragaszy et al. (2004)
			Cebus apella		X		X	X	X			X	Carosi & Visalberghi (2002)
			Cebus apella	X			X	X	X			X	Carosi & Visalberghi (2002)
			Cebus apella		X		X		X			X	Lima et al. (2017)
			Cebus apella		X		X		X		X		Westergaard (1992)
			Cebus apella		X		X			X	X		Brindle (2018)
			Cebus apella	X			X			X	X		Brindle (2018)
			Cebus apella		X		X		X			X	Fragaszy et al. (2004)
			Cebus apella	X			X		X			X	Fragaszy et al. (2004)
			Cebus capucinus		X			X		X	X		Crofoot (2018)
			Cebus capucinus	X				X		X	X		Crofoot (2018)
			Cebus capucinus		X			X	X		X		Davis & Tórrez-Herrera (2018)
			Cebus capucinus		X			X	X		X		McKinney (2018)
			Cebus capucinus	X				X		X	X		McKinney (2018)
			Cebus olivaceus		X			X		X	X		Miller (1992)
			Cebus olivaceus	X				X		X	X		Miller (1992)
			Cebus xanthosternos										
			Sapajus flavius		X			X		X	X		Brindle (2018)
			Sapajus flavius	X				X		X	X		Brindle (2018)
			Saimiri boliviensis										
			Saimiri oerstedii										
			Saimiri sciureus		X		X		X			X	Alvarez (1975)
			Saimiri sciureus		X		X		X			X	Hopf et al. (1974)
			Saimiri sciureus		X		X		X			X	King & Priscilla (1970)
			Saimiri sciureus			X			X			X	Ploog (1967)
			Saimiri sciureus		X		X		X			X	Roy (1981)
			Saimiri sciureus		X		X		X			X	Ploog et al. (1963)
			Saimiri sciureus		X		X		X			X	Travis & Holmes (1974)
			Saimiri sciureus		X		X		X		X		Thomsen (1998)
			Saimiri ustus										
			Saimiri sp.		X		X		X		X		Bernhards (1998)
		Callitrichidae	*Callimico goeldii*		X		X			X	X		Anzenberger (2021)
			Callimico goeldii	X			X			X	X		Anzenberger (2021)
			Callithrix argentata										
			Callithrix aurita										
			Callithrix emiliae										
			Callithrix geoffroyi										
			Callithrix humeralifera										
			Callithrix jacchus		X		X		X			X	Rothe (1975)
			Callithrix jacchus		X		X			X	X		Soltis (1998)
			Callithrix jacchus		X		X			X	X		Anzenberger (1992)
			Callithrix jacchus	X			X			X	X		Anzenberger (1992)
			Callithrix jacchus		X			X		X	X		Digby (1992)

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Callithrix jacchus	X				X		X	X		Digby (1992)
			Callithrix jacchus		X		X		X		X		Radespiel (1992)
			Callithrix jacchus	X			X		X			X	Dittrich (1968)
			Callithrix jacchus		X		X	X		X	X		Anzenberger (2021)
			Callithrix jacchus	X			X	X		X	X		Anzenberger (2021)
			Callithrix jacchus		X		X			X	X		Dixson (2021)
			Callithrix jacchus	X			X			X	X		Dixson (2021)
			Callithrix kuhli										
			Callithrix mauesi										
			Callithrix penicillata										
			Callithrix pygmaea		X		X			X	X		Anzenberger (2021)
			Callithrix pygmaea	X			X			X	X		Anzenberger (2021)
			Leontopithecus chrysomelas		X		X			X	X		Thomsen (1998)
			Leontopithecus chrysopygus										
			Leontopithecus rosalia		X		X	X		X	X		Beck & Rettberg-Beck (2021)
			Leontopithecus rosalia	X			X	X		X	X		Beck & Rettberg-Beck (2021)
			Saguinus bicolor										
			Saguinus fuscicollis		X		X		X		X		Knogge (1998)
			Saguinus fuscicollis		X			X		X	X		Heymann (1998)
			Saguinus fuscicollis		X		X	X		X	X		Heymann (1992)
			Saguinus fuscicollis	X			X	X		X	X		Heymann (1992)
			Saguinus fuscicollis	X			X		X		X		Küderling (1992)
			Saguinus fuscicollis		X		X			X	X		Epple (1992)
			Saguinus fuscicollis	X			X			X	X		Epple (1992)
			Saguinus fuscicollis		X			X		X	X		Nevo (2018)
			Saguinus fuscicollis	X				X		X	X		Nevo (2018)
			Saguinus fuscicollis melanoleucus										
			Saguinus geoffroyi										
			Saguinus imperator										
			Saguinus labiatus		X		X			X	X		Epple (1992)
			Saguinus labiatus	X			X			X	X		Epple (1992)
			Saguinus leucopus										
			Saguinus midas										
			Saguinus mystax		X		X	X		X	X		Heymann (1992)
			Saguinus mystax	X			X	X		X	X		Heymann (1992)
			Saguinus mystax		X			X		X	X		Heymann (1998)
			Saguinus mystax		X			X		X	X		Huck (2018)
			Saguinus mystax	X				X		X	X		Huck (2018)
			Saguinus niger										
			Saguinus oedipus		X		X		X			X	Pook (1976)
			Saguinus oedipus oedipus		X		X		X		X		Benning (1992)
			Saguinus tripartitus										
	Catarrhini	**Cercopithecinae**	*Allenopithecus nigroviridis*										
			Cercopithecus albogularis		X		X			X	X		Böer (1992)
			Cercopithecus albogularis	X			X			X	X		Böer (1992)
			Cercopithecus ascanius										
			Cercopithecus campbelli		X		X		X		X		Loser (1997)

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Cercopithecus campbelli lowei		X			X	X			X	Hunkeler et al. (1972)
			Cercopithecus cephus										
			Cercopithecus cephus cephus										
			Cercopithecus cephus ngottoensis										
			Cercopithecus diana										
			Cercopithecus erythrogaster										
			Cercopithecus erythrogaster erythrogaster										
			Cercopithecus erythrotis										
			Cercopithecus hamlyni										
			Cercopithecus lhoesti										
			Cercopithecus mitis										
			Cercopithecus mona										
			Cercopithecus neglectus		X		X		X		X		Adoyo (1997)
			Cercopithecus nictitans										
			Cercopithecus petaurista										
			Cercopithecus pogonias										
			Cercopithecus preussi										
			Cercopithecus solatus										
			Cercopithecus wolfi										
			Chlorocebus aethiops		X		X		X			X	Girolami (1985)
			Chlorocebus aethiops		X		X		X			X	Schiørring (1977)
			Chlorocebus aethiops		X			X	X			X	Struhsaker (1967)
			Chlorocebus aethiops		X			X	X		X		Hauser (1993)
			Chlorocebus aethiops		X		X		X			X	Seier et al. (1989)
			Chlorocebus pygerythrus		X		X		X		X		Gerald (1998)
			Chlorocebus pygerythrus cynosurus										
			Chlorocebus sabaeus			X		X	X			X	McGuire (1974)
			Chlorocebus tantalus										
			Erythrocebus patas	X			X		X			X	Rowell (1978)
			Erythrocebus patas	X			X		X			X	Rowell (1978)
			Miopithecus talapoin		X		X		X			X	Dixson & Herbert (1977)
			Miopithecus talapoin		X		X		X			X	Keverne (1979)
			Miopithecus talapoin		X		X		X			X	Keverne et al (1978)
			Miopithecus talapoin		X		X		X			X	Posada & Colell (2005)
			Miopithecus talapoin		X		X		X			X	Wolfheim & Rowell (1972)
			Miopithecus talapoin	X			X		X			X	Wolfheim & Rowell (1972)
			Miopithecus talapoin		X		X		X		X		Zimmermann (1992)
			Miopithecus talapoin	X			X		X		X		Zimmermann (1992)
			Cercocebus agilis										
			Cercocebus galeritus		X		X		X			X	Mitchell et al. (1988)
			Cercocebus galeritus		X		X		X			X	Mitchell et al. (1987)
			Cercocebus galeritus	X			X		X			X	Mitchell et al. (1987)
			Cercocebus torquatus		X		X		X		X		Böer (1993)
			Cercocebus torquatus atys		X		X		X			X	Bernstein (1971)
			Lophocebus albigena		X			X	X			X	Wallis (1983)
			Lophocebus aterrimus										
			Macaca arctoides		X		X		X			X	Anderson & Chamove (1981)

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Macaca arctoides		X		X		X			X	Adams & Schoel (1982)
			Macaca arctoides		X		X		X			X	Allyn et al. (1976)
			Macaca arctoides			X	X		X			X	Anderson & Chamove (1985)
			Macaca arctoides		X		X	X	X			X	Bertrand (1969)
			Macaca arctoides	X			X	X	X			X	Bertrand (1969)
			Macaca arctoides		X		X		X			X	Kanagava et al. (1972)
			Macaca arctoides		X		X		X			X	Kling & Dunne (1976)
			Macaca arctoides	X			X		X			X	Kling & Dunne (1976)
			Macaca arctoides		X		X		X			X	Linnankoski et al. (1992)
			Macaca arctoides		X		X		X			X	Linnankoski et al. (1993)
			Macaca arctoides		X		X		X			X	Linnankoski et al. (1995)
			Macaca arctoides		X		X		X			X	Linnankoski et al. (1981)
			Macaca arctoides		X		X		X			X	Linnankoski & Leinonen (1985)
			Macaca arctoides		X		X		X			X	Nieuwenhuijsen et al. (1988)
			Macaca arctoides	X			X		X			X	Nieuwenhuijsen et al. (1988)
			Macaca arctoides		X		X		X			X	Nieuwenhuijsen et al. (1988)
			Macaca arctoides	X			X		X			X	Nieuwenhuijsen et al. (1988)
			Macaca arctoides		X		X		X			X	Nieuwenhuijsen et al. (1986)
			Macaca arctoides	X			X		X			X	Nieuwenhuijsen et al. (1986)
			Macaca arctoides		X		X		X			X	Nieuwenhuijsen et al. (1987)
			Macaca arctoides		X		X		X			X	Trollope & Jones (1975)
			Macaca assamensis										
			Macaca brunnescens										
			Macaca cyclopis										
			Macaca fascicularis		X		X		X			X	Weinbauer et al. (1990)
			Macaca fascicularis		X		X		X		X		Zumpe (1992)
			Macaca fascicularis	X			X		X		X		Zumpe (1992)
			Macaca fascicularis		X			X	X		X		van Noordwijk (1997)
			Macaca fascicularis		X		X		X			X	Hamilton (1914)
			Macaca fuscata		X		X		X			X	Crowley et al. (1993)
			Macaca fuscata		X		X		X			X	Crowley et al. (1992)
			Macaca fuscata		X			X	X			X	Domingo-Roura et al. (2004)
			Macaca fuscata			X			X			X	Fedigan (1976)
			Macaca fuscata		X		X		X			X	Hanby et al. (1971)
			Macaca fuscata		X			X	X			X	Inoue (2012)
			Macaca fuscata		X		X		X			X	Matsubayashi (1974)
			Macaca fuscata		X		X		X			X	Minami (1975)
			Macaca fuscata			X	X		X			X	Ogura (2012)
			Macaca fuscata		X		X		X			X	Ogura & Matsuzawa (2012)
			Macaca fuscata	X			X		X			X	Rendall & Taylor (1991)
			Macaca fuscata		X			X	X			X	Stephenson (1973)
			Macaca fuscata		X			X	X			X	Stephenson (1974)
			Macaca fuscata		X			X	X			X	Thomsen (2014)
			Macaca fuscata		X			X	X			X	Thomsen & Soltis (2004)
			Macaca fuscata	X				X		X		X	Thomsen & Soltis (2004)
			Macaca fuscata		X		X	X	X			X	Thomsen et al. (2006)
			Macaca fuscata	X			X		X			X	Hill (1997)

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Macaca fuscata	X				X	X			X	Vasey & Duckworth (2006)
			Macaca fuscata	X					X			X	Vasey & Pfaus (2005)
			Macaca fuscata		X		X		X			X	Wolfe (1978)
			Macaca fuscata		X			X	X		X		Hauser (1992)
			Macaca fuscata	X			X		X		X		Rendall (1992)
			Macaca fuscata		X			X	X		X		Fujita (1997)
			Macaca fuscata		X			X	X		X		Kustukake (1997)
			Macaca fuscata fuscata		X			X	X		X		Watanabe (1997)
			Macaca fuscata fuscata		X		X		X		X		Soltis (1997)
			Macaca fuscata yakui		X			X	X		X		Hanya (1997)
			Macaca fuscata yakui		X			X	X		X		Hayakawa (1997)
			Macaca fuscata yakui		X			X	X		X		Hill (1997)
			Macaca fuscata yakui		X		X		X		X		Sugiura (1997)
			Macaca fuscata yakui		X			X	X		X		Tanaka (1997)
			Macaca fuscata yakui		X		X		X		X		Tanaka (1997)
			Macaca fuscata yakui		X			X	X		X		Soltis (1997)
			Macaca hecki										
			Macaca leonina										
			Macaca maura		X			X	X		X		Matsumura (1997)
			Macaca maura	X			X		X		X		Petit (1992)
			Macaca maura		X			X	X		X		Germani (2019)
			Macaca maura	X				X		X	X		Germani (2019)
			Macaca mulatta		X		X		X			X	Weinbauer et al. (1990)
			Macaca mulatta		X		X		X			X	Abbott et al. (1984)
			Macaca mulatta			X	X		X			X	Aceto & Bowman (1993)
			Macaca mulatta	X			X		X			X	Akers & Conway (1979)
			Macaca mulatta		X		X		X			X	Altmann (1962)
			Macaca mulatta		X		X		X			X	Bayne & McCully (1989)
			Macaca mulatta		X		X		X			X	Baysinger et al (1972)
			Macaca mulatta	X			X		X			X	Baysinger et al (1972)
			Macaca mulatta		X		X			X		X	Bowden & McKinney (1974)
			Macaca mulatta	X			X			X		X	Baysinger et al (1972)
			Macaca mulatta		X		X			X		X	Brandt & Mitchell (1973)
			Macaca mulatta		X		X		X			X	Brandt et al. (1971)
			Macaca mulatta		X		X		X			X	Carpenter (1942)
			Macaca mulatta	X			X		X			X	Carpenter (1942)
			Macaca mulatta	X			X		X			X	Chappel & Meier (1974)
			Macaca mulatta		X		X		X			X	Claus et al. (1980)
			Macaca mulatta		X			X	X			X	Dubuc et al. (2013)
			Macaca mulatta		X		X		X			X	Freedman & Rosvold (1962)
			Macaca mulatta	X			X		X			X	Freedman & Rosvold (1962)
			Macaca mulatta		X		X		X			X	Gilbeau & Smith (1985)
			Macaca mulatta		X		X		X			X	Glick et al. (1982)
			Macaca mulatta		X		X		X			X	Goldfoot (1977)
			Macaca mulatta		X		X		X			X	Goldfoot (1981)
			Macaca mulatta	X			X		X			X	Goosen (1981)
			Macaca mulatta		X		X		X			X	Harlow (1975)

Semiorder	Infraorder	(Sub)family	Latin name	Sex			Living environment		Masturbation occurence		Source type		Reference
				Female	Male	Unknown	Captive	Wild	Present	Absent	Questionnaire	Publication	
			Macaca mulatta	X			X		X			X	Harlow (1975)
			Macaca mulatta			X	X		X			X	Harlow et al. (1965)
			Macaca mulatta		X		X		X			X	Harlow et al. (1966)
			Macaca mulatta	X			X		X			X	Harlow et al. (1966)
			Macaca mulatta		X		X		X			X	Harlow et al. (1972)
			Macaca mulatta			X	X		X			X	Harlow et al. (1964)
			Macaca mulatta		X		X		X			X	Harrison et al. (1989)
			Macaca mulatta		X		X		X			X	Keverne (1974)
			Macaca mulatta		X		X		X			X	Keverne & Michael (1971)
			Macaca mulatta		X		X		X			X	Koford (1965)
			Macaca mulatta		X		X		X			X	Leibo et al. (2007)
			Macaca mulatta	X			X		X			X	Louis et al. (1981)
			Macaca mulatta		X		X		X			X	Loy et al. (1984)
			Macaca mulatta	X			X		X			X	Loy et al. (1984)
			Macaca mulatta		X		X		X			X	Maple et al. (1974)
			Macaca mulatta		X		X		X			X	Mason & Spoonholz (1963)
			Macaca mulatta		X		X		X			X	Mehlman et al. (1997)
			Macaca mulatta		X		X		X			X	Masserman (1966)
			Macaca mulatta		X		X		X			X	Michael & Saayman (1967)
			Macaca mulatta	X			X		X			X	Michael & Saayman (1967)
			Macaca mulatta		X		X		X			X	Michael et al. (1971)
			Macaca mulatta		X		X		X			X	Michael et al. (1974)
			Macaca mulatta		X		X		X			X	Missakian (1972)
			Macaca mulatta	X			X		X			X	Mitchell & Brandt (1975)
			Macaca mulatta		X		X		X			X	Mitchell & Brandt (1975)
			Macaca mulatta			X	X		X			X	Mitchell et al. (1966)
			Macaca mulatta		X			X	X			X	Neville (1968)
			Macaca mulatta		X		X		X			X	Ortmann et al. (1986)
			Macaca mulatta		X		X		X			X	Perachio et al. (1969)
			Macaca mulatta		X		X		X			X	Phoenix (1974)
			Macaca mulatta	X			X		X			X	Phoenix (1974)
			Macaca mulatta		X		X		X			X	Phoenix (1980)
			Macaca mulatta		X		X		X			X	Pomerantz (1990)
			Macaca mulatta		X		X		X			X	Pomerantz (1991)
			Macaca mulatta		X		X		X			X	Pomerantz (1993)
			Macaca mulatta		X			X	X			X	Prakash (1962)
			Macaca mulatta		X		X		X			X	Redican & Mitchell (1973)
			Macaca mulatta		X		X		X			X	Ruiz de Elvira et al. (1982)
			Macaca mulatta		X		X		X			X	Sackett (1974)
			Macaca mulatta			X	X		X			X	Sidowski (1970)
			Macaca mulatta			X	X		X			X	Singh & Pirta (1980)
			Macaca mulatta		X		X		X			X	Slimp et al. (1978)
			Macaca mulatta		X		X		X			X	Stoffer et al. (1973)
			Macaca mulatta			X	X		X			X	Strobel (1979)
			Macaca mulatta		X		X		X			X	Suomi (1977)
			Macaca mulatta			X	X		X			X	Zimmermann et al. (1975)
			Macaca mulatta			X	X		X			X	Zimmermann et al. (1975)

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	Infraorder	(Sub)family	Latin name	Female	Male	Unknown	Captive	Wild	Present	Absent	Questionnaire	Publication	Reference
			Macaca mulatta		X		X		X			X	Eisler et al. (1993)
			Macaca mulatta		X		X		X		X		Gerald (1998)
			Macaca mulatta		X			X	X		X		Boonratana (1992)
			Macaca mulatta		X			X	X		X		Hauser (1992)
			Macaca mulatta		X		X		X		X		Zumpe (1992)
			Macaca mulatta	X			X		X		X		Zumpe (1992)
			Macaca mulatta		X			X	X		X		Hill (1997)
			Macaca mulatta		X		X		X		X		Swam (1998)
			Macaca mulatta		X		X		X			X	Erwin & Mitchell (1975)
			Macaca mulatta		X			X	X			X	Fisler (1967)
			Macaca mulatta		X		X		X			X	Fittinghoff et al. (1974)
			Macaca mulatta		X		X		X			X	Fontenot et al. (2006)
			Macaca munzala										
			Macaca nemestrina		X		X		X			X	Crowley et al. (1974)
			Macaca nemestrina		X		X		X			X	Reite et al. (1981)
			Macaca nemestrina		X		X		X			X	Tokuda et al. (1968)
			Macaca nemestrina		X		X		X			X	Crowley (1983)
			Macaca nemestrina	X			X		X			X	Crowley (1983)
			Macaca nemestrina leonina										
			Macaca nemestrina siberu										
			Macaca nigra		X		X		X			X	Dixson (1977)
			Macaca nigra	X			X		X			X	Dixson (1977)
			Macaca nigra		X				X			X	Thierry et al. (2000)
			Macaca nigra	X					X			X	Thierry et al. (2000)
			Macaca nigra		X		X		X		X		Petit (1992)
			Macaca nigra		X		X		X		X		Curran (2018)
			Macaca nigrescens										
			Macaca ochreata										
			Macaca pagensis										
			Macaca radiata		X		X		X			X	Crowley et al. (1975)
			Macaca radiata		X			X	X			X	Makwana (1980)
			Macaca radiata		X			X	X			X	Rahaman & Parthasarathy (1969)
			Macaca radiata		X		X		X			X	Rosenblum & Smiley (1984)
			Macaca radiata	X			X		X			X	Rosenblum & Smiley (1984)
			Macaca radiata		X		X		X		X		Silk (1992)
			Macaca radiata	X				X		X	X		Silk (1992)
			Macaca radiata		X			X		X	X		Silk (1992)
			Macaca silenus		X		X		X			X	Lindburg (1990)
			Macaca silenus	X			X		X			X	Lindburg (1990)
			Macaca silenus			X	X		X			X	Mallapur et al. (2005)
			Macaca silenus			X	X		X			X	Mallapur et al. (2005)
			Macaca silenus			X	X		X			X	Mallapur et al. (2007)
			Macaca silenus		X		X		X			X	Skinner & Lockard (1979)
			Macaca silenus		X		X			X	X		Heiduck (1992)
			Macaca silenus	X			X			X	X		Heiduck (1992)
			Macaca silenus		X			X	X		X		Kumar (1997)
			Macaca silenus		X		X		X		X		Loser (1997)

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Macaca sinica										
			Macaca sylvanus		X			X	X			X	Burton (1972)
			Macaca sylvanus		X		X		X		X		Angst (1992)
			Macaca sylvanus		X		X		X		X		Paul & Küster (1992)
			Macaca sylvanus		X		X		X		X		Rümenas (1992)
			Macaca sylvanus		X			X	X		X		Paul (1997)
			Macaca thibetana		X			X	X			X	Zhao (1993)
			Macaca tonkeana	X			X		X		X		Preüschoft (1992)
			Macaca tonkeana		X		X		X		X		Thierry (1992)
			Macaca tonkeana	X			X		X		X		Thierry (1992)
			Mandrillus leucophaeus		X		X		X			X	Mootnick & Baker (1994)
			Mandrillus leucophaeus		X		X		X			X	Böer (1987)
			Mandrillus leucophaeus			X	X		X			X	Hearn et al. (1988)
			Mandrillus leucophaeus		X		X		X			X	Priest (1991)
			Mandrillus leucophaeus		X		X		X		X		Böer (1992)
			Mandrillus sphinx			X	X		X			X	Chamove et al. (1988)
			Mandrillus sphinx		X		X		X			X	Kawata (1980)
			Mandrillus sphinx		X			X	X		X		White (1997)
			Mandrillus sphinx		X		X		X		X		Dixson (2021)
			Mandrillus sphinx	X			X			X	X		Dixson (2021)
			Papio anubis		X			X	X			X	Bercovitch (1989)
			Papio anubis		X		X		X			X	Elton (1979)
			Papio anubis		X		X		X			X	Elton & Anderson (1977)
			Papio anubis		X		X		X			X	Goodwin et al. (2006)
			Papio anubis		X			X	X		X		Phillips-Conroy (1997)
			Papio cynocephalus		X		X		X			X	Bramblett (1978)
			Papio cynocephalus		X		X		X			X	Coelho & Bramblett (1981)
			Papio cynocephalus		X			X	X			X	Hausfater (1975)
			Papio cynocephalus		X			X	X		X		Strier (1992)
			Papio cynocephalus cynocephalus		X			X	X		X		Noë-Slijter & Noë (1997)
			Papio cynocephalus papio		X		X		X		X		Petit (1992)
			Papio cynocephalus anubis		X			X	X		X		Kuntz (1998)
			Papio hamadryas		X		X		X			X	Kessel & Brent (2001)
			Papio hamadryas		X			X		X	X		Boug (1997)
			Papio hamadryas		X			X	X		X		Angst (1992)
			Papio hamadryas		X		X		X		X		Weldon (2018)
			Papio hamadryas		X		X			X	X		Thomsen (1992)
			Papio hamadryas	X			X			X	X		Thomsen (1992)
			Papio hamadryas, P. cynocephalus, & hybrids		X		X		X		X		Colmenares (1992)
			Papio hamadryas, P. cynocephalus, & hybrids	X			X		X		X		Colmenares (1992)
			Papio papio										
			Papio ursinus		X		X		X			X	Bielert (1972)
			Papio ursinus		X		X		X			X	Bielert & Anderson (1985)
			Papio ursinus		X		X		X			X	Bielert & Girolami (1986)
			Papio ursinus		X		X		X			X	Bielert et al. (1986)
			Papio ursinus		X		X		X			X	Bielert et al. (1989)
			Papio ursinus		X		X		X			X	Bielert & van der Walt (1982)

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Papio ursinus		X			X	X			X	Bolwig (1959)
			Papio ursinus		X		X		X			X	Girolami & Bielert (1987)
			Papio ursinus		X			X	X			X	Saayman (1970)
			Papio ursinus		X			X	X		X		Byrne (1992)
			Papio sp.		X		X		X			X	Coelho & Bramblett (1982)
			Papio sp.			X	X		X			X	Johnson et al. (2015)
			Rungwecebus kipunji										
			Theropithecus gelada		X			X	X		X		Ramsay (2019)
			Theropithecus gelada	X				X		X	X		Ramsay (2019)
		Colobinae	*Colobus angolensis*										
			Colobus angolensis palliatus										
			Colobus guereza										
			Colobus polykomos										
			Colobus satanas										
			Colobus vellerosus										
			Nasalis larvatus		X			X		X	X		Boonratana (1992)
			Nasalis larvatus	X				X		X	X		Boonratana (1992)
			Nasalis larvatus		X			X	X		X		Yeager (1993)
			Piliocolobus badius		X			X	X			X	Starin (2004)
			Piliocolobus badius	X				X	X			X	Starin (2004)
			Piliocolobus badius		X			X	X			X	Struhsaker (1975)
			Piliocolobus badius		X			X		X	X		Stanford (1992)
			Piliocolobus badius	X				X		X	X		Stanford (1992)
			Piliocolobus badius		X			X	X		X		Korstjens (1997)
			Piliocolobus foai										
			Piliocolobus gordonorum										
			Piliocolobus kirkii		X			X	X		X		Warkentin & Georgiev (2018)
			Piliocolobus pennantii										
			Piliocolobus preussi										
			Piliocolobus rufomitratus										
			Piliocolobus tephrosceles										
			Piliocolobus tholloni										
			Presbytis comata										
			Presbytis melalophos										
			Procolobus verus		X			X	X		X		Krebs (1997)
			Pygathrix cinerea		X		X			X	X		Rudolph (2018)
			Pygathrix cinerea	X			X			X	X		Rudolph (2018)
			Pygathrix nemaeus		X		X			X	X		Rudolph (2018)
			Pygathrix nemaeus	X			X			X	X		Rudolph (2018)
			Rhinopithecus avunculus										
			Rhinopithecus bieti										
			Rhinopithecus brelichi										
			Rhinopithecus roxellana		X		X		X			X	Clarke (1991)
			Semnopithecus entellus		X			X	X			X	Hrdy (1977)
			Semnopithecus entellus		X			X	X		X		Paul (1997)
			Semnopithecus entellus		X			X	X		X		Borries (1998)
			Semnopithecus entellus	X			X		X			X	Dittrich (1978)

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	Infraorder	(Sub)family	Latin name	Female	Male	Unknown	Captive	Wild	Present	Absent	Questionnaire	Publication	Reference
			Trachypithecus auratus										
			Trachypithecus cristatus										
			Trachypithecus delacouri										
			Trachypithecus francoisi										
			Trachypithecus geei										
			Trachypithecus germaini										
			Trachypithecus johnii		X			X	X			X	Poirer (1969)
			Trachypithecus johnii		X			X	X			X	Poirer (1970)
			Trachypithecus laotum										
			Trachypithecus obscurus										
			Trachypithecus phayrei										
			Trachypithecus pileatus		X			X		X	X		Stanford (1992)
			Trachypithecus pileatus	X				X		X	X		Stanford (1992)
			Trachypithecus poliocephalus										
			Trachypithecus vetulus										
		Hylobatidae	*Bunopithecus hoolock*	X			X		X			X	Mootnick & Baker (1994)
			Hoolock leuconedys		X		X			X	X		Kumar (2021)
			Hoolock leuconedys	X			X			X	X		Kumar (2021)
			Hylobates agilis		X		X		X			X	Cheyne (2004)
			Hylobates agilis	X			X		X			X	Cheyne (2004)
			Hylobates agilis		X		X		X			X	Cheyne (2006)
			Hylobates agilis	X			X		X			X	Cheyne (2006)
			Hylobates agilis	X			X		X			X	Mootnick & Baker (1994)
			Hylobates agilis		X		X		X			X	Mootnick & Baker (1994)
			Hylobates agilis		X		X		X			X	Mootnick & Baker (1994)
			Hylobates agilis		X		X		X			X	Mootnick & Baker (1994)
			Hylobates klossii										
			Hylobates lar	X			X		X			X	Mootnick & Baker (1994)
			Hylobates lar		X			X		X	X		Reichard (1998)
			Hylobates moloch										
			Hylobates muelleri		X		X		X			X	Cheyne (2004)
			Hylobates muelleri	X			X		X			X	Cheyne (2004)
			Hylobates muelleri		X		X		X			X	Cheyne (2006)
			Hylobates muelleri	X			X		X			X	Cheyne (2006)
			Hylobates muelleri	X			X		X			X	Mootnick & Baker (1994)
			Hylobates pileatus		X		X		X			X	Mootnick & Baker (1994)
			Nomascus concolor		X		X		X			X	Mootnick & Baker (1994)
			Nomascus concolor		X		X			X	X		Böer (1992)
			Nomascus concolor	X			X			X	X		Böer (1992)
			Nomascus gabriellae										
			Nomascus leucogenys										
			Nomascus nasutus										
			Nomascus siki										
			Symphalangus syndactylus		X		X		X			X	Mootnick & Baker (1994)
		Ponginae	*Pongo abelii*		X		X		X			X	Gruber (2014)
			Pongo abelii		X			X	X			X	MacKinnon (1979)
			Pongo abelii	X				X	X			X	Rijksen (1978)

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Pongo abelii		X			X	X			X	MacKinnon (1974)
			Pongo pygmaeus		X		X		X			X	Harrisson (1960)
			Pongo pygmaeus		X			X	X			X	Galdikas (1981)
			Pongo pygmaeus		X		X		X			X	de Silva (1970)
			Pongo pygmaeus		X		X		X			X	MacKinnon (1974)
			Pongo pygmaeus	X			X		X			X	MacKinnon (1974)
			Pongo pygmaeus		X		X		X		X		Jaffe (2018)
			Pongo pygmaeus	X			X			X	X		Jaffe (2018)
			Pongo sp.		X		X		X			X	Nadler (1988)
			Pongo sp.	X			X		X			X	Nadler (1988)
			Pongo sp.		X		X		X			X	Maple (1980)
			Pongo sp.		X			X	X		X		van Schaik (1997)
			Pongo sp.		X		X			X	X		Böer (1992)
			Pongo sp.	X			X			X	X		Böer (1992)
			Pongo sp.		X			X	X		X		Kunz (2019)
			Pongo sp.	X				X	X		X		Kunz (2019)
		Homininae	*Gorilla beringei*		X			X		X	X		Stewart (1992)
			Gorilla beringei	X				X		X	X		Stewart (1992)
			Gorilla beringei		X			X	X			X	Fossey (1983)
			Gorilla beringei		X			X	X			X	Fossey (1983)
			Gorilla gorilla gorilla		X		X		X			X	Riess et al. (1949)
			Gorilla gorilla gorilla	X			X		X			X	Riess et al. (1949)
			Gorilla gorilla gorilla	X			X		X			X	Patterson et al. (1991)
			Gorilla gorilla gorilla	X			X		X			X	Sarfaty et al. (2012)
			Gorilla gorilla gorilla		X		X		X			X	Mead-Moehring & Moore-Jansen (2006)
			Gorilla gorilla gorilla		X		X		X			X	Hess (1973)
			Gorilla gorilla gorilla	X			X		X			X	Hess (1973)
			Gorilla gorilla gorilla	X			X		X			X	Atsalis et al. (2004)
			Gorilla gorilla gorilla		X		X		X			X	Casanova (1992)
			Gorilla gorilla gorilla		X		X		X			X	Clark et al. (2012)
			Gorilla gorilla gorilla	X			X		X			X	Clark et al. (2012)
			Gorilla gorilla gorilla		X		X		X			X	Schaller (1963)
			Gorilla gorilla gorilla		X		X		X			X	Schaller (1963)
			Gorilla gorilla gorilla		X		X		X		X		Weiche (1998)
			Gorilla gorilla gorilla		X		X		X		X		Perry (1992)
			Gorilla gorilla gorilla	X			X		X		X		Perry (1992)
			Gorilla gorilla gorilla		X		X		X			X	Beck & Power (1988)
			Gorilla gorilla graueri										
			Gorilla gorilla		X		X		X		X		Böer (1992)
			Gorilla gorilla		X			X		X	X		Harcourt (1992)
			Gorilla gorilla	X				X		X	X		Harcourt (1992)
			Gorilla gorilla		X		X		X		X		Donkin (1998)
			Gorilla sp.		X		X		X			X	Gould & Bres (1986)
			Gorilla sp.	X			X		X			X	Gould & Bres (1986)
			Gorilla sp.		X		X		X			X	Gould (1982)
			Gorilla sp.	X			X		X			X	Gould (1982)
			Gorilla sp.	X			X		X			X	Schaller (1963)

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Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Gorilla sp.		X		X		X			X	Schaller (1963)
			Gorilla sp.		X		X		X		X		Meder (1998)
			Homo sapiens		X			X	X			X	Kinsey et al. (1948)
			Homo sapiens	X				X	X			X	Kinsey et al. (1953)
			Homo sapiens neanderthalensis										
			Pan paniscus		X		X		X			X	de Waal (1987)
			Pan paniscus		X		X		X			X	de Waal (1990)
			Pan paniscus	X			X		X			X	Sannen et al. (2005)
			Pan paniscus		X		X		X		X		Thomsen (1998)
			Pan paniscus	X				X	X		X		Hohmann (1992)
			Pan paniscus		X		X		X		X		Thomsen & Fruth (1997)
			Pan paniscus		X		X		X			X	de Waal & Lanting (1997)
			Pan paniscus	X			X		X			X	de Waal & Lanting (1997)
			Pan troglodytes			X	X		X			X	Cronin et al. (2016)
			Pan troglodytes	X			X		X			X	de Waal (1988)
			Pan troglodytes		X		X		X			X	Fitzgerald (1977)
			Pan troglodytes	X			X		X			X	Fitzgerald (1977)
			Pan troglodytes			X	X		X			X	Freeman & Ross (2014)
			Pan troglodytes		X		X		X			X	Fritz et al. (1992)
			Pan troglodytes			X	X		X			X	Gallup (1971)
			Pan troglodytes		X		X		X			X	Gentry et al. (1988)
			Pan troglodytes	X			X		X			X	Garaham & Struthers (1988)
			Pan troglodytes		X		X		X			X	Guerrier (2011)
			Pan troglodytes		X		X		X			X	King et al. (1980)
			Pan troglodytes	X			X		X			X	King et al. (1980)
			Pan troglodytes			X	X		X			X	Kollar (1972)
			Pan troglodytes		X		X		X			X	Kollar et al. (1968)
			Pan troglodytes	X			X		X			X	Kollar et al. (1968)
			Pan troglodytes		X		X		X			X	Kollar et al. (1968)
			Pan troglodytes	X			X		X			X	Kollar et al. (1968)
			Pan troglodytes		X		X		X			X	Kraemer et al. (1982)
			Pan troglodytes		X		X		X			X	Leger (1977)
			Pan troglodytes	X			X		X			X	Leger (1977)
			Pan troglodytes	X			X		X			X	Lemmon et al. (1975)
			Pan troglodytes		X		X		X			X	Lopresti-Goodman et al. (2013)
			Pan troglodytes		X		X		X			X	Riesen (1971)
			Pan troglodytes		X		X		X			X	Rogers & Davenport (1969)
			Pan troglodytes	X			X		X			X	Savage & Malick (1977)
			Pan troglodytes		X		X		X			X	Savage & Malick (1977)
			Pan troglodytes		X		X		X			X	Shefferly & Fritz (1992)
			Pan troglodytes		X		X		X		X		Böer (1992)
			Pan troglodytes		X		X	X	X		X		Hauser (1992)
			Pan troglodytes		X			X	X		X		Stanford (1992)
			Pan troglodytes	X				X	X		X		Stanford (1992)
			Pan troglodytes		X		X		X		X		Peignot (1997)
			Pan troglodytes		X		X		X		X		Wrogemann (1998)
			Pan troglodytes		X		X		X			X	Schapiro et al. (2005)

				Sex			Living environment		Masturbation occurence		Source type		
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Unknown**	**Captive**	**Wild**	**Present**	**Absent**	**Questionnaire**	**Publication**	**Reference**
			Pan troglodytes		X		X		X			X	van Hoof (1967)
			Pan troglodytes	X			X		X			X	van Hoof (1967)
			Pan troglodytes		X			X	X			X	van Lawick-Goodall (1968)
			Pan troglodytes	X				X	X			X	van Lawick-Goodall (1968)
			Pan troglodytes		X		X			X		X	Vonk & Vedder (2013)
			Pan troglodytes	X					X			X	Wrangham (1993)
			Pan troglodytes schweinfurthii		X			X	X			X	Nishida (1997)
			Pan troglodytes schweinfurthii	X				X	X			X	Nishida (1997)
			Pan troglodytes schweinfurthii		X			X	X			X	O'Hara & Lee (2006)
			Pan troglodytes schweinfurthii		X			X	X			X	Nakamura (2018)
			Pan troglodytes troglodytes		X		X		X		X		Jaffe (2018)
			Pan troglodytes troglodytes	X			X			X	X		Jaffe (2018)
			Pan troglodytes vellerosus										
			Pan troglodytes verus		X		X		X		X		Jaffe (2018)
			Pan troglodytes verus	X			X		X		X		Jaffe (2018)
			Pan troglodytes verus		X			X	X		X		Yamakoshi (1997)

Note that Table 02.02 includes data for taxa that were not included in the taxonomy and subsequent phylogenetic analyses (see section 2.4.1). Table 02.03 highlights these cases.

Table 02.03. Overview of available data on masturbation presence and absence in species not present within the 10kTrees phylogenies. See following page.

				Sex			Living environment		Masturbation occurrence		Source type		
Semiorder	Infraorder	(Sub)family	Latin name	Female	Male	Unknown	Captive	Wild	Present	Absent	Questionnaire	Publication	Reference
Strepsirrhini	**Lemuriformes**	**Lemuridae**	*Eulemur rufifrons*		X			X	X		X		Peckre et al. (2018)
			Eulemur rufifrons	X				X		X	X		Peckre et al. (2018)
		Indriidae	*Avahi meridionalis*		X			X		X	X		Campera (2021)
			Avahi meridionalis	X				X		X	X		Campera (2021)
		Lepilemuridae	*Lepilemur fleuretae*		X			X		X	X		Campera (2021)
			Lepilemur fleuretae	X				X		X	X		Campera (2021)
Haplorrhini	**Tarsiiformes**	**Tarsiidae**	*Tarsius tarsier*		X		X			X	X		Hidayatik (2018)
			Tarsius tarsier	X			X			X	X		Hidayatik (2018)
			Tarsius sp.		X					X	X		Sajuthi (2018)
			Tarsius sp.	X						X	X		Sajuthi (2018)
		Callicebinae	*Plecturocebus cupreus*		X			X		X	X		Heymann (1998)
			Plecturocebus cupreus		X			X		X	X		Dolotovskaya & Heymann (2021)
			Plecturocebus cupreus	X				X		X	X		Dolotovskaya & Heymann (2021)
		Atelinae	*Ateles chamek*	X			X		X		X		Brindle (2018)
		Cebidae	*Sapajus flavius*		X			X		X	X		Brindle (2018)
			Sapajus flavius	X				X		X	X		Brindle (2018)
			Saimiri sp.		X		X		X		X		Bernhards (1998)
		Callitrichidae	*Saguinus labiatus*		X		X			X	X		Epple (1992)
			Saguinus labiatus	X			X			X	X		Epple (1992)
	Catarrhini	**Cercopithecinae**	*Papio hamadryas, P. cynocephalus, & hybrids*		X		X		X		X		Colmenares (1992)
			Papio hamadryas, P. cynocephalus, & hybrids	X			X		X		X		Colmenares (1992)
			Papio sp.		X		X		X			X	Coelho & Bramblett (1982)
			Papio sp.			X	X		X			X	Johnson et al. (2015)
		Hylobatidae	*Hoolock leuconedys*		X		X			X	X		Kumar (2021)
			Hoolock leuconedys	X			X			X	X		Kumar (2021)
		Ponginae	*Pongo sp.*		X		X		X			X	Nadler (1988)
			Pongo sp.	X			X		X			X	Nadler (1988)
			Pongo sp.		X		X		X			X	Maple (1980)
			Pongo sp.		X			X	X		X		van Schaik (1997)
			Pongo sp.		X		X			X	X		Böer (1992)
			Pongo sp.	X			X			X	X		Böer (1992)
			Pongo sp.		X			X	X		X		Kunz (2019)
			Pongo sp.	X				X	X		X		Kunz (2019)
		Homininae	*Gorilla sp.*		X		X		X			X	Gould & Bres (1986)
			Gorilla sp.	X			X		X			X	Gould & Bres (1986)
			Gorilla sp.		X		X		X			X	Gould (1982)
			Gorilla sp.	X			X		X			X	Gould (1982)
			Gorilla sp.	X			X		X			X	Schaller (1963)
			Gorilla sp.		X		X		X			X	Schaller (1963)
			Gorilla sp.		X		X		X		X		Meder (1998)

2.5 Discussion

This database represents the first large-scale, comparative collection documenting the diversity and forms of masturbation in both female and male primates. I was able to collate the largest amount of information on apes, followed by the other catarrhines, which was expected given how well studied these groups are. Neotropical primates were more mixed, with some species providing a wealth of data and others none at all. I garnered the least information on strepsirrhines and tarsiers. In terms of sex, I was able to obtain far more reports for males than for females.

Unsurprisingly, species with more data overall tended to also have more reports indicating that masturbation was present. For example, 96.4 % of reports for rhesus macaques (*Macaca mulatta*), and 95.9 % of reports for chimpanzees, stated that masturbation occurred. Conversely, species with less data overall tended to have a larger proportion of reports indicating masturbation absence. This probably reflects the fact that reports of masturbation absence needed to be sought via targeted questionnaires, rather than being found in the literature, since reports claiming that a behaviour does not occur are less likely to be written or published.

2.5.1 Observer bias

It is important to recognise that the database is subject to various biases. Masturbation remains a relatively rare behaviour across the primate order and, as such, has not been examined as thoroughly as others. With the exception of a handful of studies, if masturbation is noted or described, it is as an aside to the main aims and direction of a research article. This increases the likelihood that instances of masturbation may have been missed during my literature search, a problem amplified by the common use of oblique language to describe autosexuality. It is also highly likely that some studies will have been missed altogether, as euphemistic language would not have been picked up by the search terms used.

Despite a thorough, targeted questionnaire campaign designed to fill the gaps in the database, there are still little or no data for certain important radiations within the primate order. The relatively complete coverage of apes by comparison to strepsirrhines may reflect that the former have been studied in greater detail than the latter. Similarly, masturbation is documented for woolly monkeys (*Lagothrix spp.*), muriquis (*Brachyteles spp.*) and three of five species of spider monkey (*Ateles spp.*); given how closely related these taxa are, it is thus likely that missing information for the remaining two atelid species reflects a lack of observation or reporting, rather than non-occurrence. Conversely, human observers may label a behaviour more readily as masturbation if displayed by catarrhines – because their morphology and psychology are similar to our own, while we differ much more from platyrrhines, and even more so from tarsiers and strepsirrhines.

In certain clades, such as strepsirrhines and callitrichids, non-sexual behaviours, such as genital scent-marking, may conceal cases that would otherwise be considered masturbation. I employed a conservative approach, opting to exclude cases in which masturbation was uncertain, to establish as much confidence as possible in the database. This may be problematic in instances where the boundaries between behaviours are blurred, for example if an individual was sexually aroused and gained pleasure while anogenitally rubbing. Future research on masturbation in clades who routinely manipulate the ano-genital region would be instructive.

While it is entirely possible that masturbation is extremely rare, or non-existent, in certain clades, it is likely underreported for (i) species most active at night (e.g. night monkeys, *Aotus spp.;* lorises, *Loris spp.*; and aye-ayes, *Daubentonia madagascariensis*), (ii) species that spend much of their time inside tree-hollows (e.g. galagos, lorises, and tamarins, *Saguinus spp.*) or leaf-nests (e.g. mouse lemurs, *Microcebus spp.;* and aye-ayes), and (iii) small-bodied species which are often less easily observable (e.g. many strepsirrhines and callitrichids). Indeed, many of the strepsirrhines in which masturbation has been confirmed are either diurnal or common in captivity, and thus more easily observed. The database is therefore likely biased towards diurnal species, or nocturnal species that are regularly observed in zoos. Similarly, the relative paucity of data for arboreal diurnal species, such as colobines (*Colobus spp.;* 0 data sources, Table 02.01) and guenons (*Cercopithecus spp.;* 4 data sources, Table 02.01), by comparison to more terrestrial species, such as baboons (*Papio spp.;* 27 data sources, Table 02.01), may reflect the fact that it is more difficult to observe primates high in the canopy than on the ground. Overall, this suggests that the reported occurrence, or lack thereof, of masturbation in this dataset may have been influenced by the level of ease with which different species may be observed.

2.5.2 Limitations

Maximising species-level data entailed a trade-off with gathering individual-level information, and the fact that most sources were only used to gain species- and sex-level differences means that intra-specific variability may be harder to pick up in some circumstances. However, the majority of data collated for this research were garnered from pre-existing literature, most of which did not directly examine masturbation, making it difficult to definitively ascribe behaviour(s) to single individuals within a study, or sometimes even to know how many individuals were being described.

By the criteria presented here, a single report of masturbation for a given species overrode any reports of absence. While this allows us to accurately describe the phenotypic potential for a species to masturbate, it is a simplistic approach. For example, rhesus macaques, who masturbate regularly, are classed the same as Senegal bushbaby's (*Galago senegalensis*), for whom there is only one report of masturbation. This highlights an important issue with phylogenetic comparative methods, which often require that, regardless of the amount of intraspecific variability, a species is condensed down to one data point.

A final bias concerns humans, for whom data was restricted to two classic sources (Kinsey et al., 1948, 1953). While these landmark works are comprehensive, they do not represent cross-cultural norms, given that the studies were conducted with American citizens. Moreover, cultural attitudes have changed dramatically since they were published, and it is therefore important to view the findings through the lens of the prevailing zeitgeist. Ultimately, however, it is important to remember that sexual behaviour reflects a continuum. Imposing a discrete ordering system on an uninterrupted scale will be messy and can be misleading. The same is true when facets of sexual behaviours are classified so as to fit into categories of sexual orientation such as 'straight' or 'LGBTQAI+', another problematic attempt of essentialising a continuous natural spectrum (Bryson et al. 2018).

It is hoped that this database will provide the framework and impetus for future behavioural studies to incorporate an assessment of masturbation status into research protocols. Increased observation effort will provide greater confidence that absence reports truly reflect a lack of occurrence and, where masturbation is present, facilitate the collection of sufficiently detailed data to calculate masturbation rates, for at least a representative sample of taxa.

2.6 Chapter summary

In Chapter 02, I first discussed historical definitions of masturbation, before developing the working definition used in the present work. I then compiled and categorised the scattered published information pertaining to masturbation in the primate order. Where there was a scarcity of information for a given clade or taxa, data were supplemented with questionnaire responses from primatologists, zoo staff, and others with extensive experience with a given taxa. Finally, I described the patterns of data availability and coverage. Together, these sources provide a total of 569 separate reports of masturbation from across the primate order, in both females and males.

CHAPTER 03

THE NATURAL HISTORY OF PRIMATE MASTURBATION: WHO, HOW, AND WHERE?

3.1 Abstract

Many vertebrate animals engage in masturbation, but it is particularly prevalent in primates. The purpose of this chapter is threefold, aiming to: (i) identify the sex and genera in which masturbation is observed across the primate order, (ii) describe the forms this behaviour takes, and (iii) examine the environment in which it occurs. I found that masturbation was present in 19 of the 45 genera for which information is available on females (42.2 %), and 36 of the 51 genera for which information is available on males (70.6 %), with the highest prevalence in catarrhines, and lowest prevalence in tarsiers. I then subset the data to examine the form masturbation took in the individuals in which it was observed (94/163 reports for females, 307/381 reports for males). The results of these analyses indicate that the genitals, especially the clitoris and penis, are the most targeted body parts, and self-stimulation is most frequently carried out with the hands and fingers. Substrates and objects were also used by both sexes, although females were over four times more likely than males to use either. Bodily motions (such as rubbing, thrusting, and pressing) and manual techniques (such as holding, stroking, patting, and pulling) were favoured means of stimulation. Masturbation was associated with varying degrees of excitement and occasionally facial expressions and gestures, and was sometimes directed at other individuals or objects. Orgasm was reported far more often in males than in females and was sometimes associated with ejaculate consumption. In most instances, masturbatory episodes tended to be fairly short, lasting no longer than a minute.

Masturbation occurred in wild-living individuals, as well as captives, indicating that this behaviour is not a pathological outcome of captivity. Together, the results of this chapter map the masturbatory landscape of the primate order, highlighting the distribution, diverse forms, and context of this widespread behaviour.

3.2 Introduction

To date, there has been no systematic, comparative research into the wide variety of forms masturbation can take, across any group of animals. This is a crucial first step in forming research questions and hypotheses regarding its ultimate function. This chapter first discusses the value of studying the natural history of masturbation (section 3.2.1), before briefly illustrating some of the diverse forms it takes across the wider animal kingdom (section 3.2.2). Next, the primate order is examined in detail, utilising the large-scale, comparative database compiled in Chapter 02, taking the analytical approach described in section 3.3. First, the presence and absence of masturbation is mapped in females and males (section 3.4). Following this, the forms of masturbation are reviewed with respect to body parts stimulated, devices used, techniques, associated traits, and temporal context (section 3.5). Finally, the broader context of masturbation is described (section 3.6), both in terms of living environment and demographics. Understanding the natural history of masturbation will provide a solid base for exploration of its evolutionary trajectory within the primate order (Chapter 04) and its potential functional significance (Chapter 05).

3.2.1 The natural history of masturbation

Natural history can be defined as "*the observational study of organisms in their environment*" (Barrows et al., 2016, p. 592). Once highly-valued for its own sake and a respected component of scientific endeavour, the discipline has become unfashionable of late. The 19th century saw the emergence of avowed naturalists, who studied, documented and classified the world around them, and many important biological advances during this time were built on these foundations (Barrows et al., 2016). Indeed, natural history was once described as

> "*at once the beginning and end of biological study. The beginning, because almost everyone who has left an impress in biological research has been drawn to these studies by contact with nature and by the love of first hand knowledge, – the end, because all forms of biological experiment and observation lead finally towards the greater problems the aggregate of which we call Life.*" (Jordan, 1916, p. 3)

More recently, however, the study of natural history appears to be in decline (cf. Schmidly, 2005; Suarez & Tsutsui, 2004; Tewksbury et al., 2014), and natural historians are often dismissed as 'old fashioned', or even uninformed about advances in scientific methodology. The proportion of researchers with PhDs in natural history-related fields in the US declined steeply between the 1960s and 2000s (Figure 03.01), and undergraduate courses have followed suit, with biology degrees incorporating less and less natural history (Tewksbury et al., 2014). Correspondingly, the number of natural history articles published is also declining sharply (McCallum & McCallum, 2006), and it has been suggested that this reflects a worrying trend towards greater disconnect from nature in the general population (Balmford et al., 2009; Tewksbury et al., 2014).

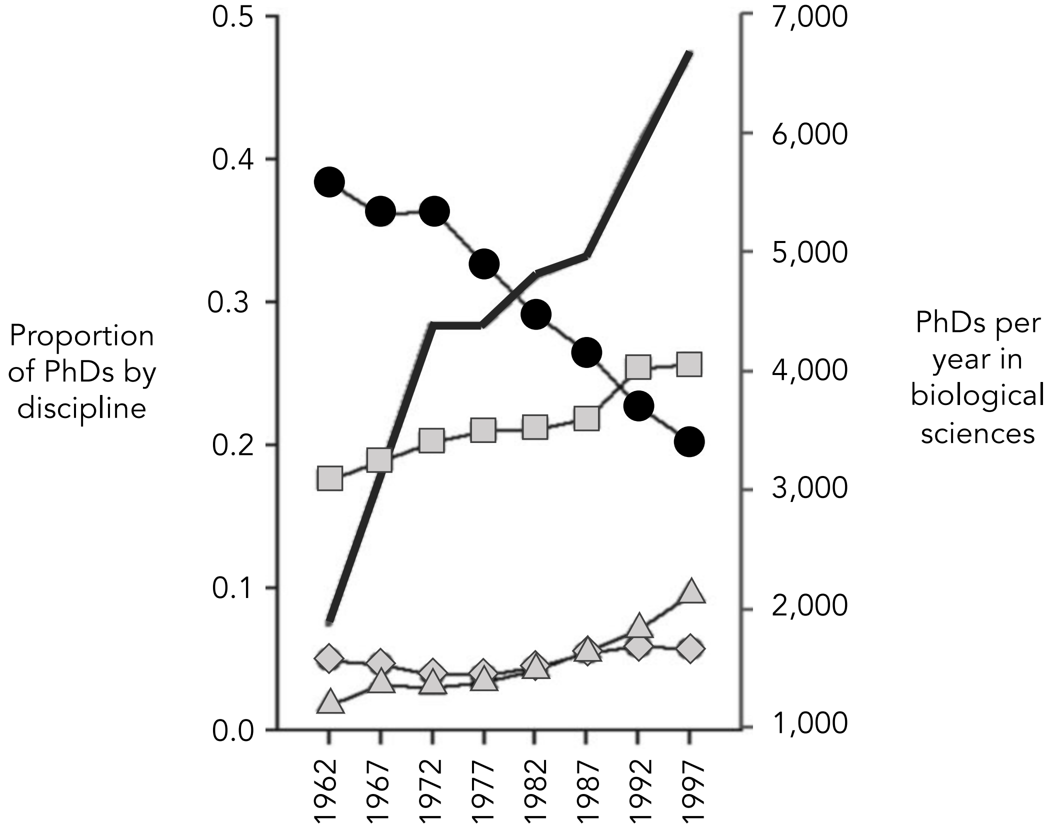

Figure 03.01. The number of biology PhDs issued by US institutions between 1962 and 1997 (solid black line); and the proportion of natural history-related degrees (solid black circles), microbiology and molecular biology (grey squares), biophysics and neurology (grey triangles), and genetics (grey diamonds). Figure adapted from Tewksbury et al., 2014.

Despite this shift, it is important to remember that the scientific method and natural history are not mutually exclusive. In order to study an underlying biological process, such as how a trait has evolved, we must first comprehend the diversity in the product of that process (i.e. its natural history). As summarised by Jordan (1916): "*observation comes first and then experiment and both lead from the gathering of facts to the contemplation of causes. Experiment is not necessarily nobler than observation because it comes later.*"

(Jordan, 1916, p. 3). A deep understanding of the natural history of an organism, process, or behaviour is a crucial first step in beginning to ask scientific questions. With this in mind, it is essential to understand the diverse forms and variability of masturbation across the animal kingdom, before forming research questions and hypotheses.

To date, there has been no systematic, cross-taxa comparison of the forms of masturbation across any group of animals. Even comparative data collection on the presence/absence of masturbation has been limited in scope, and has almost universally ignored female masturbation. Unsurprisingly, hypotheses regarding the functions of masturbation have often been based on observations of a single species, and designed to account for masturbation in males, even if it is possible to extrapolate them to females, too (Thomsen, 2000; Thomsen, 2004; Waterman, 2010; Wikelski & Bäurle, 1996). Identifying different types of masturbation, and the contexts in which they occur, will help us to understand why masturbation occurs and what its potential functions might be, if any. It is commonly assumed, for example, that masturbation is a pathological behaviour, or an artefact of captivity (Dittrich, 1968; Laqueur, 2003); understanding the broader context of this behaviour, in a sample of different species, would allow this belief to be addressed. If self-stimulation has only been reported in captive animals, the idea cannot be refuted, but the presence of masturbation in healthy, free-living populations would indicate that masturbation cannot simply be a consequence of captivity.

Documenting the natural history of masturbation will also help to develop our understanding of what it actually is, by establishing clearer boundaries for this behaviour. Given how widely self-stimulation varies between species, many researchers may not recognise the behaviour when they see it. An approach that values and encourages continued observation and documentation is more likely to reveal reports that challenge existing conceptions of what constitutes masturbation, enabling our understanding to be refined. Establishing a clear, incontrovertible means of classifying the behaviour will allow researchers to easily include masturbation in research protocols and ethograms, thus greatly increasing data yield.

Understanding, and communicating, the natural history and forms of masturbation across the animal kingdom has an additional benefit, not rooted in scientific research. Many members of the public are unaware, and often shocked, that animals other than humans masturbate (personal observation). Imparting an understanding that masturbation is not a strange, human aberration, but is a perfectly 'natural' behaviour may help to combat cultural stigma and taboos surrounding masturbation.

3.2.2 Heads, shoulders, flippers and paws: masturbation by any means

With the exception of a handful of studies, research into masturbation in other animals is still nascent, and little attention has been paid to broad cross-taxa patterns, in terms of form and context. However, masturbation is widespread across the animal kingdom, appearing in a multitude of forms and contexts. Masturbation has been reported across a variety of non-primate mammals, as well as in reptiles and birds (see Chapter 01). While data are too scant to provide a comprehensive review of masturbation in other animals with respect to its prevalence in different clades and sexes, or trends regarding its form and context, illustrative examples may be used to paint a broad picture.

Vast morphological variability necessitates a diverse array of means by which self-stimulation can be attained, incorporating different body parts, stimulation devices, and techniques. Even animals without the ability to touch their genitals with prehensile appendages masturbate. Male red deer (*Cervus elaphus*) shed their antlers in spring and develop a new pair in the summer, ready for the autumn rutting season (Darling, 1937). By this time, the new antlers have hardened and, intriguingly, constitute a highly sensitive erogenous zone (Ford & Beach, 1951). The stags may then masturbate to ejaculation by "*lowering the head and gently drawing the tips of the antlers to and fro through the herbage (...) ejaculation follows about five seconds after the penis is erected, so that the whole act takes ten to fifteen seconds*" (Darling, 1937, p. 161). A stag may masturbate multiple times per day in this manner, even in the presence of their own harem of females, with whom they could copulate (Darling, 1937). Different techniques are demonstrated by cetaceans, who stimulate themselves in a plethora of ways. Bottlenose dolphins (*Tursiops truncatus*) hold their erect penises in the water jets of their enclosures, rub them on the floor, and have even been observed enveloping them in live eels (McBride & Hebb, 1948). While a, now infamous, YouTube clip shows a captive Amazon river dolphin (*Inia geoffrensis*) thrusting his penis into the remains of a decapitated fish (Figure 03.02; Vit Kol, 2015). Other animals make up for their lack of manual dexterity by using other parts of their bodies, such as the mouth.

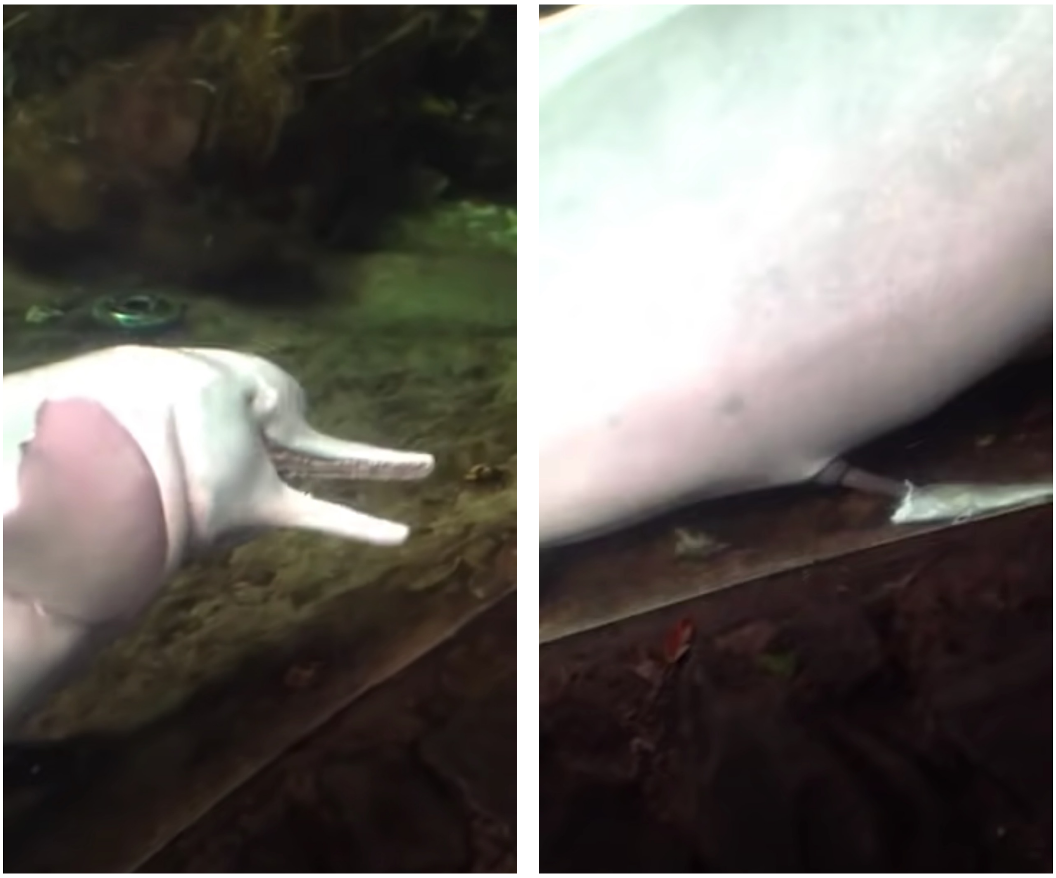

Figure 03.02. A male Amazon river dolphin (*Inia geoffrensis*) inserting his penis into the body cavity of a decapitated fish. Stills taken from YouTube footage (Vit Kol, 2015).

Masturbation may also be heavily context-dependent in different animals. For example, when female North American porcupines (*Erethizon dorsatum*) are in oestrus, excited males have been observed to hold their genitals with their forepaws, rub them on substrates within their cage, and straddle long sticks "*as a child does a broomstick*" (Shadle, 1946, p.159), stimulating their genitals and soaking the stick with urine and glandular secretions in the process. Consequently, when the stick is sufficiently odorous, it becomes "*a source of sexual stimulation*" for both sexes – although whether this refers to physical or mental stimulation is unclear (Shadle, 1946, p. 160).

3.3. Analytical approach

3.3.1 Definitions of behaviours

I opted to follow the descriptions of masturbation provided in the original sources when compiling and categorising data, rather than attempting to standardise them according to my own interpretations, since this could bias the database. By collating non-standardised data in this way I hope to (i) present the data in the greatest level of detail possible (which varies by source) and (ii) gain a better understanding of the ways in which observations can be categorised and reported most effectively in future research protocols. For example, it might be recommended that instead of consolidating these body parts under the single category of 'genitalia', or specifying them in too great a level of detail (e.g. labia majora, labia minora, perineum etc.), that researchers should in future only differentiate between the clitoris, other areas of the vulva, and vagina.

While this approach does not affect my analyses where sources use globally accepted categories (e.g. female and male), there are implications in cases where authors take different approaches, or differ in their level of precision (as discussed in Chapter 02, section 2.4.2). In these instances, the data must be treated with caution, since some categories are not mutually exclusive. For example, in the case discussed above, females who touch their clitoris would not be represented within the group that were described as touching their genitalia, even though the clitoris forms part of the genitals. While I could take the approach of grouping all reports that identify a specific part of the genitalia together with those that only refer to 'the genitals', this would significantly reduce the level of detail in which the different facets of masturbatory behaviour could be examined.

Similarly, authors may use different terminology to describe the same thing. For example, the masturbatory techniques 'handle' and 'fondle' are likely very similar, while 'pat' and 'slap' may or may not be the same action, depending on the force with which the hand makes contact with the body. This may lead to underestimates of the frequency of a given behaviour, if it is distributed across multiple categories.

It is also important to note that most sources did not cover all variables. For example, a report may state that the genitals were stimulated for 30 seconds, without including any information about which stimulation device was used, or whether there were associated traits or physiological correlates. The following results only examine the data that were reported (i.e. a failure to mention a behaviour in a report was not assumed to indicate its absence). Conversely, some reports include multiple different descriptions of the same event, so that one episode may cover multiple categories (for example when masturbation events involved a combination of different behaviours). An example of this would be if a female masturbated by manually rubbing her nipples, while also stimulating her clitoris on a substrate and/or inserting an object into her vagina. Together, this means that each category of behaviour does not always tally to 100 %. It is important to bear in mind, therefore, that the following results indicate the percentage of occasions when a given behaviour happened, but that does not mean that the behaviour was the only one that occurred. In other words, behaviours were not always mutually exclusive.

3.3.2 Calculating summaries

Given the potential biases associated with missing data, the calculation of percentages to describe the relative frequency of different behaviours or categories could be carried out in one of two ways. The first approach would be to calculate the percentage values from only the sources that specify the relevant data (e.g. if only half of the sample report whether or not female orgasm occurred, the percentage of orgasm presence versus absence would be reported from that sample). However, this approach is vulnerable to potential reporting biases if (i) a behaviour is difficult to assess, and therefore the author does not feel confident in reporting it, even if they have been looking out for it; (ii) a behaviour is subtle or cryptic and thus easily missed, so the reporter does not notice it; or (iii) a behaviour is common or unremarkable, so the reporter does not think to record it. A physiological correlate associated with masturbation that may be affected by such bias is female orgasm, which may be difficult to assess, while also being cryptic and easily missed, but very likely to be reported in cases where it is conspicuous. In this case, if percentages were only calculated based only on confirmed presence or absence reports, female orgasm would be dramatically overestimated. The second approach, and the one adopted here, is to calculate percentages from the whole sample of individuals that masturbate, not just those for which data are available for a particular variable. This approach is likely to underestimate the occurrence of behaviours as a proportion of the whole sample (since behaviours may occur but go unreported), but should adequately highlight key trends.

3.3.3 Pseudoreplication

In most cases, there were insufficient data to characterise the autosexual behaviour of a particular species. For this reason, data were combined across taxa, in order to maximise the data available for analysis.

While pseudoreplication is not controlled for in these analyses, its presence is taken into account when the results are interpreted, particularly when observed patterns may reflect disproportionate representation of a given species. For example, taxa with the most sources confirming masturbation presence or absence are likely overrepresented within the analyses, especially rhesus macaques (*Macaca mulatta*), chimpanzees (*Pan troglodytes*), Japanese macaques (*Macaca fuscata*), stump-tailed macaques (*Macaca arctoides*), Western gorillas (*Gorilla gorilla*) and chacma baboons (*Papio ursinus*), all of which are represented by at least 10 sources (Chapter 02, section 2.4.3). Additionally, certain taxa may be more likely to be represented in particular categories. For instance, rhesus macaques are likely to be overrepresented in captivity, since they are common subjects for biomedical research. Similarly, the apes are likely overrepresented in summaries of masturbatory tool use.

Importantly, problems with pseudoreplication only apply to analyses presented in sections 3.4.2 (*Individual phenotype*) onwards. For analyses of masturbation occurrence across genera (section 3.4.1), a single value of presence or absence was assigned to each genus, on the basis of at least one report confirming masturbation presence, so pseudoreplication will not be an issue in these analyses.

3.3.4 Statistical analysis

Because of the combined difficulties outlined above (non-standardised behavioural definitions, missing data, and pseudoreplication in the sample), the summaries presented in the following section are purely descriptive, with no formal statistical tests carried out. Importantly, the following analyses are not designed to provide an authoritative or systematic overview of how primates masturbate, but instead aim to illustrate the range of autosexual behaviours that have been reported, and to provide a starting point for future analyses in the hope that they will be employed as part of a more systematic and quantitative approach.

3.4 Who? Masturbation across the primate order

3.4.1 Presence and absence of masturbation

The database compiled in the present study collates the scattered literature on autosexual behaviour across the primate order, charting where it is present and absent, as well as the forms it takes. Occurrence data can be visualised over a phylogeny, thus providing information on how masturbation is distributed in relation to the evolutionary relationships between species, with shading illustrating masturbation presence or absence for females and males separately (section 3.4.1; Figure 03.03). In addition to examining which species of primate masturbate, and which do not, the individual phenotypes of those that do masturbate are considered with respect to age-class and dominance-rank (section 3.4.2).

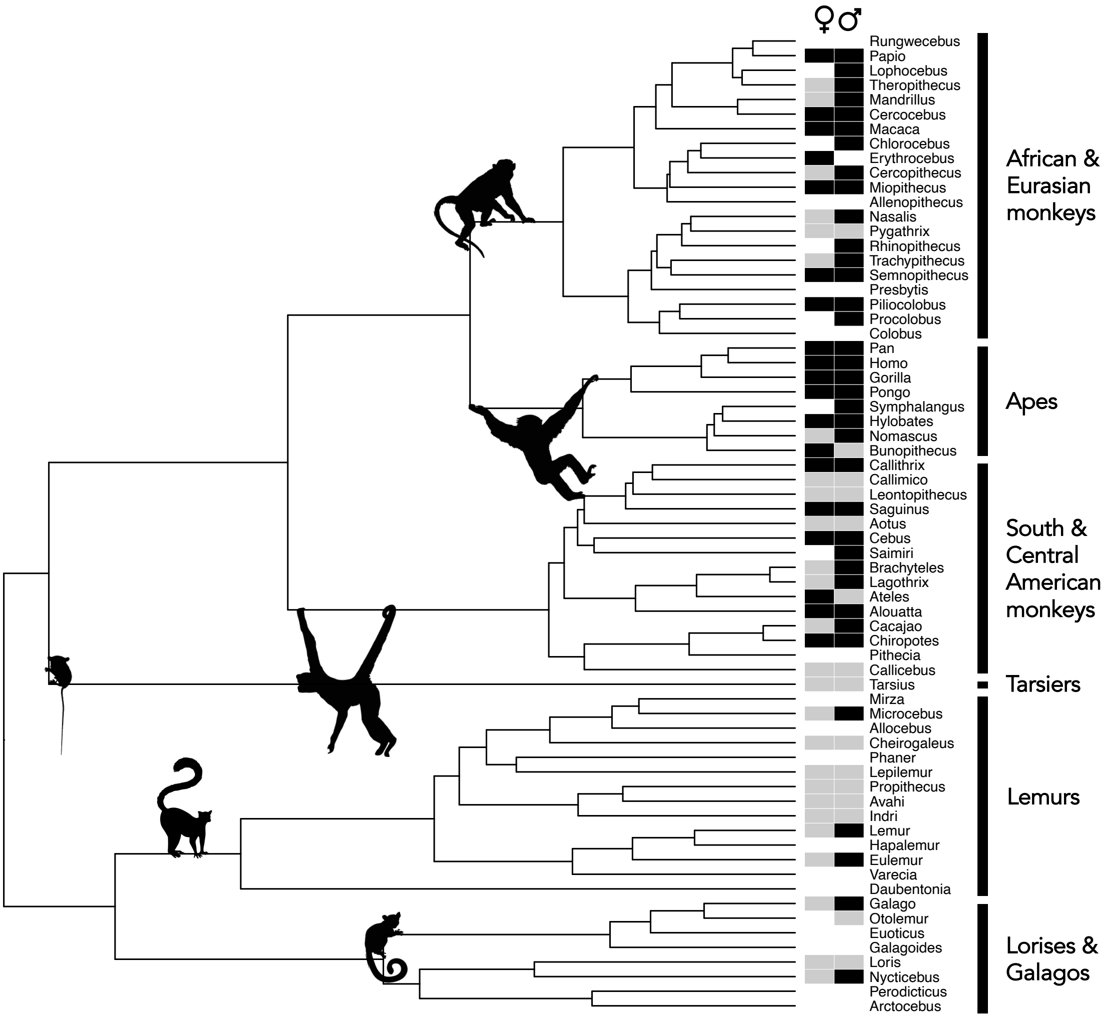

Figure 03.03. Phylogeny of 68 genera of the primate order, with reported presence (black squares) or absence (grey squares) of masturbation in females (♀) and males (♂) in at least one species of that genus. Empty tips indicate a lack of data. Maximum Clade Credibility tree created from a sample of 10,000 molecular phylogenies from the 10kTrees project (Arnold et al., 2010).

Information regarding females was available for 45 genera (67.2 %), and masturbation occurred in 19 of these (42.2 %), while it was absent in 26 (57.8 %). Notably, there is not a single genus of strepsirrhine (lorises and galagos, lemurs) or tarsier in which females have been reported to masturbate. Female masturbation is therefore not reported in a large proportion of primate radiations (tarsiers, lemurs, lorises and galagos) while occurring in the remainder (platyrrhines and catarrhines).

Information was available for males of 51 genera (76.1 %), and masturbation occurred in 36 of these (70.6 %) while it was absent in 15 (29.4 %). Male masturbation therefore occurs in most major primate radiations, with tarsiers being the exception.

Therefore, within the major primate radiations, autosexual behaviour is never observed in tarsiers of either sex, or in female strepsirrhines, while being almost entirely absent in male strepsirrhines. Platyrrhines largely masturbate, albeit with certain exceptions. Masturbation occurs much more commonly, and almost universally, in all genera of African and Eurasian monkeys, small apes, and large apes.

3.4.2 Individual phenotype

Patterns of individual variation in autosexual behaviour in female and male primates are summarised in Table 03.01.

Table 03.01. An overview of female and male masturbation in relation to two other axes of individual variation, namely age and dominance rank, where percentages are relative to the total number of reports in which masturbation was present for the respective sex (n = 94 for females, n = 307 for males). See following page.

Individual phenotype		**Females** Reports (n)	**Females** Percentage	**Males** Reports (n)	**Males** Percentage
Age	Adult	58	61.70%	161	52.61%
	Subadult	8	8.51%	77	25.16%
	Juvenile	15	15.96%	45	14.71%
	Infant	5	5.32%	25	8.17%
Dominance	High	2	2.13%	14	4.58%
	Medium	3	3.19%	5	1.63%
	Low	4	4.26%	14	4.58%

Age-class was given in 72 reports on females, and 188 reports on males. In reports that confirmed masturbation presence, by far the largest age-group who masturbated were adults, in both females (61.7 %) and males (52.6 %). The next largest demographic were juveniles for females (16.0 %, 14.7 % of males), and subadults for males (25.2 %, 8.5 % of females). It is important to note that many observers may not have distinguished a ‘subadult’ category for females of some species, since they do not always have a discernible ‘subadult’ stage, instead transitioning directly to adulthood after the juvenile period (e.g. in baboons). Infants of both sexes also masturbated, but were reported less than other age ranges (5.3 % of female reports, 8.2 % of male reports).

Information on dominance rank was provided in 8 reports on females, and 39 reports on males. Masturbation reports did not appear to vary in frequency between dominance ranks, with no marked differences between low- (4.3 % and 4.6 % for female and male reports, respectively), middle- (3.2 % and 1.6 % for female and male reports, respectively), or high-ranking individuals (2.1 % and 4.6 % of female and male reports, respectively). It is likely, therefore, that this varies between species, an examination of masturbation occurrence across different ranks within species would be instructive in exploring whether masturbation is a sexual outlet, or may serve an adaptive function for those with fewer copulatory opportunities (e.g. the Sexual Arousal and Sperm Quality hypotheses). Studies documenting dominance rank in masturbating individuals are listed in table 03.02.

Table 03.02. An overview of studies that document the dominance rank of masturbating individuals. See following pages.

				Sex		Dominance rank				
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**High**	**Middle**	**Low**	**All/mixed**	**Reference**
Strepsirrhini	**Lemuriformes**	**Lemuridae**	*Eulemur fulvus fulvus*		X	X				Ganzhorn (1992)
		Cheirogaleidae	*Microcebus murinus*		X			X		Zimmermann (1992)
	Lorisiformes	**Lorisidae**	*Nycticebus coucang*		X			X		Zimmermann (1992)
		Galagidae	*Galago senegalensis*		X			X		Zimmermann (1992)
Haplorrhini	**Platyrhhini**	**Alouattinae**	*Alouatta palliata*	X				X		Whitehead (1992)
		Cebidae	*Cebus apella*		X			X		Westergaard (1992)
		Callitrichinae	*Callithrix jacchus*		X	X	X			Radespiel (1992)
			Callithrix jacchus		X	X				Rothe (1975)
			Saguinus oedipus oedipus		X		X			Benning (1992)
	Catarrhini	**Cercopithecinae**	*Macaca arctoides*		X	X				Kling & Dunne (1976)
			Macaca arctoides		X				X	Nieuwenhuijsen et al. (1986)
			Macaca arctoides		X				X	Nieuwenhuijsen et al. (1987)
			Macaca fuscata		X				X	Hanby et al. (1971)
			Macaca fuscata		X				X	Inoue (2012)
			Macaca fuscata	X					X	Rendall (1992)
			Macaca fuscata		X	X				Stephenson (1973)
			Macaca fuscata		X				X	Thomsen & Soltis (2004)
			Macaca maura	X				X		Petit (1992)
			Macaca mulatta		X			X		Boonratana (1992)
			Macaca mulatta		X				X	Dubuc et al. (2013)
			Macaca mulatta		X		X	X		Fisler (1967)
			Macaca mulatta		X				X	Ruiz de Elvira et al. (1982)
			Macaca nemestrina		X			X		Crowley (1983)
			Macaca nemestrina		X				X	Crowley et al. (1974)
			Macaca nigra		X	X	X			Curran (2018)
			Macaca nigra		X	X	X			Petit (1992)
			Macaca silenus		X				X	Skinner & Lockard (1979)
			Macaca sylvanus		X				X	Angst (1992)
			Macaca sylvanus		X				X	Paul & Küster (1992)
			Macaca sylvanus		X	X				Rümenas (1992)
			Macaca tonkeana	X			X			Preüschoft (1992)

				Sex		Dominance rank				
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**High**	**Middle**	**Low**	**All/mixed**	**Reference**
			Macaca tonkeana	X			X	X		Thierry (1992)
			Macaca tonkeana		X				X	Thierry (1992)
			Miopithecus talapoin		X				X	Keverne (1979)
			Miopithecus talapoin		X				X	Keverne et al. (1978)
			Miopithecus talapoin	X				X		Zimmermann (1992)
			Miopithecus talapoin		X			X		Zimmermann (1992)
			Papio hamadryas, P. cynocephalus, & hybrids	X		X				Colmenares (1992)
			Papio hamadryas, P. cynocephalus, & hybrids		X	X	X			Colmenares (1992)
			Papio cynocephalus papio		X				X	Petit (1992)
			Papio hamadryas		X	X				Weldon (2018)
			Papio ursinus		X			X		Bolwig (1959)
			Theropithecus gelada		X			X		Ramsay (2019)
		Colobinae	*Piliocolobus badius*		X	X		X		Starin (2004)
		Homininae	*Gorilla beringei*		X			X		Fossey (1983)
			Gorilla beringei		X			X		Fossey (1983)
			Pan paniscus	X		X	X			Hohmann (1992)
			Pan troglodytes		X				X	Stanford (1992)
			Pan troglodytes		X				X	van Hoof (1967)

3.5 How? Forms of masturbation

To help understand the range of variation in how primates masturbate, five different aspects of autosexual behaviour are considered: the body parts that are stimulated, such as the genitals or nipples (section 3.5.1); the stimulation device that is used, such as the hand or objects in the environment (section 3.5.2); the technique, such as rubbing or holding (section 3.5.3); a range of associated traits and physiological correlates, such as whether vocalisations or orgasm occur (section 3.5.4); and finally the temporal context, including the duration and frequency of masturbation (section 3.5.5).

3.5.1 Stimulated body parts

A variety of body parts are stimulated during primate autosexual behaviour (Table 03.03). Data describing stimulated body parts were available in 68 reports on females, and 160 reports on males.

Table 03.03. An overview of the body parts stimulated by female and male primates during masturbation, where percentages are relative to the total number of reports in which masturbation was present for the respective sex (n = 94 for females, n = 307 for males). See following page.

Body part stimulated		Females		Males	
		Reports (n)	Percentage	Reports (n)	Percentage
Sex nonspecific	Anus	4	4.26%	1	0.33%
	Genitals	23	24.47%	22	7.19%
	Glabella	0	0.00%	1	0.33%
	Nipples	7	7.45%	2	0.65%
	Rump	1	1.06%	0	0.00%
	Thigh	1	1.06%	0	0.00%
	Urethra	1	1.06%	1	0.33%
Female-specific	Anogenital-swelling	4	4.26%	-	-
	Breasts	5	5.32%	-	-
	Clitoris	28	29.79%	-	-
	Labia	2	2.13%	-	-
	Vagina	15	15.96%	-	-
	Vulva	6	6.38%	-	-
Male-specific	Glans-penis	-	-	1	0.33%
	Penis	-	-	152	49.67%
	Testicles	-	-	10	3.27%

Unsurprisingly, genitalia were the primary focus of stimulation for both sexes, and were mentioned without further specification (i.e. rather than specifically mentioning a clitoris or penis, for example), in 24.5 % of female reports, and 7.2 % of male reports. The reporting discrepancy between females and males is likely accounted for by the fact that penis tends to be far more conspicuous than the external genitalia of females. Possible exceptions include female atelids, who possess hypertrophied clitorises (Campbell, 2016), and male gorillas, whose external genitalia are incredibly small for their body size (Dixson, 1987).

Both sexes also stimulated their nipples (7.5 % of female reports, 0.7 % of male reports) – highly sensitive, specialised areas of the mammary glands – although females did so more often, perhaps due to greater tactile sensitivity (Robinson & Short, 1977). Surprisingly, histological evidence indicates that the nipple skin itself is not densely innervated. Instead, the high sensitivity may be related to a rich network of nerves present in the deep dermis, as well as the occurrence of specific mechanoproteins – sensory structures responsible for different types of mechanosensitivity, such as touch, pressure, and vibration (Gutiérrez-Villanueva et al., 2020). In human females "*kissing the nipples [or] touching them with the penis*" can lead to orgasm (Grafenberg, 1950), while three periovulatory rhesus macaque females were observed "*sucking their own nipple*s" (Carpenter, 1942, p. 152).

Other body parts stimulated by both sexes were the anus (4.3 % of female reports, 0.3 % of male reports), rump (1.1 % of female reports), thigh (1.1 % of female reports), urethra (1.1 % of female reports, 0.3 % of male reports), and, rather unusually, the glabella (0.3 % of male reports).

Some authors specified which areas of the genitals were stimulated, as presented below. It is important to note that these reports are separate to those in which authors simply reported 'genital' stimulation, so the actual rates of genital touching of some form are higher than those presented here.

Unsurprisingly, for females, the clitoris – which has been described as "*the most pivotal structure for female sexual pleasure*" (Pauls, 2015, p. 376) – received the most attention (29.8 % of reports). The clitoris, or 'clitoral complex', is a densely innervated structure, consisting of a glans, prepuce, body (or corpora), crura, bulbs, suspensory ligaments and root (Mazloomdoost & Pauls, 2015). A female stump-tailed macaque would "*stimulate her clitoris with her fingertips*" (Linnankoski et al., 1981, p. 212), while the clitoris of a Japanese macaque was "*rolled against the side of her ischial callosity or pulled and rolled between her thumb and the side of her index finger*" (Wolfe, 1984, p. 152). A wild chimpanzee, Fifi, "*was often seen to make thrusting movements of her pelvis whilst rubbing her clitoris against a branch on the ground*" (van Lawick-Goodall, 1968, p. 221), and a Hanuman langur (*Semnopithecus entellus*) frequently rubbed and pulled her clitoris, which soon extended to 2 cm in length (Dittrich, 1968). Females also stimulated the vagina (16.0 % of reports), vulva (6.4 % of reports), breasts (5.3 % of reports), anogenital swelling (4.3 % of reports), and labia (2.1 % of reports).

For males, the penis was the centre of attention (49.7 % of reports), followed by the testicles (3.3 % of reports). A male stump-tailed macaque "*kept his hand around the penis and moved either the hand or himself rhythmically as when mounting a female (…) After ejaculation the males kept the hand around the penis for about 1 min, which was the usual duration of a tieing* *[intromission]*" (Linnankoski et al., 1981, p. 219). Chimpanzees handle the penis or scrotum (Leger, 1977), and howler monkeys (*Alouatta palliata*) rub the scrotum against the heel of the foot, branches, or the terminal portions of the tail (Collias & Southwick, 1952).

Word clouds can be used as an (imprecise) visual aid, to help illustrate broad qualitative patterns within the database. Figure 03.04 depicts the body parts stimulated by primates during masturbation, with those that are more often reported represented by larger text (note that the word clouds are employed purely as illustrative devices, and are not to scale).

Figure 03.04. Illustrative word cloud, depicting the different body parts stimulated by primates during masturbation. Descriptors that are more often reported are represented by larger text (not to scale). Created with www.wordclouds.co.uk.

3.5.2 Stimulation devices

The type of stimulation device used by primates is highly variable, and includes limbs and extremities, as well as external tools (Table 03.04). Data describing stimulation devices were available from 65 reports on females, and 131 reports on males. The first part of Table 03.04 provides an overview across different body parts, objects and substrates, while the second part provides further information for the object and substrate categories, respectively.

Table 03.04. An overview of stimulation devices utilised by female and male primates during masturbation, where percentages are relative to the total number of reports in which masturbation was present for the respective sex (n = 94 for females, n = 307 for males).

		Females		Males	
Stimulation devices		Reports (n)	Percentage	Reports (n)	Percentage
	Feet	5	5.32%	20	6.54%
	Hands/Fingers	40	42.55%	107	34.97%
	Mouth	5	5.32%	48	15.69%
	Tail	9	9.57%	1	0.33%
	Leg	0	0.00%	2	0.65%
	Limb	0	0.00%	1	0.33%
	Object	11	11.70%	8	2.61%
	Substrate	32	34.04%	24	7.84%
Object types					
Natural objects	Bark	1	1.06%	0	0.00%
	Leaf	1	1.06%	0	0.00%
	Stick	1	1.06%	1	0.33%
	Stone(s)	1	1.06%	2	0.65%
	Straw	1	1.06%	0	0.00%
	Twig	1	1.06%	0	0.00%
	Wood	1	1.06%	0	0.00%
Water sources	Water-stream	2	2.13%	0	0.00%
Food	Food	2	2.13%	3	0.98%
Toys	Ball	1	1.06%	0	0.00%
	Doll	1	1.06%	0	0.00%
	Toys	1	1.06%	0	0.00%
Human objects	Baskets	1	1.06%	1	0.33%
	Bed	1	1.06%	0	0.00%
	Chair	1	1.06%	0	0.00%
	Clothing	1	1.06%	0	0.00%
	Pillow	1	1.06%	0	0.00%
	Douche	1	1.06%	0	0.00%
	Vibrator	1	1.06%	0	0.00%
	55-Gallon-drum	0	0.00%	1	0.33%
Substrate types					
	Branch	6	6.38%	3	0.98%
	Enclosure-environment	12	12.77%	12	3.92%
	Ground	6	6.38%	1	0.33%

Body parts were the predominant tools for stimulation used by both females (62.8 % of reports) and males (58.5 % of reports), in particular hands and fingers (42.6 % of female reports, 35.0 % of male reports). Interestingly, while half of all masturbators in a troop of Japanese macaques used both hands for stimulation, the other half preferred either the right or the left hand (Inoue, 2012). Fine motor control enabled a male gorilla to stimulate his penis by "*working it back and forth between index finger and thumb*" (Schaller, 1963, p. 277). A vervet monkey (*Chlorocebus pygerythrus*) adopted a rather more elaborate approach, by manipulating his penis "*with one or both hands by pulling on it, sliding his hand(s) along its shaft, or while supporting his penis with the fingers of one hand moving the thumb of this same hand rapidly back and forth over the glans penis at its junction with the shaft*" (Struhsaker, 1967, p. 19).

For females, the next most utilised body part was the tail (9.6 % of reports), followed by the feet and mouth (both 5.3 % of reports). By contrast, males were second-most likely to employ their mouths for stimulation (15.7 % of reports), as exemplified by an infant vervet monkey, who "*placed his head between his legs and grasped his erect penis with his mouth*" (Struhsaker, 1967, p. 20). The relative high occurrence of autofellatio, by comparison to its female counterpart, autocunnilingus, is presumably related to the fact that reaching the female genitalia orally is a significantly more challenging manoeuvre than reaching the penis. The feet (6.5 % of reports), legs (0.7 % of reports), other unspecified limbs (0.3 % of reports), and tail (0.3 % of reports) are also used by males for stimulation.

Both sexes also used objects and substrates to assist with masturbation. Substrates were used over four times more frequently by females (34.0 % of reports) than males (7.8 % of reports). This is likely due to anatomical differences between the sexes that (i) make it easier for females to stimulate themselves on substrates in the environment – which may be especially true for females with anogenital swellings, which protrude significantly – and (ii) make it more difficult more females to reach their genitalia manually. The most used substrate type was the enclosure environment for both females (12.8 % of reports) and males (3.9 % of reports). For example, in an inventive display, male orangutans (*Pongo sp.*) at the Yerkes Primate Centre masturbated by "*thrusting into the holes of chain-link fencing for stimulation*" (Maple, 1980, p. 118), while female and male Müller's gibbons (*Hylobates muelleri*) rubbed their clitorises or penises against their cage mesh (Cheyne, 2004). However, branches (6.4 % of reports for females and 1.0 % of reports for males) and the ground (6.4 % of reports for females, 0.3 % of reports for males) are also used.

Similarly, the use of objects as sexual tools is over four times as common in females (11.7 % of reports) as it is in males (2.6 % of reports). This reflects a trend in humans, where the majority of the sex toy market is aimed at women. There are various potential explanations for this. First, while male masturbation tends to focus on the penis, and occasionally the testes, female masturbation may be distributed across a wide range of body parts, including (but not limited to) the clitoris, other areas of the vulva, and the vagina. For this reason, there are a greater range of potential ways in which females may stimulate themselves, whereas manual stimulation alone may be adequate for males. Another important difference between the sexes is that the penis is within far easier reach (for most species) than female genitalia. Tools may therefore be used by females as an extension of the body.

Objects could be classed into various categories. Natural objects (bark, leaves, sticks, stones, straw, twigs, and wood) were used in 7.6 % of female reports, and 1.0 % of male reports, such as "*pieces of liana bitten off to an appropriate size*", which are used by female orangutans to stimulate the vagina (Bagemihl, 1999, p. 69). Water sources were used in 2.1 % of female, but not male, reports, as demonstrated by an adolescent chimpanzee who "*was seen to back into the touch-release water spigot in her cell in such a way that it sprayed water into her vagina*" (Kollar et al., 1968, p. 453). Food was used in 2.1 % of female reports and 1.0 % of male reports. Toys (balls, dolls, and unspecified toys) were used in 3.2 % of female, but not male, reports. Finally, human objects (baskets, beds, chairs, clothing, pillows, vaginal douches, vibrators, 55-gallon drums) were utilised in 7.5 % of female reports and 0.7 % of male reports. Interestingly, tool use in wild primates tends to be more limited than in those in captivity (see Table 03.05). The increase in masturbatory creativity in captive primates may be a result of increased access to novel items, or alternatively an imaginative way to pass the time in an under-stimulating environment.

A potential source of bias in this data comes from the fact that apes are more likely to use tools than most other primates, and are therefore likely overrepresented within the sample of individuals that use objects to assist with masturbation. Figure 03.05 illustrates the devices used by primates during masturbation.

Table 03.05. Studies documenting substrates and objects employed to masturbate with by wild-living primates. See following page.

				Sex		Substrates & objects used			
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Female**	**Male**	**Substrate**	**Object**	**Additional detail**	**Reference**
Haplorrhini	**Platyrrhini**	**Pitheciinae**	*Chiropotes satanas*	X		X			Norconk (1992)
		Alouattinae	*Alouatta palliata*	X		X			Altmann (1959)
			Alouatta palliata	X		X		Branch	Collias & Southwick (1952)
			Alouatta palliata		X	X		Branch	Collias & Southwick (1952)
			Alouatta palliata	X		X			Whitehead (1992)
		Atelinae	*Ateles geoffroyi*	X		X		Branch	Davis & Tórrez-Herrera (2018)
	Catarrhini	**Cercopithecinae**	*Chlorocebus aethiops*		X	X			Struhsaker (1967)
			Macaca sylvanus		X		X	Stones	Burton (1972)
		Homininae	*Pan troglodytes*	X		X		Branch, ground	van Lawick-Goodall (1968)
			Pan troglodytes schweinfurthii		X		X	Wadge of chewed ficus	Nakamura (2018)

Figure 03.05. Illustrative word cloud, depicting the devices used by primates for masturbation. Descriptors that are more often reported are represented by larger text (not to scale). Created with www.wordclouds.co.uk.

3.5.3 Techniques

The techniques that individuals use to masturbate also vary, as shown in Table 03.06. Data describing technique were available from 46 reports on females, and 69 reports on males.

Table 03.06. An overview of masturbatory techniques employed by female and male primates, where percentages are relative to the total number of reports in which masturbation was present for the respective sex (n = 94 for females, n = 307 for males).

		Females		**Males**	
Techniques		Reports (n)	Percentage	Reports (n)	Percentage
General	Manipulate	3	3.19%	8	2.61%
	Stimulate	1	1.06%	0	0.00%
	Vibrate	0	0.00%	1	0.33%
Manual	Clutch	1	1.06%	0	0.00%
	Fiddle	0	0.00%	1	0.33%
	Fondle	0	0.00%	1	0.33%
	Fumble	0	0.00%	1	0.33%
	Groom	0	0.00%	2	0.65%
	Handle	0	0.00%	2	0.65%
	Hold	5	5.32%	5	1.63%
	Pat	2	2.13%	1	0.33%
	Pick	0	0.00%	1	0.33%
	Play-With	1	1.06%	0	0.00%
	Poke	1	1.06%	0	0.00%
	Pull	2	2.13%	5	1.63%
	Pump	0	0.00%	1	0.33%
	Roll	0	0.00%	1	0.33%
	Scratch	1	1.06%	3	0.98%
	Slap	1	1.06%	0	0.00%
	Slide-hand	0	0.00%	1	0.33%
	Stroke	0	0.00%	8	2.61%
	Touch	1	1.06%	1	0.33%
	Tug	0	0.00%	1	0.33%
Oral	Chew	0	0.00%	1	0.33%
	Lick	0	0.00%	6	1.96%
	Mouth	0	0.00%	1	0.33%
	Suck	2	2.13%	12	3.92%
Bodily	Contract	0	0.00%	1	0.33%
	Press	2	2.13%	3	0.98%
	Rub	38	40.43%	35	11.44%
	Slide	1	1.06%	0	0.00%
	Tense-Muscles	1	1.06%	0	0.00%
	Thrust	2	2.13%	10	3.27%
Insertions	Insert	7	7.45%	0	0.00%
	Penetrate	1	1.06%	0	0.00%

The most commonly employed techniques involved bodily motion of some sort, in both female (46.8 %) and male reports (16.0 %). Of these, rubbing (40.4 % of female reports, 11.4 % of male reports), thrusting (2.1 % of female reports, 3.3 % of male reports), and pressing (2.1 % of female reports, 1.0 % of male reports) were most common. For example, a bonnet macaque (*Macaca radiata*) female would "*stand bipedally with her right hand pressed between her legs; from the ventral side she would thrust rapidly against her genitally placed hand*" (Rosenblum & Smiley, 1984, p. 491). Contracting, sliding and tensing-of-muscles also occurred. The finding that rubbing was nearly four times as common in females than males is likely related to the fact that females utilised substrates as stimulation devices far more often than males.

Manual techniques were the next most frequently employed (16.0 % of female reports, 11.4 % of male reports). Holding (5.3 % of reports), patting (2.3 % of reports), and pulling (2.1 % of reports) were the most common techniques used by females, whereas stroking (2.6 % of reports), holding (1.6 % of reports), and pulling (1.6 % of reports) were favoured manual methods for males. Oral techniques were employed by both sexes. Both females and males were reported to suck various body parts (2.1 % and 3.9 % of reports, respectively), and males also licked (2.0 % of reports), chewed (0.3 % of reports) and mouthed (0.3 % of reports). General techniques such as manipulating (3.2 % of female reports, 2.6 % of male reports), stimulating (1.1 % of female reports) and vibrating (0.3 % of male reports), were also described. Finally, a female-specific behaviour was insertion (7.5 % of reports) or penetration (1.1 % of reports), although these are arguably the same action, termed differently, which would increase the percentage of female reports describing this technique to 8.6 %. An example of this behaviour came from a Celebes crested macaque (*Macaca nigra*) who was observed "*slapping her rump with one hand and each time inserting a finger into her vagina*" (Dixson, 1977, p. 71).

Figure 03.06 highlights the techniques used by female and male primates during masturbation.

Figure 03.06. Illustrative word cloud, depicting the masturbatory techniques used by primates. Descriptors that are more often reported are represented by larger text (not to scale). Created with www.wordclouds.co.uk.

The results presented here provide a good example of the inherent complications with collating data from pre-existing literature, and the need to interpret these results with caution, since descriptors may be used in different ways by different authors. For example, while one author may use the term ‘rubbing’ only to describe a backwards and forwards movement of the body on a surface (whether that surface be a body part, a substrate, or an object), others may use the term ‘rubbing’ to describe movements of the hand on the genitals (or nipples, etc.). In other cases, different terms may be used for the same action. For example, the differences between the terms manipulating and stimulating, inserting and penetrating, and mouthing and sucking, are unclear.

3.5.4 Associated traits and physiological correlates

The associated traits and physiological correlated of masturbation across primates are summarised in Table 03.07.

Table 03.07. An overview of the traits and physiological correlates of masturbation in female and male primates, where percentages are relative to the total number of reports in which masturbation was present for the respective sex (n = 94 for females, n = 307 for males). * Includes low-moderate and moderate-high. See following page.

		Females		Males	
Physiological correlates		Reports (n)	Percentage	Reports (n)	Percentage
Excitement	Little (or 'no')	5	5.32%	19	6.21%
	Moderate* (or 'yes')	6	6.38%	15	4.90%
	High	2	2.13%	2	0.65%
		13		36	
Vocalisation	Yes	3	3.19%	12	3.92%
	No	10	10.64%	23	7.52%
Facial expressions	Yes	6	6.38%	18	5.88%
	No	8	8.51%	14	4.58%
Gestures	Yes	15	15.96%	13	4.25%
	No	1	1.06%	7	2.29%
Genital condition	Enlarged external genitalia	5	5.32%	-	-
	Flaccid penis	-	-	9	2.94%
	Erect penis	-	-	73	23.86%
Directed masturbation	Conspecific	4	4.26%	24	7.84%
	Human	9	9.57%	13	4.25%
	Object	0	0.00%	2	0.65%
Orgasm	Yes	6	6.38%	135	44.12%
	No	0	0.00%	26	8.50%
	Maybe	1	1.06%	0	0.00%
Ejaculation	Yes	-	-	135	44.12%
	No	-	-	26	8.50%
	Maybe	-	-	2	0.65%
Consumption of ejaculate	Yes	-	-	62	20.26%
	No	-	-	3	0.98%

Data on excitement were available from 13 reports on females, and 30 reports on males. Vocalisation data were available from 13 female reports, and 32 male reports.

Surprisingly, masturbation is often a rather lackadaisical affair, given that the lowest numbers of females and males showed a high degree of excitement when stimulating themselves (2.1 % of female reports, 0.7 % of male reports). Instead, most females tended to show moderate (6.4 % of reports) or low excitement (5.3 % of reports), and most males showed little or no excitement (6.2 % of reports) or moderate levels (4.9 % of reports). Similarly, very few individuals were reported to vocalise during autoerotic activity (3.2 % of female reports, 3.9 % of male reports).

Information on facial expressions was provided in 13 reports on females, and 31 reports on males, while information on gestures was available from 17 reports on females and 23 reports on males. Some primates displayed distinctive facial expressions, including grimacing, lip-smacking, round-mouth, and teeth-chattering during masturbation (6.4 % of female reports, 5.9 % of male reports, Figure 03.06). Similarly, certain gestures or body positions were adopted (16.0 % of female reports, 4.3 % of male reports), such as presenting, thrusting, arching of the back and quivering. Figure 03.07 illustrates the terms used to describe the gestures and facial expressions displayed by masturbating primates.

Figure 03.07. Illustrative word cloud, depicting the gestures and facial expressions of masturbating primates. Descriptors that are more often reported are represented by larger text (not to scale). Created with www.wordclouds.co.uk

Data on genital condition was available from four reports on females, and 72 reports on males. Enlarged external genitalia were sometimes reported in female primates (5.3 % of reports), for example swollen labia or engorged clitorises, but not commonly. In males, masturbation tended to be associated with an erect penis (23.9 % of reports), rather than a flaccid one (2.9 % of reports). Often, flaccid penises became erect after some stimulation, unless the endeavour was abandoned.

On occasion, masturbation was directed at other individuals or objects. Data on directed masturbation was provided in 9 reports on females, and 40 reports for males. Females most commonly directed their autoerotic activities towards human observers or keepers (9.6 % of reports), and sometimes towards conspecifics (4.3 % of reports), likely reflecting bias in the dataset towards captive primates. Male masturbation was more frequently levelled towards members of their own species (7.8 % of reports) than humans (4.9 % of reports). For example, a masturbating male stump-tailed macaque "*often established eye contact with some visible female; he teeth-chattered and stared at her during genital manipulation and ejaculation*" (Linnankoski et al. (1981), p. 219). On rare occasions, objects were the unwitting target of directed masturbation (0.7 % of reports). Please see Table 03.08 for a studies documenting masturbation directed at other individuals or objects.

Table 03.08. Studies documenting masturbation directed at other individuals or objects. See following pages.

				Sex		**Direction of masturbation**				
Semiorder	**Infraorder**	**(Sub)family**	***Latin name***	**Female**	**Male**	**Conspecific**	**Object**	**Human**	**None**	**Reference**
Haplorrhini	**Platyrhhini**	**Cebidae**	*Cebus capucinus*		X	X				McKinney (2018)
			Saimiri sciureus		X	X				Travis & Holmes (1974)
	Catarrhini	**Cercopithecinae**	*Cercocebus galeritus*	X		X				Mitchell et al. (1987)
			Cercocebus galeritus		X		X			Mitchell et al. (1988)
			Cercocebus galeritus		X	X				Mitchell et al. (1987)
			Macaca arctoides		X	X				Nieuwenhuijsen et al. (1986)
			Macaca arctoides		X	X				Nieuwenhuijsen et al. (1988)
			Macaca arctoides		X	X				Nieuwenhuijsen et al. (1988)
			Macaca arctoides		X	X				Linnankoski & Leinonen (1985)
			Macaca arctoides		X	X				Linnankoski et al. (1981)
			Macaca arctoides		X	X				Linnankoski et al. (1993)
			Macaca arctoides		X	X				Trollope & Jones (1975)
			Macaca fuscata		X	X				Inoue (2012)
			Macaca mulatta		X				X	Glick et al. (1982)
			Macaca mulatta		X	X				Fittinghoff et al. (1974)
			Macaca mulatta		X	X				Carpenter (1942)
			Macaca mulatta		X	X				Harrison et al. (1989)
			Macaca mulatta		X	X				Pomerantz (1990)
			Macaca mulatta		X	X				Pomerantz (1991)
			Macaca nigra		X				X	Curran (2018)
			Macaca radiata	X		X				Rosenblum & Smiley (1984)
			Macaca radiata		X	X				Rosenblum & Smiley (1984)
			Macaca silenus	X		X				Lindburg (1990)
			Macaca silenus		X	X				Lindburg (1990)
			Papio hamadryas		X				X	Weldon (2018)
			Theropithecus gelada		X				X	Ramsay (2019)
		Colobinae	*Rhinopithecus roxellana*		X	X				Clarke (1991)
		Hylobatidae	*Bunopithecus hoolock*	X				X		Mootnick & Baker (1994)
			Hylobates agilis	X				X		Cheyne (2006)
			Hylobates agilis	X				X		Cheyne (2004)
			Hylobates agilis	X				X		Mootnick & Baker (1994)
			Hylobates agilis		X			X		Cheyne (2006)

				Sex		Direction of masturbation				
Semiorder	**Infraorder**	**(Sub)family**	***Latin name***	**Female**	**Male**	**Conspecific**	**Object**	**Human**	**None**	**Reference**
			Hylobates agilis		X			X		Cheyne (2004)
			Hylobates agilis		X		X			Mootnick & Baker (1994)
			Hylobates agilis		X	X				Mootnick & Baker (1994)
			Hylobates agilis		X	X				Mootnick & Baker (1994)
			Hylobates lar	X				X		Mootnick & Baker (1994)
			Hylobates muelleri	X				X		Cheyne (2006)
			Hylobates muelleri	X				X		Cheyne (2004)
			Hylobates muelleri	X				X		Mootnick & Baker (1994)
			Hylobates muelleri		X			X		Cheyne (2006)
			Hylobates muelleri		X			X		Cheyne (2004)
			Hylobates pileatus		X			X		Mootnick & Baker (1994)
			Nomascus concolor		X			X		Mootnick & Baker (1994)
			Symphalangus syndactylus		X			X		Mootnick & Baker (1994)
		Ponginae	*Pongo pygmaeus*		X	X				Harrisson (1960)
			Pongo pygmaeus pygmaeus		X			X		de Silva (1970)
			Pongo sp.		X	X				Maple (1980)
		Homininae	*Gorilla gorilla gorilla*	X		X				Perry (1992)
			Gorilla gorilla gorilla		X			X		Weiche (1998)
			Gorilla sp.		X			X		Meder (1998)
			Pan troglodytes	X					X	Lemmon et al. (1975)
			Pan troglodytes		X			X		Shefferly & Fritz (1992)
			Pan troglodytes		X			X		Lopresti-Goodman et al. (2013)
			Pan troglodytes		X	X				Kraemer et al. (1982)
			Pan troglodytes		X	X				Kollar et al. (1968)
			Pan troglodytes schweinfurthii		X				X	Nakamura (2018)

Establishing whether autosexual behaviour induces orgasms in female primates is a more complex matter than in males, where ejaculation makes things rather more obvious. Accordingly, information on whether orgasm occurred was available from eight female reports, and 136 male reports. This may account for the fact that orgasm is stated with certainty only in 6.4 % of cases of female masturbation, and potential orgasm in 1.1 % of reports. However, on some occasions, orgasm is rather more conspicuous. Such as when a female Hanuman langur demonstrated convulsive tremors of her whole body after stimulating herself, in a display that went far beyond that observed during heterosexual encounters: "*neither [Hanuman langurs] nor other monkey species experience an orgasm of this intensity during normal mating*" (translated from Dittrich, 1968, p. 303). In stark contrast to the paucity of clear female orgasms, male orgasm and ejaculation were present in 44.1 % of reports, and absent in just 8.5 %, this suggests that male autosexual behaviour leads to ejaculation in 83.9 % of cases where occurrence of ejaculation was reported. Please see Table 03.09 for studies documenting whether male masturbation occurred with versus without ejaculation.

Table 03.09. Studies documenting whether masturbation occurred with versus without ejaculation in male primates. Please see following pages.

				Ejaculation occurrence			
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Present**	**Absent**	**Uncertain**	**Reference**
Strepsirrhini	**Lemuriformes**	**Lemuridae**	*Eulemur fulvus fulvus*		X		Ganzhorn (1992)
Haplorrhini	**Platyrhhini**	**Pitheciinae**	*Cacajao melanocephalus*	X			Bezerra et al. (2011)
		Alouattinae	*Alouatta palliata*			X	Altmann (1959)
			Alouatta palliata			X	Collias & Southwick (1952)
		Atelinae	*Brachyteles arachnoides*	X			Strier (1997)
		Cebidae	*Saimiri sciureus*	X			Hopf et al. (1974)
			Saimiri sciureus	X			Thomsen (1998)
			Saimiri sciureus	X			Travis & Holmes (1974)
			Saimiri sp.	X			Bernhards (1998)
		Callitrichidae	*Callithrix jacchus*	X			Rothe (1975)
			Saguinus fuscicollis		X		Knogge (1997)
	Catarrhini	**Cercopithecinae**	*Cercocebus galeritus*	X			Mitchell et al. (1987)
			Chlorocebus aethiops	X			Hauser (1993)
			Chlorocebus aethiops	X			Struhsaker (1967)
			Chlorocebus pygerythrus	X			Gerald (1998)
			Lophocebus albigena	X			Wallis (1983)
			Macaca arctoides	X			Anderson & Chamove (1981)
			Macaca arctoides	X			Bertrand (1969)
			Macaca arctoides	X			Kanagava et al. (1972)
			Macaca arctoides	X			Linnankoski & Leinonen (1985)
			Macaca arctoides	X			Linnankoski et al. (1981)
			Macaca arctoides	X			Linnankoski et al. (1992)
			Macaca arctoides	X			Linnankoski et al. (1993)
			Macaca arctoides	X			Nieuwenhuijsen et al. (1986)
			Macaca arctoides	X			Nieuwenhuijsen et al. (1987)
			Macaca arctoides	X			Nieuwenhuijsen et al. (1988)
			Macaca arctoides	X			Nieuwenhuijsen et al. (1988)
			Macaca arctoides	X			Trollope & Jones (1975)
			Macaca fascicularis	X			Hamilton (1914)
			Macaca fascicularis	X			van Noordwijk (1997)
			Macaca fascicularis	X			Zumpe (1992)
			Macaca fuscata	X			Domingo-Roura et al. (2004)
			Macaca fuscata	X			Fujita (1997)
			Macaca fuscata	X			Hanby et al. (1971)
			Macaca fuscata	X			Inoue (2012)
			Macaca fuscata	X			Kustukake (1997)
			Macaca fuscata	X			Matsubayashi (1974)
			Macaca fuscata	X			Stephenson (1973)

Semiorder	Infraorder	(Sub)family	Latin name	Ejaculation occurrence Present	 Absent	 Uncertain	Reference
			Macaca fuscata	X			Stephenson (1974)
			Macaca fuscata	X			Thomsen (2014)
			Macaca fuscata	X			Thomsen & Soltis (2004)
			Macaca fuscata	X			Thomsen et al. (2006)
			Macaca fuscata fuscata	X			Soltis (1997)
			Macaca fuscata fuscata	X			Watanabe (1997)
			Macaca fuscata yakui	X			Hanya (1997)
			Macaca fuscata yakui	X			Hayakawa (1997)
			Macaca fuscata yakui	X			Hill (1997)
			Macaca fuscata yakui	X			Soltis (1997)
			Macaca fuscata yakui	X			Sugiura (1997)
			Macaca fuscata yakui	X			Tanaka (1997)
			Macaca fuscata yakui	X			Tanaka (1997)
			Macaca maura		X		Matsumura (1997)
			Macaca mulatta	X			Abbott et al. (1984)
			Macaca mulatta	X			Altmann (1962)
			Macaca mulatta	X			Boonratana (1992)
			Macaca mulatta	X			Carpenter (1942)
			Macaca mulatta	X			Dubuc et al. (2013)
			Macaca mulatta	X			Erwin & Mitchell (1975)
			Macaca mulatta	X			Fisler (1967)
			Macaca mulatta	X			Fittinghoff et al. (1974)
			Macaca mulatta	X			Fontenot et al. (2006)
			Macaca mulatta	X			Freedman & Rosvold (1962)
			Macaca mulatta	X			Gerald (1998)
			Macaca mulatta	X			Gilbeau & Smith (1985)
			Macaca mulatta	X			Glick et al. (1982)
			Macaca mulatta	X			Goldfoot (1977)
			Macaca mulatta	X			Hauser (1992)
			Macaca mulatta	X			Hill (1997)
			Macaca mulatta	X			Keverne (1974)
			Macaca mulatta	X			Keverne & Michael (1971)
			Macaca mulatta	X			Koford (1965)
			Macaca mulatta	X			Leibo et al. (2007)
			Macaca mulatta	X			Loy et al. (1984)
			Macaca mulatta	X			Michael et al. (1971)
			Macaca mulatta	X			Ortmann et al. (1986)
			Macaca mulatta	X			Phoenix (1974)

Semiorder	Infraorder	(Sub)family	Latin name	Ejaculation occurrence Present	 Absent	 Uncertain	Reference
			Macaca mulatta	X			Phoenix (1980)
			Macaca mulatta	X			Pomerantz (1990)
			Macaca mulatta	X			Pomerantz (1991)
			Macaca mulatta	X			Pomerantz (1993)
			Macaca mulatta	X			Ruiz de Elvira et al. (1982)
			Macaca mulatta	X			Slimp et al. (1978)
			Macaca mulatta	X			Swam (1998)
			Macaca mulatta	X			Zumpe (1992)
			Macaca mulatta		X		Mitchell & Brandt (1975)
			Macaca mulatta		X		Perachio et al. (1969)
			Macaca nemestrina	X			Crowley et al. (1974)
			Macaca nemestrina	X			Tokuda et al. (1968)
			Macaca nigra	X			Petit (1992)
			Macaca nigra	X			Thierry et al. (2000)
			Macaca nigra		X		Curran (2018)
			Macaca nigra		X		Dixson (1977)
			Macaca radiata	X			Makwana (1980)
			Macaca radiata	X			Makwana (1980)
			Macaca radiata		X		Rosenblum & Smiley (1984)
			Macaca silenus	X			Mallapur et al. (2005)
			Macaca silenus		X		Skinner & Lockard (1979)
			Macaca sylvanus	X			Angst (1992)
			Macaca sylvanus	X			Burton (1972)
			Macaca sylvanus	X			Paul (1997)
			Macaca sylvanus	X			Paul & Küster (1992)
			Macaca sylvanus	X			Rümenas (1992)
			Macaca thibetana		X		Zhao (1993)
			Macaca tonkeana	X			Thierry (1992)
			Mandrillus sphinx	X			Kawata (1980)
			Miopithecus talapoin	X			Dixson & Herbert (1977)
			Miopithecus talapoin	X			Posada & Colell (2005)
			Miopithecus talapoin	X			Wolfheim & Rowell (1972)
			Miopithecus talapoin	X			Zimmermann (1992)
			Papio anubis	X			Bercovitch (1989)
			Papio anubis	X			Phillips-Conroy (1997)
			Papio cynocephalus	X			Hausfater (1975)
			Papio cynocephalus anubis	X			Kuntz (1998)
			Papio cynocephalus cynocephalus	X			Noë-Slijter & Noë (1997)

				Ejaculation occurrence			
Semiorder	**Infraorder**	**(Sub)family**	**Latin name**	**Present**	**Absent**	**Uncertain**	**Reference**
			Papio cynocephalus papio	X			Petit (1992)
			Papio hamadryas	X			Angst (1992)
			Papio hamadryas	X			Weldon (2018)
			Papio hamadryas, P. cynocephalus, & hybrids	X			Colmenares (1992)
			Papio ursinus	X			Bielert (1972)
			Papio ursinus	X			Bielert & Anderson (1985)
			Papio ursinus	X			Bielert & Girolami (1986)
			Papio ursinus	X			Bielert & van der Walt (1982)
			Papio ursinus	X			Bielert et al. (1986)
			Papio ursinus	X			Bielert et al. (1989)
			Papio ursinus	X			Bolwig (1959)
			Papio ursinus	X			Byrne (1992)
			Papio ursinus	X			Girolami & Bielert (1987)
			Papio ursinus		X		Saayman (1970)
			Theropithecus gelada	X			Ramsay (2019)
		Colobinae	*Piliocolobus badius*	X			Starin (2004)
			Piliocolobus badius		X		Korstjens (1997)
			Piliocolobus badius		X		Struhsaker (1975)
			Piliocolobus kirkii		X		Warkentin & Georgiev (2018)
			Procolobus verus	X			Krebs (1997)
			Rhinopithecus roxellana	X			Clarke (1991)
			Semnopithecus entellus	X			Borries (1998)
			Semnopithecus entellus	X			Hrdy (1977)
			Semnopithecus entellus	X			Paul (1997)
			Trachypithecus johnii	X			Poirer (1969)
			Trachypithecus johnii	X			Poirer (1970)
		Hylobatidae	*Hylobates agilis*		X		Mootnick & Baker (1994)
			Nomascus concolor	X			Mootnick & Baker (1994)
		Homininae	*Gorilla beringei*		X		Fossey (1983)
			Gorilla gorilla		X		Donkin (1998)
			Gorilla gorilla gorilla	X			Hess (1973)
			Gorilla gorilla gorilla	X			Weiche (1998)
			Gorilla gorilla gorilla		X		Schaller (1963)
			Gorilla gorilla gorilla		X		Schaller (1963)
			Homo sapiens	X			Kinsey et al. (1948)
			Pan paniscus	X			Thomsen (1998)
			Pan paniscus		X		de Waal (1987)
			Pan paniscus		X		de Waal (1990)

Semiorder	Infraorder	(Sub)family	Latin name	Ejaculation occurrence Present	 Absent	 Uncertain	Reference
			Pan paniscus		X		de Waal & Lanting (1997)
			Pan troglodytes	X			Hauser (1992)
			Pan troglodytes	X			Kollar et al. (1968)
			Pan troglodytes	X			Peignot (1997)
			Pan troglodytes	X			Riesen (1971)
			Pan troglodytes	X			Rogers & Davenport (1969)
			Pan troglodytes	X			Schapiro et al. (2005)
			Pan troglodytes	X			Stanford (1992)
			Pan troglodytes		X		van Lawick-Goodall (1968)
			Pan troglodytes schweinfurthii		X		Nakamura (2018)
			Pan troglodytes schweinfurthii		X		Nishida (1997)
			Pan troglodytes verus		X		Yamakoshi (1997)

Data regarding ejaculate consumption was available for 67 reports on males. As well as being composed of spermatozoa, parasperm, accessory gland, and immune cells, ejaculate contains various molecules, including hormones, proteins, water, salts, sugars and fats (Perry, Sirot, & Wigby, 2013). Conceivably, therefore, its consumption may provide some nutritional benefit, or help to prevent moisture loss (Waterman, 2010). Indeed, it was often consumed (20.3 % of male reports), such as in common marmosets (*Callithrix jacchus*), where semen is "*either licked up by the ejaculating male himself or by his brothers and sisters*" (Rothe, 1975, p. 258).

3.5.5 Temporal context

The temporal context of masturbation varies across the primate order (Table 03.10).

Table 03.10. An overview of the temporal context of masturbation in female and male primates, where percentages are relative to the total number of reports in which masturbation was present for the respective sex (n = 94 for females, n = 307 for males). See following page.

Temporal factors		Females		Males	
		Reports (n)	Percentage	Reports (n)	Percentage
Duration	< 1 min	9	9.57%	17	5.56%
	≥ 1, < 2	9	9.57%	15	4.90%
	≥ 2, < 3 min	0	0.00%	2	0.65%
	≥ 3, < 5 min	1	1.06%	4	1.31%
	≥ 5 min	1	1.06%	1	0.33%
Frequency	Rare	7	7.45%	9	2.94%
	Occasional	2	2.13%	3	0.98%
	Frequent	3	3.19%	19	6.21%
Seasonal	Yes	0	0.00%	15	4.90%
	No	0	0.00%	5	1.63%

Data on masturbation duration were provided in 20 reports for females, and 39 reports for males. The majority of masturbatory episodes were a rather bounded affair, lasting for less than one minute (9.6 % of female reports, 5.6 % of male reports), or between one and two minutes (9.6 % of female reports, 4.9 % of male reports). It could, however, extend to over five minutes (1.1 % of female reports, 0.3 % of males report), as illustrated by a female Temminck's red colobus monkey (*Procolobus badius temmickii*) who "*would sit and continually (for periods up to 15 min) move her fingers in and out of her genitalia whilst simultaneously flicking her tongue in and out of her mouth, scraping it against her top teeth*" (Starin, 2004, p. 115).

Information on masturbation frequency was available from 16 reports for females, and 63 reports for males. In females, masturbation was most frequently described as rare (7.5 % of reports), but was also described as frequent (3.2 % of reports) or occasional (2.1 % of reports). By contrast, male masturbation was most commonly described as frequent (6.2 % of reports), followed by rare (2.7 % of reports) or occasional (1.0 % of reports). Masturbation was described as seasonal for 4.9 % of male reports, and aseasonal for 1.6 %.

Unfortunately, there were not enough studies documenting whether masturbation took place pre- or post-copulation to examine this in a meaningful way.

3.6 Where? Context of masturbation

Here, the environmental context in which autosexual behaviour occurs is examined, with respect to captivity status (section 3.6.1; Table 03.11), housing condition (section 3.6.2; Table 03.12), and grouping arrangement (section 3.6.3; Table 03.12).

3.6.1 Captivity status

Table 03.11. An overview of the number of reports of masturbation presence and absence in captivity and the wild, where the percentage is relative to the total number of reports for the respective sex and living condition.

		Females		**Males**	
Masturbation occurrence		Captive	Wild	Captive	Wild
Masturbation present	Reports (n)	76	17	222	88
	Percentage	74.51%	35.42%	87.40%	73.33%
Masturbation absent	Reports (n)	26	31	32	32
	Percentage	25.49%	64.58%	12.60%	26.67%

The hypothesis that masturbation is an abnormal behaviour, reflecting a pathological condition, has been – and still is – a widespread conceptualisation with respect to humans (Laqueur 2003). Given that early animal behaviourists typically observed captive subjects, it is unsurprising that difficult-to-explain behaviour was seen to result from confinement (Chapter 01, Table 01.01). The Pathology Hypothesis of autosexual behaviour predicts that masturbation occurs exclusively, or at an inflated rate, in captivity rather than in the wild.

Indeed, reported instances of masturbation are nearly three times more frequent for captive primates (*n* = 298) than wild animals (*n* = 105) (Table 03.11). However, since my dataset lacks measures of how well studied each species is in a given environment, this does not tell us much. For example, for certain primates, such as rhesus macaques, there are far more records of masturbation in captivity than in the wild because they are common zoo animals and preferred subjects of biomedical research. A more appropriate measure than using absolute numbers is to compare how many studies on captive versus wild primates report masturbation, or the lack thereof. Thus, in my database, masturbation is reported in 74.5 % of studies on captive females, and 87.4 % of studies on captive males, versus 35.4 % of studies on wild females, and 73.3 % of studies on wild males (Table 03.11). These data highlight the inadequacy of the Pathology Hypothesis to explain autosexuality in primates, when masturbation is reported in over a third of studies on wild females, and over two thirds of reports on wild males. Indeed, for certain species, masturbation is only recorded in the wild (see Table 02.02 in Chapter 02), namely: red-fronted lemurs (*Eulemur rufifrons*), Madame Berthe's mouse lemurs (*Microcebus berthae*), mantled howler monkeys (*Alouatta palliata*), black bearded sakis (*Chiropotes satanas*), white-fronted capuchins (*Cebus albifrons*), white-faced capuchins (*C. capucinus*), green monkeys (*Chlorocebus sabaeus*), grey-cheeked mangabeys (*Lophocebus albigena*), geladas (*Theropithecus gelada*), proboscis monkeys (*Nasalis larvatus*), Western red colobuses (*Piliocolobus badius*), Zanzibar red colobuses (*P. kirkii*), olive colobuses (*Procolobus verus*), Nilgiri langurs (*Trachypithecus johnii*) and Eastern gorillas (*Gorilla beringei*). However, this likely reflects the fact that these species are well-studied in the wild, rather than indicating that masturbation does not occur in captivity.

Nevertheless, these data suggest that there may be an influence of captivity on the prevalence of reported masturbation. Two things may be causing this pattern, which are not mutually exclusive. First, the prevalence of masturbation in captivity may reflect a reporting bias. Specifically, the preponderance of reports on captive animals masturbating may have influenced researchers working with caged animals to view the behaviour as non-natural and even bordering on a pathology, given that it is commonly characterised as stemming from "frustration", "boredom", "stress", "social deprivation", "restricted mating opportunity", "stereotypy" and "hypersexuality". Second, the prevalence of masturbation in captivity may reflect a genuinely pathological effect as a consequence of poor housing and rearing conditions. For instance, rhesus macaques raised in isolation display a higher rate of autoerotic behaviours, in more abnormal forms, than wild-born individuals (Fittinghoff et al., 1974). Isolates also tend to masturbate in agonistic contexts, for example during an experiment when placed in a cage with another individual, one male "*suddenly crouched bipedally, spread his thighs, and grasped his scrotum with both hands, lifting it towards the other animal*" he then "*paused before his opponent and masturbated briefly before attacking*" (Fittinghoff, 1974, p. 126).

In order to understand the specific aspects of captivity associated with masturbation, I filtered the data to only include reports in which masturbation is present in captive individuals. I opted to include semi-free ranging primates in this category, since they cannot be classed as truly wild, and often have a history of captivity, such as formerly trafficked individuals that are moved to sanctuaries.

3.6.2 Captive environment

Data on the environment of captive primates are provided in Table 03.12.

Table 03.12. An overview of female and male masturbation in various captive environments, where percentages are relative to the total number of reports in which masturbation was present in captivity for the respective sex (n = 76 for females, n = 222 for males). See following page.

Masturbation occurrence		**Females**		**Males**	
		Captive	Wild	Captive	Wild
Masturbation present	Reports (n)	76	17	222	88
	Percentage	74.51%	35.42%	87.40%	73.33%
Masturbation absent	Reports (n)	26	31	32	32
	Percentage	25.49%	64.58%	12.60%	26.67%

Data on grouping was available from 56 reports on females, and 156 reports on males. Of captive primates in which masturbation was reported, the highest proportion were grouped socially (52.6 % of female reports, 41.4 % of male reports), followed by those living in isolation (11.8 % of female reports, 17.12 % of male reports).

Information on living-environment was available from 47 reports on females, and 104 reports on males, and on rearing environment from 12 reports on females and 57 reports on males. Of captive primates in which masturbation was reported, there were more reports on females housed in a combination of indoor and outdoor enclosures (27.6 %, versus 14.0 % of males), whereas most male cases involved indoor housing (22.5 %, versus 11.8 % of females). More cases involved females and males reared in captivity (10.5 % and 16.2 %, respectively), than those born in the wild (4.0 % and 9.0 %, respectively).

Thirty-three reports on females provided information on exposure to the public, and 70 reports on males. More reports indicated females had been exposed to the public in some way, for example those housed in zoos or sanctuaries open to the public, than had not (22.4 % versus 14.5 %). Similar numbers of reports described males who had (14.4 %) and had not (15.3 %) been exposed to the public.

Finally, 33 reports on females provided information on experimental manipulation, and 98 reports on males. A greater number of reports came from both males and females that had been subject to some form of experimental manipulation (26.3 % of females, 32.4 % of males) than those that had not (7.9 % of females, 7.2 % of males). Presumably largely due to the fact that experimental manipulation is less likely to be discussed if it did not occur. Manipulation included non-physiologically-invasive treatments, such as being raised in isolation or a becoming a subject in behavioural trials, to physiologically-invasive experimentation, such as electric-shock punishment, forcible drugging, and surgical operations (typically neurosurgery or castration).

Still, not all autosexual behaviour is a product of housing constraints, given that the females of at least 11 species, and males of at least 24, who masturbate in captivity also masturbate in the wild: *Microcebus murinus* (M), *Galago senegalensis* (M), *Cacajao melanocephalus* (M), *Cebus apella* (F, M), *Callithrix jacchus* (F, M), *Saguinus fuscicollis* (F, M), *Cercopithecus campbelli* (M), *Chlorocebus aethiops* (M), *Macaca arctoides* (F, M), *M. fascicularis* (M), *M. fuscata* (F, M), *M. maura* (F), *M. mulatta* (F, M), *M. radiata* (F, M), *M. silenus* (M), *M. sylvanus* (M), *Mandrillus sphinx* (M), *Papio anubis* (M), *P. cynocephalus* (M), *P. hamadryas* (M), *P. ursinus* (M), *Pongo abelii* (M), *P. pygmaeus* (M), *Gorilla gorilla (*F, M), *Pan paniscus* (F), and *P. troglodytes* (F, M).

3.7 Discussion

3.7.1 Occurrence and forms

Data on the occurrence of masturbation across the primate order indicate that it is most common in catarrhine primates, in particular the large apes, in which masturbation presence is reported for every genus. The platyrrhines present a more mixed picture, in which masturbation appears to be more common in larger monkeys, but still occurs in certain smaller genera, such as *Callithrix* and *Saguinus*. Masturbation is less common still in the strepsirrhines, being completely absent in females, and present only in 5 genera of males (*Microcebus, Lemur, Eulemur, Galago* and *Nycticebus*). Finally, neither female nor male tarsiers have been reported to masturbate. These findings thus largely confirm a statement in the seminal book *Primate Sexuality* that "*the available information on masturbation in primates indicates that this behavior occurs more frequently in males than in females, in anthropoids [haplorrhines minus tarsiers] rather than prosimians [strepsirrhines plus tarsiers], and especially among the Old World monkeys and apes, rather than in New World monkeys*" (Dixson, 2012, p. 188).

In addition, the data show considerable diversity in the form of self-stimulation, including the use of tools. While a synopsis of masturbation across the whole spectrum of animals does not yet exist, it is unlikely that those with paws, hooves, flippers or wings, instead of prehensile hands, will match the multiplicity of masturbatory techniques in primates. Lower occurrence of masturbation in certain primate clades may reflect a lack of sampling effort. Alternatively, it may reflect a lack of multimale-multifemale mating systems, with correspondingly reduced selection pressures in terms of competition over mates or disease transmission.

Moreover, observed intraspecific variability might be connected to the 'cultural profiles' of a given population which are constituted of socially transmitted suites of behaviours (Whiten, 2017). The presence or absence of genital self-stimulation could be homologous to mechanisms by which moral principles, social identity, and templates of in-group/out-group characteristics are brought about in human communities (Bryson et al., 2020). For example, Japanese macaque females (famous for culturally transmitted potato washing) perform sitting mounts during which they rub their genitals against the backs of the mountees – but this only occurs in certain groups (e.g. Arashiyama) and not in others (e.g. Minoo) (Leca et al., 2014). Arbitrary behavioural conventions such as these develop as a consequence of their shared meaning within a social group, and may gain further significance as markers of group identity, rather than serving an adaptive function. The apparent arbitrariness of female mount style in Japanese macaques suggests that cultural factors may be a cause of intraspecific variation, because ecological factors can be ruled out (Leca et al., 2014). It is possible, therefore, that certain *forms* of masturbation are also socially transmitted within-groups. Further research across different populations of the same species would help shed light on this possibility.

Relatedly, greater behavioural variability and arbitrariness may indicate that traits are non-adaptive, because adaptive traits tend to be more canalised (Acasuso-Rivero et al, 2019). It could therefore be argued that the diversity in masturbatory forms across the primate order shows support for the Sexual Outlet hypothesis, which states that masturbation is a non-adaptive byproduct of high underlying libido, rather than an adaptative behaviour itself. However, given that behavioural traits tend to express the greatest variance and least canalisation of all traits (Acasuso-Rivero et al, 2019), this interpretation should be considered carefully. Moreover, the results presented here are pooled across the primate order; in order to examine this avenue more thoroughly, analyses should be conducted within-species.

Interestingly, the data suggest that ejaculation is present in the majority of male masturbation. It is likely that this presents an inflated view of ejaculation rate, since ejaculation is more likely to be reported if it is observed. Nevertheless, the fact that ejaculation appears to be common provides support for the Sperm Quality and Pathogen Avoidance hypotheses, both of which require that masturbation must induce ejaculation, but not the Sexual Arousal hypothesis, which predicts that ejaculation will not occur. Support for the Sexual Outlet hypothesis is equivocal, since masturbation may still provide an outlet even if ejaculation does not occur.

3.7.2 Living environment

The database includes nearly three times as many reports of masturbation presence among captive individuals than in those observed in the wild. However, many of the species in the database are commonly kept in zoos, or for biomedical research, so the preponderance of reports in captive individuals likely reflects the fact that these species are simply better studied in captivity. Instead, I compared the proportion of reports indicating masturbation presence in captivity with the proportion of reports indicating masturbation presence in the wild. Examined in this way, male masturbation was reported to a similar degree, regardless of living environment, whereas female masturbation was reported far more in captive individuals. Still, the fact that masturbation is reported at high rates in healthy, free-living individuals refutes the hypothesis that it is a pathological consequence of captivity.

The discrepancy between observations in captive, versus wild, female primates may be explained by the fact that masturbation is more cryptic in females than males, and may therefore be even harder to spot in the field, where primates are usually less easily observed. This reflects a broader challenge in the compilation of the database: establishing whether the relatively low number of reports for females, by comparison to males, truly indicates lower rates of masturbation.

3.7.3 Absence of evidence

The absence of female masturbation in some clades is difficult to understand. The lack of reports may truly be indicative of that fact that females masturbate less than males, and not at all in certain taxa, however, this is more likely to reflect a sampling bias. There is no reason to suspect that female primates do not masturbate, given that they possess the same neuroendocrinological mechanisms for desire, arousal and orgasm as males (Calabrò et al., 2019). Likewise, masturbation should not be more costly for females, not least because it does not usually include ejaculation (aside from 'female ejaculation', which is a healthy element of sexuality for some women; Addiego et al., 1981). It may be that, for female primates, absence of evidence is not evidence of absence. Certainly, female masturbation is often less conspicuous than that of males. In males, arousal is usually accompanied by penile erection, and whilst the vulva and clitoris may become enlarged, they are not nearly so prominent. Autosexual behaviours may also be more subtle in females. For example, Ford & Beach (1951) note that when a Lesu woman of New Ireland – an island in Papua New Guinea – becomes aroused "*she then sits down and bends her right leg so that her heel presses against her genitalia (…) they never use their hands for manipulation*" (p. 158). Indeed, my data indicate that females are more likely to utilise substrates, such as tree branches or the ground, to stimulate themselves, which may be harder to observe.

3.7.4 Future directions

While my data on the forms and context of masturbation reveal certain broad patterns across the primate order, they are too sparse to lend real credence to any conclusions. Gathering more data is an obvious next step, but this should be collected through targeted research campaigns – in which questions regarding masturbation are incorporated into the research methods and protocols of behavioural studies, both in captivity and the wild – rather than via further literature searches.

The data presented in this chapter were collated from research articles and questionnaires that tended to examine a single species, or a few related species. The database is thus dependent on comparison across studies. This approach works well when variables can be compared like with like, but this was often not the case. For example, while many studies specified the exact body part stimulated (such as the clitoris or penis), others simply referred to the genitalia. Similarly, some studies reported the frequency of masturbation descriptively (e.g. 'frequent', 'occasional', 'rare'), whereas others recorded the rate in terms of number of events per day, week, month, or year. Attempting to systematically reconcile these studies would be subject to significant bias, likely varying in line with the assumptions of a given researcher, as to what constitutes high- or low-frequencies of masturbation. For this reason, I was unable to use some of the data, for certain behavioural categories, when examining trends across the primate order. Future research should establish clear protocols and terminology that are applicable to the entire primate order, or even the broader animal kingdom, thus facilitating cross-taxa comparison.

3.8 Chapter summary

In Chapter 03, I began by discussing the importance of natural history studies, before briefly describing the natural history of masturbation across the animal kingdom. I then outlined the descriptive, analytical approach employed throughout the chapter to explore the natural history of primate masturbation using the database compiled in Chapter 02. Next, I reviewed *who* masturbates across the primate order, charting its presence and absence across different species and individual phenotypes, finding that masturbation is never observed in tarsiers or female strepsirrhines, and is rare in male strepsirrhines, while being relatively common in platyrrhines, and very common in catarrhines, of both sexes. I then explored *how* primates masturbate, by looking at the wide-ranging, diverse forms it takes. Finally, I examined *where* masturbation occurs, finding that it is common in both captivity and the wild.

CHAPTER 04

EVOLUTION OF MASTURBATION: WHEN?

4.1 Abstract

Masturbation occurs throughout the primate order, suggesting that it may be a phylogenetically ancient trait. Despite this, no study has examined the evolutionary history of this common behaviour. In this chapter, female and male masturbation are examined independently within a comparative, phylogenetic framework for the first time, by testing for phylogenetic signal and running a series of models to reconstruct the ancestral state of masturbation occurrence at eight key nodes within the primate order. Analyses were conducted with data on masturbation occurrence for females of 49 species, and males of 83 species, using Bayesian phylogenetic Markov chain Monte Carlo techniques. It was found that masturbation has a strong phylogenetic signal in both female and male primates, and that both sexes showed similar evolutionary patterns. Although it was not possible to ascertain the occurrence of masturbation in the earlier stages of primate evolution, analyses consistently indicate masturbation was present in the ancestor of all platyrrhines and catarrhines and appears to have been retained at all subsequent nodes, albeit with varying probabilities. These findings suggest that masturbation is an ancient trait in the primate order, raising questions about its potential ultimate function.

4.2 Introduction

Understanding the evolutionary history of a trait can help to uncover what might be driving its evolution, retention, or loss, as well as shedding light on the behaviour and ecology of ancient species. While there are several theories as to the adaptive function of masturbation (Chapter 01), it is not yet known whether this common behaviour exhibits a phylogenetic signal and, to date, no study has ever examined it within an evolutionary phylogenetic framework. This chapter begins by providing an introduction to inference of evolutionary history (section 4.2.1) and a general overview of the phylogenetic approach (section 4.3). I then go on to describe the analytical methods employed in this chapter (section 4.4). Finally, I use these methods to examine whether masturbation shows a phylogenetic signal (section 4.5.1) and conduct the first ever examination of the evolutionary history of masturbation occurrence, reconstructing its ancestral state at eight key nodes across the primate order, in both females (section 4.5.2) and males (section 4.5.3). The findings are discussed in section 4.6. Establishing whether masturbation has a phylogenetic signal, and understanding its evolutionary history, will lay the groundwork for further phylogenetic analyses examining the potential adaptive function(s) of masturbation (Chapter 05).

4.2.1 Inferring evolutionary history

Phylogenetic approaches play a vital role in the study of evolutionary biology, by allowing evolutionary processes, and the function and evolution of specific traits, to be inferred from data on contemporary species (Pagel, 1999a). Using these methods, it is possible to uncover both what the past may have been like, and how the diversity of extant taxa came to be (Pagel, 1999a). There are various ways in which evolutionary history can be investigated using statistical models, whether it be through the reconstruction of ancestral states, via estimation of the timing of evolutionary events, or by tests of correlated evolution. Phylogenetic methods are particularly useful for understanding the evolution of typically non-fossilising traits, such as soft tissue, behaviour, or social systems.

Soft tissue does occasionally turn up in the fossil record. For instance, an unusually well-preserved *Psittacosaurus* – a non-avian dinosaur from the Early-Cretaceous period – has shown that these dinosaurs had cloacas, in common with many other vertebrate animals (Vinther et al., 2021). However, discoveries like this are the exception to the rule, and phylogenetic methods are a vital technique for understanding the past when palaeontological records are not available. For example, ancestral state reconstructions indicate that the baculum (or, penis bone) first evolved in mammals between 95 and 145 million years ago – after placental and non-placental mammals split, but before the most recent common ancestor of primates and carnivores first evolved – and that both the ancestral carnivore and primate had a baculum (Brindle & Opie, 2016). Fossil bacula are notoriously difficult to find since they are not attached to the rest of the skeleton and are often very small. As such, uncovering the evolutionary history of the penis bone would be highly unlikely through fossil evidence alone. Another study utilised phylogenetic methods to show that brain mass, which is difficult to measure from the fossil record, increased early on in primate evolution, with subsequent increases and decreases in mass occurring in all major clades (Montgomery et al., 2010).

Behavioural patterns and phenotypes can occasionally be captured within palaeontological records. For example, herbivore coprolites from the Late-Cretaceous period have been found to contain backfilled burrows, a signature behaviour of paracoprid dung beetles (dung-rollers), the only extant taxa known to make caches in this way (Chin & Gill, 1996). This find not only elucidates the behavioural phenotypes of ancient dung-beetles, but also suggests that they had an important association with dinosaurs. Nevertheless, behaviour is usually difficult to capture via the palaeontological record alone.

Phylogenetic research on a different taxonomic class found that the ancestral passerine (songbird) was likely migratory, but that this behaviour was subsequently lost in many lineages, since over 85 % of extant species within the order are non-migratory (Dufour et al., 2020). Another study found that birdsong, historically characterised as a largely male trait, was present in the female common ancestors of all passerines (Odom et al., 2014). It would not have been possible to uncover the behaviour of these long-extinct birds without the application of phylogenetic methods.

Complex combinations of behaviours can give rise to broader social and mating systems within a group of species. These systems can also be difficult to infer from the fossil record, but may be understood via phylogenetic methods. For example, reconstructions of primate mating systems indicate that the ancestral primate was polygynandrous, with polygyny and monogamy evolving later on in primate evolution (Opie et al., 2012). By examining patterns of coevolution between mating systems, the researchers were able to establish that, while monogamy was a derived state, once primates transitioned into monogamous systems, they never transitioned out of them (Opie et al., 2012).

Phylogenetic methods are therefore a vital tool when trying to understand the evolution and diversity of life on earth, particularly when examining traits that cannot be frequently or accurately inferred from the fossil record. Masturbation occurrence is an ideal candidate for examination within a phylogenetic framework, since it is likely to be a functional, adaptive trait, that cannot be inferred from palaeontological data. Utilising the large-scale, comparative database collated in Chapter 02, it is now possible to reconstruct the evolutionary history of primate masturbation for the first time. In order to do this, it is important to first understand the basics behind the principles and practice of phylogenetic approaches.

4.3 Phylogenetic approaches

Here, I first discuss phylogenetic signal and how it can be measured (section 4.3.1), before outlining the basic concepts behind phylogenetic trees (section 4.3.2) and how they can be inferred (section 4.3.3). I go on to describe how Bayesian Markov chain Monte Carlo methods offer a means of sampling from a distribution of trees (section 4.3.4), before explaining how these can be consolidated into a single tree where necessary (section 4.3.5). Finally, I consider how these methods can be applied to infer ancestral states and correlated evolution across a phylogeny (section 4.3.6) before identifying a method that helps find the best fitting model of trait evolution (section 4.3.7).

4.3.1 Phylogenetic signal

In order to assess whether a phylogenetic approach can be adopted to study the evolution of a trait, it is important to ask whether that trait shows an association with phylogeny, i.e. do species with shared ancestry have more similar trait values? Historically, there has been a tendency not to consider phylogeny when studying behavioural traits, because they have traditionally been perceived to be inherently more labile and susceptible to homoplasy (Atz, 1970; cf. Rendall & Di Fiore, 2007). Indeed, reflecting this view, before the 21st century, only 4-6 % of phylogenetic studies examined behavioural phenotypes (Proctor, 1996; Sanderson et al., 1993). However, this view has now been recognised as oversimplistic, and an important assumption that should be tested, given that, where studied, the degree of phylogenetic signal seen in behavioural traits is often similar to that of other trait systems (Fleagle & Reed, 1999; Kamilar & Cooper, 2013; Ossi & Kamilar, 2006; Rendall

& Di Fiore, 2007). Of course, this is not always the case (see, for example, Blomberg et al., 2003); but the fact that certain behavioural traits are demonstrably affected by phylogeny makes them equally as valid candidates for phylogenetic research as morphological traits.

One approach to assessing the extent to which trait distribution among species is influenced by phylogeny is provided by the statistic D (Fritz & Purvis, 2010). D is a diagnostic parameter that measures the degree of statistical dependence of a binary trait on the shared evolutionary history of species, and is often described as the 'phylogenetic signal' of a trait. D assumes that a strong phylogenetic signal corresponds to a Brownian motion (also known as 'random-walk') model of evolution across the phylogeny. This carries several corresponding assumptions, namely that trait change at any point in evolutionary history is independent of previous change and change in other lineages, and that rates of evolution are stable across time and accumulate in proportion to branch length (Nunn, 2011). A value of 1 corresponds to phylogenetic randomness, whereas a value of 0 indicates that trait evolution is strongly linked to phylogeny. High phylogenetic signal indicates that closely related species express similar trait values, and this similarity decreases as phylogenetic distance increases.

4.3.2 Tree thinking: basic concepts

Phylogenetic trees can be used to illustrate the evolutionary relationships between species. Phylogenies are composed of branches, nodes and tips. The tips of a phylogenetic tree represent extant taxa. The branches represent species lineages. Nodes symbolise speciation events when an ancestral branch splits into two (dichotomous) or more (polytomous) descendent branches. Polytomies can be *hard*, in which case they denote a true speciation event of one lineage into three or more lineages simultaneously, or *soft*, in which case they may represent uncertainty around the divergence times of a group of taxa (Nunn, 2011).

Different types of phylogenetic tree convey different information, and are thus useful for different types of analysis. *Cladograms* display the topology of a tree, i.e. the evolutionary relationships between species, rather than information about the distance between tips/nodes. *Chronograms* (also known as ultrametric trees) are dated phylogenies where the branch lengths are proportional to time. *Phylograms* have branch lengths proportional to the rate of character change, such as the degree of molecular change in DNA sequences, rather than time.

4.3.3 How are trees inferred?

Early systematists constructed phylogenies largely based on their own 'biological intuition' and scholarly training, rather than by following a clearly defined procedure (Felsenstein, 1982). This was much lamented by the evolutionary biologist A. J. Cain, who complained that "*young taxonomists are trained like performing monkeys, almost wholly by imitation*", a fact he argues "*would have shocked Linnaeus*" who "*knew perfectly well what his principles were*" (Cain, 1959). Fortunately, systematics has developed significantly since then, and it is safe to say that modern taxonomists are no longer in danger of being labelled as 'performing monkeys'.

Phylogenetic data

Phylogenies are produced in various ways, but most commonly they are generated using morphological, genetic, or molecular data (Nunn, 2011). Crucially, phylogenetic inference should be based on *homology* (shared derived characteristics), rather than *homoplasy* (shared convergent characteristics). In other words, phylogenies should be based on shared ancestral states, rather than shared traits that have evolved in several places on the tree via convergent or parallel evolution. Behavioural traits are often passed over for inferring phylogenies due to the common idea that they may be more susceptible to convergent evolution (Rendall & Di Fiore, 2007). However, there was little support for this assumption when reviewed – behavioural traits were not particularly labile or prone towards high levels of homoplasy when compared with other trait systems (Rendall & Di Fiore, 2007). There are various methods by which phylogenetic trees can be inferred.

Maximum parsimony

One of the simplest means of constructing a phylogenetic tree is through maximum parsimony, a method which selects the tree that can account for the character states of extant taxa with the fewest evolutionary transitions (i.e. it assumes that evolution follows the principle of parsimony; Felsenstein, 1983). Parsimony works well when traits are relatively stable and branches of a phylogeny are short, because longer periods of evolutionary time (branch lengths) increase the likelihood that traits will change and that similar character states will arise via convergent evolution (Pagel, 1999a). Conversely, parsimony performs poorly when rates of evolution are high, and a phylogeny includes long branches.

Maximum likelihood

An alternative to parsimony follows the principle of maximum likelihood. Maximum likelihood methods use the observed trait data (i.e. the character states of extant taxa), a probability model of how these states evolved, and a hypothesised phylogeny with branch lengths (Nunn, 2011). Using this information, it is possible to establish the likelihood of extant taxa having their observed traits, given the proposed tree and evolutionary model. This process is repeated over many iterations, after which the tree and model parameters with the highest likelihood are chosen. In other words, maximum likelihood methods make the observed data the most likely outcome given a tree and a statistical model of the way in which evolution proceeds (Pagel, 1999b). Importantly, maximum likelihood methods do not assume that the most parsimonious route to the traits of extant taxa is the 'true' evolutionary path (Pagel, 1999b). Instead, different models of evolution may be selected, the choice of which will greatly affect the outcome. Additionally, like parsimony, maximum likelihood approaches aim to identify a single 'best' tree, rather than producing a distribution of many trees.

Bayesian methods

Bayesian methods offer an alternative means of inferring phylogenies that is not based on the optimisation procedures employed by maximum parsimony and maximum likelihood. Where maximum likelihood methods select the tree that maximises the probability of observed data, Bayesian methods assess the likelihood that a hypothetical phylogeny is accurate, given the observed data and selected evolutionary model (Nunn, 2011). In this way, Bayesian methods offer a formal statistical procedure for acquiring a distribution of trees and model parameters, sampled in proportion to their *posterior probabilities.* In this instance, the posterior probability is the likelihood that any one tree is correct, given the observed data and the *prior* (existing beliefs about evolutionary parameters or phylogenetic relationships; Nunn, 2011; Pagel et al., 2004).

4.3.4 Tree selection using Markov chain Monte Carlo methods

As discussed, phylogenetic analyses are often conducted across a single tree, but this method relies on the phylogeny being an accurate representation of the evolutionary history of a group of species. Tree-building criterion such as maximum likelihood or maximum parsimony make different assumptions as to what constitutes an optimal tree – however, the 'best' tree is not necessarily the true tree (Pagel et al., 2004). Because phylogenies are usually constructed via inferences from data, it is important to account for uncertainty in these estimates when inferring ancestral states. Bayesian Markov chain Monte Carlo (MCMC) methods offer a means of sampling from a distribution of trees while accounting for uncertainty, rather than taking the approach of optimising over a single tree (Pagel et al., 2004).

The method works by constructing a Markov chain, a mathematical system that 'jumps' from one state to another, where the probability of transitioning to a new state is a function of the current state, irrespective of previous states (Pagel & Meade, 2006). In the case of Bayesian MCMC, the states of the Markov chain are different phylogenetic trees (Nunn, 2011; Pagel et al., 2004). First, a random tree is constructed and the likelihood that it is correct – based upon the likelihood of the data given that tree and model of evolution – is estimated. Next, the tree is randomly altered in some way, for example by perturbing the branch lengths, topology, or some aspect of the model of evolution. The likelihood of this new tree is then estimated. The Metropolis-Hastings algorithm (Metropolis et al., 1953; Hastings, 1970) is used to either accept or reject the newly proposed phylogeny. If the likelihood of the new tree is higher than the old tree, it is 'accepted' (i.e. it is sampled); if it is lower than the old tree, it is accepted with a probability proportional to the difference in likelihood between the two trees (Pagel et al., 2004).

This process is repeated to create a Markov chain: a sequence of trees. If the chain is run for long enough, often for millions of iterations, it reaches the point at which the likelihood of each newly proposed tree no longer increases on average, i.e. it reaches a 'stationary distribution' (Pagel et al., 2004). Once the chain has reached this point, it explores the universe of possible trees, sampling both those that are better and worse, rather than attempting to optimise by only moving towards 'better' trees (Pagel et al., 2004). Importantly, the *burn in* period – during which the likelihood climbs before reaching stationarity – should be discarded (Nunn, 2011). In this way, the MCMC method allows us to move away from attempting to find a single 'best' tree, and towards the more nuanced approach of estimating statistical confidence in different areas of a phylogeny.

The ability to run phylogenetic analyses over this many trees makes it possible to ask comparative evolutionary questions while accounting for phylogenetic uncertainty. This has the added benefit that the results of the analysis are not constrained to a single phylogeny, or set of branch lengths, which may or may not be correct.

4.3.5 Consensus trees

Certain analyses, however, require a single tree rather than a sample. Consensus trees are created by taking a collection of phylogenies obtained via MCMC sampling, and summarising them into a single 'representative' tree. Various consensus tree construction methods are available, each with different assumptions. The present study employed the Maximum Clade Credibility (MCC) method. This method identifies the single tree from a distribution in which the product of all posterior frequencies of each clade within the tree is the highest (i.e. it has the maximum clade credibility from the sample of trees). Since the tree comes from an existing sample, its topology tends to be fully resolved.

4.3.6 Reconstructing ancestral states

The application of statistical models of trait evolution to cross-taxa datasets facilitates the estimation of evolutionary processes, such as rates of evolution, as well as the inference of ancestral states and correlated evolution among traits (Pagel et al., 2004). The reconstruction of ancestral states is an essential step in understanding the evolutionary history of a trait and complements traditional palaeontological methods by enabling the investigation of non-fossilising characters, such as behaviour. For this reason, ancestral state reconstructions have been described as 'statistical palaeontology' (Pagel, 1997).

Ancestral state reconstructions require a model of the way in which traits are believed to change over the course of evolution, and information on the evolutionary relationships between species, i.e. a phylogeny. The model of trait evolution denotes how a given trait changes across a phylogeny, while the phylogeny itself identifies the likely path along which ancestral species evolved into extant taxa (Pagel et al., 2004).

The principles underlying Bayesian ancestral state reconstructions are equivalent to those for constructing phylogenetic trees. Essentially, Bayesian analyses attempt to obtain the probability distribution of a parameter, whether it be an inference of tree topology, the rate parameters of an evolutionary model, or ancestral nodes (Nunn, 2011). This is described as the *posterior probability distribution*, because it is assigned *after* taking the relevant evidence – in this case, the data and prior probability of the hypothesis – into account. In the context of ancestral state reconstructions, this means estimating the posterior probability distribution of the transition rates between character states (for example, masturbation presence versus absence). Since the posterior probability distribution of a given parameter includes all possible variability that can result from fitting the model to different phylogenies, phylogenetic uncertainty is accounted for (Pagel et al., 2004).

Just as Bayesian methods move away from constructing a single 'best' tree, they also depart from an approach that aims to find the optimal reconstruction of ancestral states or rates of trait evolution, or correlations between traits. Instead, Bayesian methods aim to estimate the level of confidence it is possible to have in alternative hypotheses on the data, while accounting for uncertainty (Pagel et al., 2004). In doing so, observed data (i.e. the character states of extant taxa) are treated as fixed, and the hypotheses on those data (i.e. gain and loss parameters in the model of trait evolution, or ancestral state reconstructions) are allowed to vary. Similarly, the analyses can run over a collection of trees using MCMC techniques, removing reliance on a single reconstruction of evolutionary history.

Some ancestral traits have a narrow range of possible states and will therefore be inferred with a relatively high degree of certainty. By contrast, others – typically those a greater phylogenetic distance from extant taxa – may have a wider range of potential states and will therefore be inferred with lower certainty. This problem is exacerbated when confidence in the existence of an ancestral node itself is low, since it puts an upper limit on confidence in the ancestral state (Pagel et al., 2004). This tends to occur when a particular node is present in some phylogenies within the MCMC sample, but not in others.

One solution is to take the ‘most recent common ancestor’ approach, which finds the node on each tree from which a fixed set of species evolve, regardless of where that node is positioned (Pagel et al., 2004). In this way, the sample of trees used within an analysis is not constrained only to those in which the ancestral node, or nodes, of interest are present, since node placement depends on where the most recent common ancestor of a group of species occurs within a phylogeny.

The Bayesian methods described here are also applicable to other evolutionary processes, such as examining the correlated evolution of two binary traits, as will be addressed in Chapter 05.

4.3.7 Identifying best-fitting models of trait evolution

The reversible-jump MCMC (rjMCMC) method (Green, 1995) is a form of Bayesian analysis that helps find the best-fitting models of trait evolution (Pagel & Meade, 2006). The method works by constructing a Markov chain that searches the universe of potential models, over a sample of possible trees, and visits them in proportion to their posterior probability (Pagel & Meade, 2006). The models identified are usually of direct relevance to tests of alternative scenarios that describe how traits arose and coevolved, while taking phylogenetic and model uncertainty into account (Pagel & Meade, 2006). By integrating results over the model space, weighted by their probabilities, this method has the additional benefit of reducing model complexity, making them less computationally expensive to run.

4.4 Data analysis

I utilised the analytical tools and methods detailed above (i) to test whether masturbation occurrence shows an association with phylogeny (i.e. whether it has a phylogenetic signal), and (ii) to reconstruct the evolutionary history of masturbation occurrence across the primate order. All analyses were conducted separately for females and males, since there are marked differences in masturbation occurrence between the sexes in extant taxa, which may indicate that the evolutionary trajectory of masturbation occurrence is different in females and males. I also ran additional exploratory models to examine the robustness of the original models to missing data.

4.4.1 Phylogenetic signal

The phylogenetic signal (D) of female and male masturbation was calculated using the ‘phylo.d’ function within the R package ‘caper’ (Orme et al., 2018; R Core Team, 2020). Tests were run over a single Maximum Clade Credibility (MCC) tree, generated using TreeAnnotator, part of the BEAST software package (Drummond & Rambaut, 2007), using the sample of 10,000 molecular ultrametric phylogenies acquired from the 10kTrees project (Arnold et al., 2010).

4.4.2 Ancestral state reconstructions

I used a Bayesian MCMC framework to reconstruct the evolutionary history of masturbation across the primate order for females (model F1) and males (model M1), using the ‘MultiState’ function in BayesTraits (v. 3; Meade & Pagel, 2017). A reversible-jump hyperprior approach was employed, seeding from an exponential distribution with a range of 0.00 – 0.05. Hyperpriors allow the details of the prior distribution to be estimated from the data, rather than an *a priori* assumption, which is often useful where investigators have little or no information about the mean and variance of rate coefficients (Pagel & Meade, 2006). Each model was run three times, and the one with the median log marginal likelihood was selected. Models were run for 5 million iterations, with a burn in of 50,000 iterations. Analyses were conducted over a posterior distribution of 10,000 molecular ultrametric phylogenies (Arnold et al., 2010).

I reconstructed ancestral states of interest by employing the 'most recent common ancestor' approach, through the 'Add MRCA' function in BayesTraits. The nodes reconstructed were the most recent common ancestors of (A) all primates, (B) strepsirrhines, (C) haplorrhines, (D) haplorrhines excluding tarsiers, (E) platyrrhines, (F) catarrhines, (G) apes, and (H) non-ape catarrhines (Figure 04.01). Using this approach, the probability of a given state at any one node is generated. I consider probabilities > 0.70 as providing high confidence of a given state, > 0.60 as low confidence, and < 0.60 as equivocal.

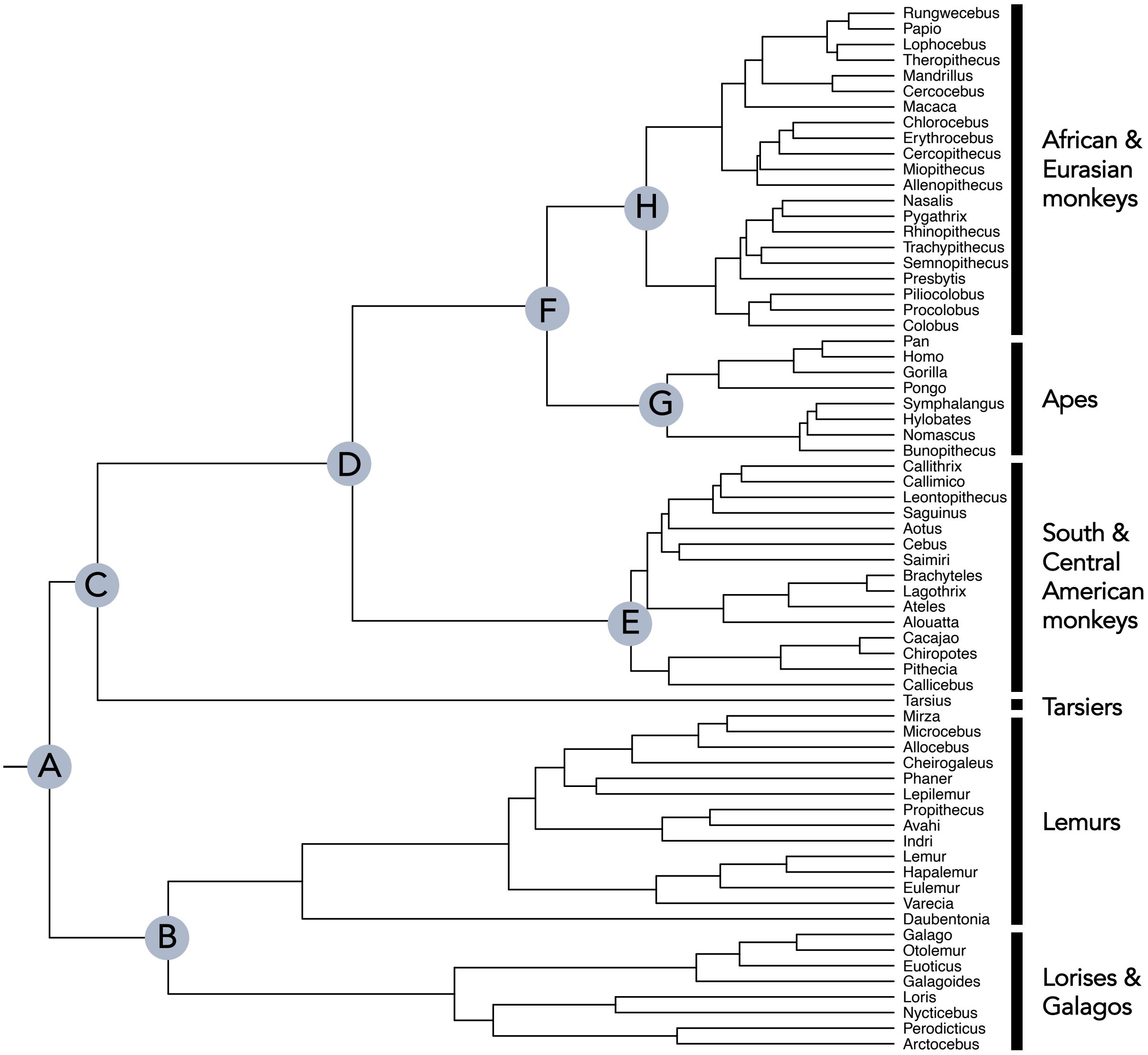

Figure 04.01. Illustrative primate phylogeny illustrating the ancestral nodes reconstructed.

4.4.3 Range of models explored

In the primary models tested for females and males (models F1 and M1, respectively), the analysis was carried out at the species level, missing data were left 'untreated', and nodes could take one of two states (masturbation present versus masturbation absent). However, given that data are missing for many important taxa and clades within the phylogeny, I also ran exploratory models in which missing data were treated differently, to assess how this affected ancestral state reconstructions in female and male primates. Specifically, I ran a total of 16 models, eight for females (F1 - F8) and eight for males (M1 - M8). For each sex, these were split evenly between analyses at the level of species (F1 - F4, M1 - M4), and genus (F5 - F8, M5 - M8). Within each of these groups of four models, a different approach to missing data was adopted: untreated (F1, F5, M1, M5), present (F2, F6, M2, M6), absent (F3, F7, M3, M7) and unknown (F4, F8, M4, M8). A summary of these different models is provided in Table 04.01, which details the different models generated and their assumptions (taxonomic level and missing data treatment). The exploratory models (F2 - F8, M2 - M8) were run following the same methodology as the original ancestral models (F1, M1), although the exponential distribution range from which the hyperpriors were seeded varied between models (F2, M2 = 0.00 – 0.0001; F3, M3, F6, M6, F7, M7 = 0.00 – 0.01; F4, M4 = 0.00 – 0.005; F5, M5 = 0.00 - 0.10; F8, M8 = 0.00 – 0.008).

Table 04.01. Overview of all models of masturbation evolution in female and male primates, according to the way missing data were treated.

Sex	Taxonomic level	Missing data treatment	Model number
Females	Species	Untreated	F1
		Present	F2
		Absent	F3
		Unknown	F4
	Genus	Untreated	F5
		Present	F6
		Absent	F7
		Unknown	F8
Males	Species	Untreated	M1
		Present	M2
		Absent	M3
		Unknown	M4
	Genus	Untreated	M5
		Present	M6
		Absent	M7
		Unknown	M8

Treatment of missing data

Since the true state of masturbation occurrence is not known where there are missing data, it would be informative to examine how model outcomes may change if the sample size increased and missing data were replaced with presence or absence data. As such, in models F2 and M2 (females and males, respectively), missing data were coded as 'masturbation present'. Whereas in models F3 and M3 (females and males, respectively), missing data were coded as 'masturbation absent'.

Finally, models F4 and M4 (females and males, respectively), were run as three-state models, in which missing data were coded as a third 'unknown' variable (i.e. masturbation present, versus masturbation absent, versus masturbation unknown). These differed from models in which data were left in an untreated form (F1 and M1), because instead of representing missing data as an 'empty cell', missing data were coded as though they were a third possible state. Of course, these three-state models do not represent a true phenotype, but they may help us to understand the weight that should be given to other model outcomes. For example, if the variable 'masturbation unknown' was reconstructed with a very low probability at a given node, it would be possible to have greater confidence in the results of the original ancestral state reconstructions at the same node. Conversely, if 'masturbation unknown' was reconstructed with a high probability at a certain node, it would highlight the need to treat the original reconstructions at the same node with caution.

Extrapolating genus-level data

While the coverage of masturbation data by species is limited (105/281 species), the coverage by genus is more comprehensive (54/68 genera; see Chapter 02, section 2.4.3). Thus, while many species are missing in the infraorders Lemuriformes, Lorisiformes, and Tarsiiformes, there is at least one representative in most genera. For example, there are only data for 1/6 species of sifaka (*Propithecus,* 17.0 %), 2/17 species of sportive lemur (*Lepilemur,*12.0 %), 3/6 species of galago (*Galago*, 33.0 %), and 1/5 species of tarsier (*Tarsius,* 20.0 %; all Chapter 02, Table 02.04). Indeed, while the database covers just 37.4 % of species within the phylogenies, 79.4 % of genera are covered. To examine how missing data at the species-level affected model outcomes, all species-level models (F1 – F4 and M1 – M4;

Table 04.02) were repeated in a series of exploratory genus-level models (F5 – F8, M5 – M8; Table 04.01). While species-level analyses included each species as a separate data point within the model, genus-level analyses grouped an entire genus into a single data-point. For example, both *Pan paniscus* (bonobos) *and P. troglodytes* (chimpanzees) could be represented by *P. paniscus* in the analysis, but would incorporate all data available for the genus *Pan*. In this instance, a single observation of masturbation presence in any species within the genus would correspond to the genus being classed as 'masturbation present', in line with my approach at the species-level (see Chapter 02).

4.5 When? Evolution of masturbation

4.5.1 Evolution of female masturbation

Masturbation showed a strong phylogenetic signal in female primates, ($p < 0.01$; Table 04.02), indicating that species with more recent shared ancestry have more similar trait values.

Table 04.02. Phylogenetic signal (D) of female and male masturbation, respectively. Values significantly > 0 indicate traits follow a model of evolution that is not significantly different from a random structure. Values significantly < 1 indicate traits follow a model of evolution not significantly different from Brownian motion.

Behavioural trait	***n***	**D**	**p (D > 0)**	**p (D < 1)**
Female masturbation	49	0.03	0.49	**< 0.01**
Male masturbation	83	0.44	0.08	**< 0.01**

The ancestral state reconstruction of female masturbation (model F1: species-level, untreated data; Table 04.03; Figure 04.02) indicates that masturbation was present in ancestral (non-tarsier) haplorrhines (node D; mean probability = 0.76), catarrhines (node F; mean probability = 0.91), apes (node G; mean probability = 0.95), and non-ape catarrhines (node H; mean probability = 0.87). Other nodes were reconstructed with less confidence, with the model indicating that masturbation was probably present in the ancestral haplorrhine (including tarsiers; node C; mean probability = 0.65) and platyrrhine (node E; mean probability = 0.63), but absent in the ancestral strepsirrhine (node B; mean probability = 0.67). The estimation of female masturbation occurrence at the root was equivocal (node A; mean probability = 0.55).

Table 04.03. Probability of female masturbation presence or absence at the root and seven key nodes of the primate phylogeny. All models were run to the species-level. Model F1 is a two-state model, in which data were run in their untreated form (i.e. masturbation presence, absence, and missing data). Model F2 is a two-state model in which missing data were coded as 'masturbation present'. Model F3 is a two-state model in which missing data were coded as 'masturbation absent'. Model F4 is a three-state model, in which missing data were coded as a third 'unknown' variable (i.e. masturbation present, versus masturbation absent, versus masturbation unknown). See following page.

	Model F1				Model F2				Model F3				Model F4					
	Present		Absent		Present		Absent		Present		Absent		Present		Absent		Unknown	
Node	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error
(A) Root	0.55	0.00	0.45	0.00	1.00	0.00	0.00	0.00	0.63	0.00	0.37	0.00	0.40	0.00	0.22	0.01	0.38	0.01
(B) Strepsirrhines	0.33	0.00	0.67	0.00	1.00	0.00	0.00	0.00	0.33	0.00	0.67	0.00	0.23	0.00	0.23	0.00	0.54	0.00
(C) Haplorrhines	0.65	0.00	0.35	0.00	1.00	0.00	0.00	0.00	0.76	0.00	0.24	0.00	0.51	0.00	0.26	0.01	0.23	0.00
(D) Haplorrhines (no tarsiers)	0.76	0.00	0.24	0.00	1.00	0.00	0.00	0.00	0.81	0.00	0.19	0.00	0.57	0.00	0.24	0.01	0.19	0.00
(E) South & Central American monkeys	0.63	0.00	0.37	0.00	1.00	0.00	0.00	0.00	0.53	0.00	0.47	0.00	0.30	0.00	0.29	0.01	0.41	0.01
(F) Catarrhines	0.91	0.00	0.09	0.00	1.00	0.00	0.00	0.00	0.95	0.00	0.05	0.00	0.88	0.00	0.08	0.00	0.04	0.00
(G) Apes	0.95	0.00	0.05	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.01	0.00	0.92	0.00	0.07	0.00	0.00	0.00
(H) African & Asian monkeys	0.87	0.00	0.13	0.00	1.00	0.00	0.00	0.00	0.62	0.01	0.38	0.01	0.52	0.01	0.12	0.00	0.36	0.01

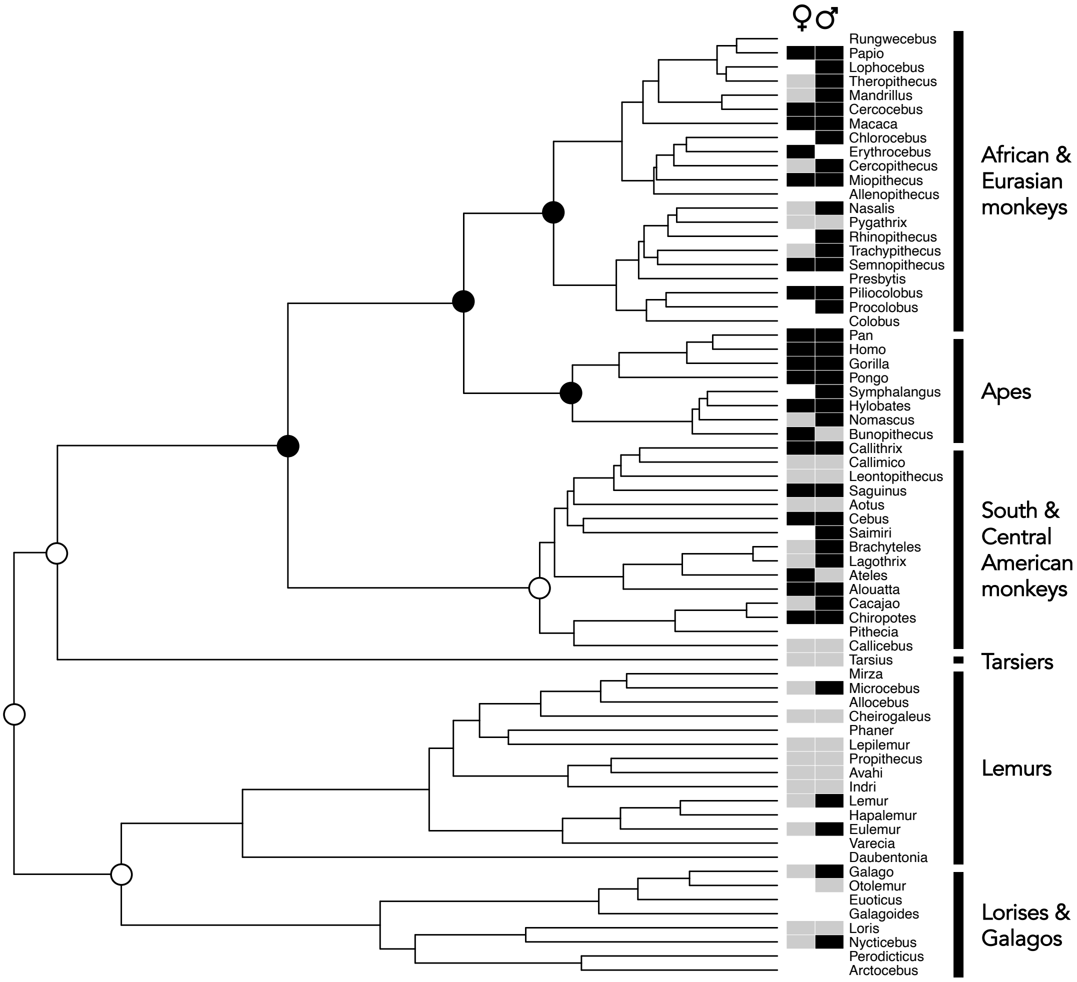

Figure 04.02. Phylogeny of 68 genera of the primate order illustrating the ancestral nodes reconstructed in female (model F1, Table 04.03) and male (model M1, Table 04.05) primates. Only one set of reconstructions is shown, since the same pattern was observed in both sexes. Black circles indicate masturbation presence, grey circles indicate masturbation absence, and empty circles indicate equivocal reconstructions. Reported presence (black squares) or absence (grey squares) of masturbation in extant females (♀) and males (♂) in at least one species of that genus is indicated at the tips of the tree. Empty tips indicate a lack of data. Maximum Clade Credibility tree created from a sample of 10,000 molecular phylogenies from the 10kTrees project (Arnold et al., 2010).

Exploratory models

Ancestral state reconstructions varied according to taxonomic level and treatment of missing data in the exploratory models (Tables 04.03 and 04.04).

Table 04.04. Probability of female masturbation presence or absence at the root and seven key nodes of the primate phylogeny. All models were run to the genus-level. Model F5 is a two-state model, in which data were run in their untreated form (i.e. masturbation presence, absence, and missing data). Model F6 is a two-state model in which missing data were coded as 'masturbation present'. Model F7 is a two-state model in which missing data were coded as 'masturbation absent'. Model F8 is a three-state model, in which missing data were coded as a third 'unknown' variable (i.e. masturbation present, versus masturbation absent, versus masturbation unknown). See following page.

	Model F5				Model F6				Model F7				Model F8					
	Present		Absent		Present		Absent		Present		Absent		Present		Absent		Unknown	
Node	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error
(A) Root	0.61	0.00	0.39	0.00	0.91	0.00	0.09	0.00	0.42	0.01	0.58	0.01	0.35	0.00	0.29	0.00	0.37	0.00
(B) Strepsirrhines	0.29	0.00	0.71	0.00	0.91	0.00	0.09	0.00	0.16	0.00	0.84	0.00	0.25	0.00	0.30	0.00	0.45	0.01
(C) Haplorrhines	0.72	0.00	0.28	0.00	0.72	0.00	0.28	0.00	0.52	0.01	0.48	0.01	0.40	0.00	0.29	0.00	0.31	0.00
(D) Haplorrhines (no tarsiers)	0.84	0.00	0.16	0.00	0.95	0.00	0.05	0.00	0.52	0.01	0.48	0.01	0.48	0.00	0.23	0.00	0.30	0.01
(E) South & Central American monkeys	0.88	0.00	0.12	0.00	1.00	0.00	0.00	0.00	0.50	0.01	0.50	0.01	0.53	0.00	0.21	0.00	0.26	0.00
(F) Catarrhines	0.90	0.00	0.10	0.00	0.99	0.00	0.01	0.00	0.58	0.01	0.42	0.01	0.56	0.01	0.12	0.00	0.32	0.01
(G) Apes	0.93	0.00	0.07	0.00	0.99	0.00	0.01	0.00	0.90	0.00	0.10	0.00	0.75	0.01	0.08	0.00	0.17	0.01
(H) African & Asian monkeys	0.87	0.00	0.13	0.00	0.99	0.00	0.01	0.00	0.38	0.01	0.62	0.01	0.41	0.01	0.13	0.00	0.46	0.01

When missing data were left untreated (as in species-level model F1), the genus-level model (F5) indicated that masturbation was absent in the ancestral strepsirrhine (node B), first evolving in the ancestral haplorrhine (node C) and remaining present in all subsequent nodes (D, E, F, G, H). Thus, the models F1 and F5 showed a similar pattern, with the only difference being the position of the node where masturbation first appeared (one node later for F1, one node earlier for F5).

When missing data were coded as 'masturbation present', both species- and genus-level models (F2 and F6, respectively) indicate that masturbation presence was the ancestral state for all primates, and was retained at every reconstructed node. This was unsurprising, given that this treatment increased the prevalence of confirmed masturbation across the order.

When missing data were coded as 'masturbation absent', the species-level model (F3) suggested that the ancestral strepsirrhine (node B) was likely to not masturbate, whereas ancestral haplorrhines (with and without tarsiers, nodes C and D), catarrhines (node F) and apes (node G) were reconstructed with a high probability of masturbating. In comparison, the genus-level 'masturbation absent' model (F7) indicated that ancestral strepsirrhines (node B) did not masturbate, and only the ancestral ape (node G) did. The F3 and F7 findings are therefore contrasting. Model F3 suggests that the F1 results are robust to the possibility that missing data largely indicate an absence of masturbation (i.e., the two models produce broadly similar results), while model F7 is only consistent with model F3 for strepsirrhines (node B) and apes (node G).

Finally, where missing data were treated as a separate state within a three-state model, masturbation was present in ancestral apes and catarrhines (nodes F and G) in the species-level model (F4), and only in the ancestral ape (node G) in the genus-level model (F8). These results suggest that the additional parameter space of a third possible state made it more difficult to assign nodes with any certainty, although model F4 remains consistent with model F1 with respect to ancestral apes and catarrhines, while model F8 indicates that, even when there is more uncertainty, the pattern of masturbation presence in the ancestral ape is very robust.

4.5.2 Evolution of male masturbation

In line with females, male masturbation showed a strong phylogenetic signal, ($p < 0.01$; Table 04.02).

The ancestral state reconstruction of male masturbation (model M1: species-level, untreated data; Table 04.05; Figure 04.02) followed the same broad pattern as female masturbation. The model indicates that masturbation was present in ancestral (non-tarsier) haplorrhines (node D; mean probability = 0.74), catarrhines (node F; mean probability = 0.92), apes (node G; mean probability = 0.95), and non-ape catarrhines (node H; mean probability = 0.97). The ancestral platyrrhine node was reconstructed with less confidence, but indicated that masturbation was likely present (node E; mean probability = 0.67). Compared to females, ancestral male haplorrhines (including tarsiers; node D; mean probability = 0.58), and strepsirrhines (node B; mean probability = 0.49), were reconstructed with lower confidence. In keeping with females, the estimation of male masturbation occurrence at the root was equivocal (node A; mean probability = 0.56).

Table 04.05. Probability of male masturbation presence or absence at the root and seven key nodes of the primate phylogeny. All models were run to the species-level. Model M1 is a two-state model, in which data were run in their untreated form (i.e. masturbation presence, absence, and missing data). Model M2 is a two-state model in which missing data were coded as 'masturbation present'. Model M3 is a two-state model in which missing data were coded as 'masturbation absent'. Model M4 is a three-state model, in which missing data were coded as a third 'unknown' variable (i.e. masturbation present, versus masturbation absent, versus masturbation unknown). See following page.

Node	Model M1				Model M2				Model M3				Model M4					
	Present		Absent		Present		Absent		Present		Absent		Present		Absent		Unknown	
	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error
(A) Root	0.56	0.00	0.44	0.00	1.00	0.00	0.00	0.00	0.43	0.00	0.57	0.00	0.36	0.00	0.21	0.00	0.43	0.00
(B) Strepsirrhines	0.49	0.00	0.51	0.00	1.00	0.00	0.00	0.00	0.33	0.00	0.67	0.00	0.23	0.00	0.23	0.00	0.54	0.00
(C) Haplorrhines	0.58	0.00	0.42	0.00	1.00	0.00	0.00	0.00	0.58	0.00	0.42	0.00	0.49	0.00	0.26	0.00	0.25	0.00
(D) Haplorrhines (no tarsiers)	0.74	0.00	0.26	0.00	1.00	0.00	0.00	0.00	0.66	0.00	0.34	0.00	0.54	0.00	0.25	0.00	0.21	0.00
(E) South & Central American monkeys	0.67	0.00	0.33	0.00	1.00	0.00	0.00	0.00	0.41	0.01	0.59	0.01	0.35	0.00	0.26	0.00	0.39	0.00
(F) Catarrhines	0.92	0.00	0.08	0.00	1.00	0.00	0.00	0.00	0.88	0.00	0.12	0.00	0.86	0.01	0.11	0.00	0.03	0.00
(G) Apes	0.95	0.00	0.05	0.00	1.00	0.00	0.00	0.00	0.88	0.00	0.12	0.00	0.79	0.00	0.17	0.00	0.04	0.00
(H) African & Asian monkeys	0.97	0.00	0.03	0.00	1.00	0.00	0.00	0.00	0.70	0.00	0.30	0.00	0.71	0.00	0.15	0.00	0.15	0.00

Exploratory models

In accordance with female models, exploratory reconstructions of male masturbation differed according to the taxonomic level a model was run at, and the way missing data were treated (Tables 04.05 and 04.06).

Table 04.06. Probability of male masturbation presence or absence at the root and seven key nodes of the primate phylogeny. All models were run to the genus-level. Model M5 is a two-state model, in which data were run in their untreated form (i.e. masturbation presence, absence, and missing data). Model M6 is a two-state model in which missing data were coded as 'masturbation present'. Model M7 is a two-state model in which missing data were coded as 'masturbation absent'. Model M8 is a three-state model, in which missing data were coded as a third 'unknown' variable (i.e. masturbation present, versus masturbation absent, versus masturbation unknown). See following page.

	Model M5				Model M6				Model M7				Model M8					
	Present		Absent		Present		Absent		Present		Absent		Present		Absent		Unknown	
Node	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error	Mean Probability	Standard Error
(A) Root	0.75	0.00	0.25	0.00	0.96	0.00	0.04	0.00	0.44	0.00	0.57	0.00	0.39	0.00	0.17	0.00	0.43	0.00
(B) Strepsirrhines	0.68	0.00	0.32	0.00	0.97	0.00	0.03	0.00	0.32	0.00	0.68	0.00	0.19	0.00	0.15	0.00	0.66	0.00
(C) Haplorrhines	0.68	0.00	0.32	0.00	0.75	0.00	0.25	0.00	0.57	0.00	0.43	0.00	0.54	0.00	0.24	0.00	0.22	0.00
(D) Haplorrhines (no tarsiers)	0.89	0.00	0.11	0.00	0.97	0.00	0.03	0.00	0.73	0.00	0.27	0.00	0.76	0.00	0.11	0.00	0.13	0.00
(E) South & Central American monkeys	0.94	0.00	0.06	0.00	0.99	0.00	0.01	0.00	0.69	0.00	0.31	0.00	0.85	0.00	0.12	0.00	0.04	0.00
(F) Catarrhines	0.97	0.00	0.03	0.00	0.99	0.00	0.01	0.00	0.90	0.00	0.10	0.00	0.93	0.00	0.03	0.00	0.04	0.00
(G) Apes	0.98	0.00	0.02	0.00	1.00	0.00	0.00	0.00	0.92	0.00	0.08	0.00	0.94	0.00	0.02	0.00	0.04	0.00
(H) African & Asian monkeys	0.98	0.00	0.02	0.00	1.00	0.00	0.00	0.00	0.94	0.00	0.06	0.00	0.96	0.00	0.01	0.00	0.02	0.00

When missing data were left untreated (as in species-level model M1), the genus-level model (M5) indicated that masturbation presence was the ancestral state for all primates (node A), was probably retained in strepsirrhines and haplorrhines (nodes B and C), and was very likely the ancestral state for all other reconstructed nodes (nodes D, E, F, G, and H). Thus, the results were similar to those from model M1 after node D (non-tarsier haplorrhines), but instead of being equivocal at the root and for ancestral strepsirrhines and haplorrhines (nodes A, B, and C), indicated that masturbation was present.

When missing data were coded as 'masturbation present', as in females, both species- and genus-level models (M2 and M6, respectively) reconstructed all nodes with masturbation presence as the ancestral state. Again, this was not surprising given that this treatment considerably increased the prevalence of confirmed masturbation across the order.

When missing data were coded as 'masturbation absent', both species- and genus-level reconstructions (models M3 and M7, respectively) suggest that masturbation was probably absent in the ancestral strepsirrhine (node B). Species-level models indicate that masturbation was present in ancestral catarrhines, apes, and non-ape catarrhines (nodes F - H), and possibly non-tarsier haplorrhines (node D). In comparison, genus-level model M7 indicates that masturbation was present in ancestral non-haplorrhine tarsiers, catarrhines, apes, and non-ape catarrhines (nodes D, F, G, and H) and probably ancestral platyrrhines (node E). These results broadly follow the same pattern, with differences being that model M3 provides more certainty that masturbation was absent in ancestral strepsirrhines (node B), and model M7 indicating that masturbation was probably present in ancestral platyrrhines (node E). Interestingly, model M7 shows the most similar results to model M1, suggesting that model M1 is robust to missing data.

Finally, when missing data were coded as 'masturbation unknown' in a three-state model, masturbation was present in ancestral catarrhines (node F), apes (node G), and non-ape catarrhines (node H) at both the species- and genus-level (models M4 and M8, respectively), as well as non-tarsier haplorrhines (node D) and platyrrhines (node E) at the genus-level (model M8). The genus-level model also indicated that ancestral strepsirrhines (node B) had an 'unknown' masturbation state, providing support for the equivocal reconstruction of this node in model M1.

4.6 Discussion

Here, I have uncovered the evolutionary history of masturbation for the first time, showing that it has a strong phylogenetic signal and is an ancient trait within the primate order. The results were also largely consistent between female and male primates, indicating that masturbation likely evolved in both sexes around the same time.

Ancestral state reconstructions (models F1 and M1) indicated that masturbation first evolved in ancestral haplorrhines – probably after the split from tarsiers – and persisted in ancestral catarrhines and all subsequent nodes (apes, and African and Eurasian monkeys). It is likely that ancestral platyrrhines also masturbated, although this node was less well resolved, particularly in females. These models suggested that masturbation was likely absent in ancestral female strepsirrhines, but were equivocal regarding males, while reconstructions of the root of the tree were inconclusive. In the following Discussion, I will briefly review my findings on phylogenetic signal (section

4.6.1), before exploring in more detail the interpretation of different modelling approaches for node reconstruction (section 4.6.2), and consider the limitation of this study, and where future work could be prioritised (section 4.6.3).

4.6.1 Phylogenetic signal

Historically, it was often assumed that – unlike morphological traits, for example – flexible behavioural traits, such as masturbation, were not subject to directional evolutionary forces, and that that the patterning of such behaviours was therefore not reflective of functional trade-offs (Atz, 1970; cf. Rendall & Di Fiore, 2007). In more recent times, however, this mindset has shifted, as many behavioural traits have been found to be just as affected by shared ancestry as morphological or genetic traits (Rendall & Di Fiore, 2007). In primates, these include, mating system (Opie et al., 2012) and territoriality (Kamilar & Cooper, 2016). This research suggests that masturbation is no different, showing a strong phylogenetic signal in both female and male primates, adding another voice to the growing consensus that behavioural traits are valid candidates for phylogenetic analyses.

4.6.2 Exploring model robustness

The models in which the data were left untreated (models F1 and M1) are the most realistic representation of masturbation occurrence across the primate order, and exploratory models (models F2 - F8, M2 - M8) should therefore be interpreted with caution. However, exploring how other treatments of missing data affect model outcomes will help test the robustness of the original models, and may indicate the way models would behave if more data became available (for instance, if it was established that gaps in the database were because a species did not masturbate). Similarly, genus-level models are a helpful means of exploring how missing data at the species-level affected model outcomes. A summary of the different model results is provided in Table 04.07 for females, and 04.08 for males.

Table 04.07. Summary of ancestral state reconstruction models for female masturbation presence or absence (models F1 - F8). Strong support for masturbation presence or absence at a given node is indicated as ++ or --, respectively. Weak support for masturbation presence or absence at a given node is indicated as + or -, respectively. Strong support for 'masturbation unknown' is indicated as UU, and weak support is indicated by U. Equivocal reconstructions are indicated as ?.

		Model							
		Species-level				**Genera-level**			
Node		F1	F2	F3	F4	F5	F6	F7	F8
(A)	Root	?	++	+	?	+	++	?	?
(B)	Strepsirrhines	-	++	-	?	--	++	--	?
(C)	Haplorrhines	+	++	++	?	++	++	?	?
(D)	Haplorrhines (no tarsiers)	++	++	++	?	++	++	?	?
(E)	South & Central American monkeys	+	++	?	?	++	++	?	?
(F)	Catarrhines	++	++	++	++	++	++	?	?
(G)	Apes	++	++	++	++	++	++	++	++
(H)	African & Eurasian monkeys	++	++	+	?	++	++	-	?

Table 04.08. Summary of ancestral state reconstruction models for male masturbation presence or absence (models M1 - M8). Strong support for masturbation presence or absence at a given node is indicated as ++ or --, respectively. Weak support for masturbation presence or absence at a given node is indicated as + or -, respectively. Strong support for 'masturbation unknown' is indicated as UU, and weak support is indicated by U. Equivocal reconstructions are indicated as ?.

		Model							
		Species-level				**Genera-level**			
Node		M1	M2	M3	M4	M5	M6	M7	M8
(A)	Root	?	++	?	?	++	++	?	?
(B)	Strepsirrhines	?	++	-	?	+	++	?	U
(C)	Haplorrhines	?	++	?	?	+	++	?	?
(D)	Haplorrhines (no tarsiers)	++	++	+	?	++	++	++	++
(E)	South & Central American monkeys	+	++	?	?	++	++	+	++
(F)	Catarrhines	++	++	++	++	++	++	++	++
(G)	Apes	++	++	++	++	++	++	++	++
(H)	African & Eurasian monkeys	++	++	++	++	++	++	++	++

Alternative treatments of missing data (models F2 - F4, M2 - M4)

In models where missing data were treated as though masturbation was present, every node was reconstructed with a high probability of masturbation presence. This is fairly unsurprising, given the large proportion of species for which data are missing. More interesting are the models in which missing data were treated as though masturbation was absent. Here, the results aligned more closely with those in which data were left untreated (i.e. the dataset included missing data), particularly those run at species-level, albeit with most nodes reconstructed with a lower probability, suggesting that the species-level models constructed with untreated data are fairly robust to missing data. If it turned out that the species for which no information is available do not masturbate, the results of the ancestral state reconstructions would not change dramatically. Conversely, if those species were later reported to masturbate, nodes where reconstructed states are equivocal in the untreated data models would be possible to reconstruct with greater confidence. In reality, however, the missing data are likely a combination of presence and absence, with the broad trends following the same patterns as the data that already exist.

Three-state models should not be interpreted as a true reflection of the way in which masturbation has evolved, since the third state, 'masturbation unknown', does not represent a true phenotype. However, they are a useful tool in understanding the weight that should be given to other models. For example, all three-state models (except female genus-level models) indicate that the mean probabilities of the ancestral catarrhine and ape having the trait 'masturbation unknown' are < 0.10. While on its own, this does not tell us much, it gives far greater credibility to the relatively high mean probabilities of masturbation presence in these models at the same nodes, all of which are ≥ 0.79. Similarly, the male, genus-level, three-state model reconstructs the ancestral strepsirrhine as 'masturbation unknown' with a mean probability of 0.66, suggesting that reconstructions with a high probability of masturbation presence at the same node in other models ought to be treated with caution.

Alternative treatments of taxonomic resolution (models F5 - F8, M5 - M8)

The main rationale for running models at the genus-level was to fill any gaps associated with missing data at the species-level, since the presence of data for a single species within a genus would allow the entire genus to be accounted for. In other words, this method would be a useful guide if species-level models were providing inconclusive results, due to the large number of species for which data were missing. However, while genus-level models tended to provide more decisive results (i.e. a greater number of nodes were reconstructed with high probabilities), species-level models also performed well, providing conclusive results despite their higher proportion of missing data. Given that species-level models more accurately reflect the true picture of masturbation occurrence across the primate order and provided clear, intuitive results, despite their increased reliance on incomplete data, greater credence should be placed on these models than on those run at the genus-level.

4.6.3 Limitations and future directions

Poorly supported nodes

Phylogenetic approaches can only capture a glimpse of the past, and the view can be incomplete or misleading when based only on present day information (Nunn, 2011). The database contains relatively little information for strepsirrhines compared to haplorrhines and, as such, the ancestral state of masturbation occurrence in the strepsirrhines was less well-resolved than for clades with more data. Similarly, of the non-tarsier haplorrhines, I have the least data for platyrrhines and, correspondingly, their ancestral state is reconstructed with a lower probability than other nodes. The uncertainty regarding the strepsirrhine ancestral state has likely had a knock-on effect on estimates of the root of the phylogeny, which are also equivocal. These equivocal results are also likely to reflect the fact that the basal primate is the most phylogenetically distant from extant taxa, which has an adverse effect on ancestral state reconstructions. Gathering more data on strepsirrhines, therefore, will be an important step towards resolving deeper nodes within the phylogenies.

Ancestral state reconstructions tended to be less well-resolved for the ancestral haplorrhine (including tarsiers) than for the ancestral non-tarsier haplorrhine. This makes sense, given that I have only scant data for the Tarsiiformes, all of which indicates that masturbation does not occur (contrary to the data for other haplorrhines). Nevertheless, there may be additional factors at play. Historically, Tarsiiformes were placed alongside the strepsirrhines, within the suborder Prosimii, but more recent taxonomic revisions generally group them alongside monkeys and apes as a member of the Haplorrhini; the latter placement is reflected in the phylogenies used for these analyses (Arnold et al., 2010). There is still debate, however, as to where tarsiers should be positioned, with molecular evidence providing support for both sides (Chatterjee et al., 2009). Irrespective, it is generally accepted that the three major lineages within the order Primates are the Strepsirrhini (lemurs, lorises, and galagos) the Haplorrhini (platyrrhines and catarrhines) and the Tarsiiformes. If Tarsiiformes are, in fact, the sister group of Strepsirrhini, the apparent absence of masturbation in this clade may be because it first evolved as a regular behaviour when strepsirrhines and haplorrhines diverged, around 63.7 million years ago (mya; Chatterjee et al., 2009).

Masturbation absence

While it looks likely that the ancestral female strepsirrhine did not masturbate (model F1), this node was not reconstructed with a high probability and the lack of strong support for masturbation absence in males at this node, or in females and males at any other node, is conspicuous. These results likely reflect the fact that there are fewer sources describing masturbation absence than presence, but it is also possible that masturbation could have been present at these nodes.

Intraspecific variability

These models reconstructed the ancestral state of masturbation as either 'present' or 'absent', however, masturbation occurs to a varying degree in different species. For example, there are 72 different sources describing masturbation in rhesus macaques (*Macaca mulatta*), but only one for black bearded sakis (*Chiropotes satanas;* see Chapter 02). Similarly, the dichotomisation of presence versus absence fails to account for the fact that masturbation is subject to a great deal of intra-specific variability, in addition to inter-specific differences. Masturbatory behaviours reflect a broad continuum, not just in terms of presence or absence, but in form, duration, and frequency (see Chapter 03). With increased data availability, future research seeking to reconstruct the ancestral states of masturbation should take a more nuanced approach, aiming to address these inter- and intra-specific differences.

4.7 Chapter summary

Chapter 04 aimed to uncover *when* masturbation first evolved within the primate order. I first illustrated that masturbation shows a phylogenetic signal in both female and male primates, indicating that more closely related species show more similar patterns of masturbation occurrence. Next, I reconstructed the evolutionary history of masturbation at eight key nodes within the primate order, using Bayesian phylogenetic methods. I found that both females and males showed similar evolutionary patterns, with masturbation likely first appearing in (non-tarsier) haplorrhines and being retained in ancestral catarrhines and all subsequent nodes. It seems likely that masturbation was present in ancestral platyrrhines, but with lower certainty than other groups. Similarly, it is unclear whether ancestral strepsirrhines masturbated, although it looks likely that it was absent in females. Finally, reconstructions at the root of the tree (i.e. the ancestral primate) were inconclusive.

CHAPTER 05

FUNCTION OF MASTURBATION: WHY?

5.1 Abstract

Masturbation – the self-stimulation of the ano-genital or breast region, carried out with an individual's own body parts or external tools – occurs throughout the animal kingdom. At first glance, however, the fitness benefits of this solitary behaviour are unclear. In this chapter, I explore two functional hypotheses that posit an adaptive benefit. The Postcopulatory Selection Hypothesis (PSH) states that masturbation increases the probability of successful fertilisation, while the Pathogen Avoidance Hypothesis (PAH) states that postcopulatory masturbation helps reduce host infection, by flushing pathogens from the genital tract. I test these two hypotheses in both females and males, drawing on the database described in Chapter 02, and in conjunction with Bayesian phylogenetic methods. Analyses of masturbation occurrence across females of 49 species, and males of 83 species, indicated that both female and male masturbation show a positive association with male testes mass, while male masturbation has coevolved with multi-male mating systems and a higher pathogen load. These findings show support for the PSH in both female and male primates, and the PAH in males, suggesting that masturbation is an adaptive trait, functioning at a macroevolutionary scale.

5.2 Introduction

Autosexual behaviour, or masturbation, is common across the animal kingdom, but appears to be particularly prevalent in the primates. However, there has been no systematic comparative research into this behaviour. Here, I utilise the new, comprehensive database charting masturbation across the primate order introduced in Chapter 02, to examine evolutionary questions related to this behaviour. This chapter begins by briefly recapping the key theories and empirical studies to date regarding the function, or lack thereof, of masturbation in primates and vertebrates more generally (section 5.2, see Chapter 01, section 1.6 for a more detailed account). Next, I outline the methodological techniques employed to test two adaptive hypotheses, the Postcopulatory Selection Hypothesis and the Pathogen Avoidance Hypothesis (section 5.3). I then describe the results of these analyses and evaluate these hypotheses in both females and males (section 5.4). This chapter concludes my initial research into the evolution of masturbation, which has shed light on the what (Chapter 02), who, how, where (Chapter 03), when (Chapter 04), and why (Chapter 05) of masturbation across the primate order.

5.2.1 An evolutionary paradox

At first glance, masturbation poses a problem for classic evolutionary theory; it does not appear to increase an individual's survival prospects and, by definition, occurs to the exclusion of reproductive partners. It can also be costly in terms of time, attention, and energy. For example, male Japanese macaques (*Macaca fuscata*) may spend up to six percent of their daily basal metabolic rate on ejaculate (Thomsen et al., 2006). The proximate driver of masturbation is not difficult to establish, since all desire for sexual activity is reinforced through the same hedonic feedback (Dixson, 2012), regardless of whether it is auto- or allosexual. But the ultimate function remains elusive.

Historical explanations for masturbation tended to focus on the *proximate* causes (i.e. why individuals are motivated to masturbate during their lifetime) rather than the *ultimate* causes (i.e. how and why masturbation has evolved in a population). Traditionally, masturbation was considered, at worst, a pathological behaviour carried out by aberrant, typically captive, individuals (Dittrich, 1969; Laquer, 2011) and, at best, a sexual outlet necessitated by high underlying libido (Dixson & Anderson, 2004).

The first of these suggestions – the result of an unfortunate turn of events that eventually characterised human masturbation as the profane, unnatural, and morally devoid practice of delinquents and psychiatric patients (see Laqueur, 2003) – is likely responsible for the common assumption that masturbation amongst nonhuman animals is the preserve of captive individuals. This explanation can be easily dismissed, at least within the primate order, since autosexuality is common in healthy, wild individuals as well as in captives (see Chapter 03).

The second suggestion, that masturbation serves as a 'sexual outlet' – a byproduct of high underlying libido, rather than an adaptation itself – deserves more credence. Indeed, data from a small sample of 22 species of primate suggest that masturbation is significantly more likely in those with greater relative testes mass, which tends to be associated with multi-male multi-female mating systems (Dixson & Anderson, 2004). Since copulation frequency is higher in such species, it may also be that sexual desire is higher in these species, leading to increased rates of masturbation (Dixson & Anderson, 2004). It is important to note, however, that this research did not take into account the statistical non-independence of data that arises on account of shared evolutionary history, and examined residual testes weights to control for body weight, which can yield biased parameter estimates (it would be better to employ a multiple regression with body mass included as a covariate: see Freckleton, 2002). However, the Sexual Outlet Hypothesis does not explain why an individual might masturbate directly pre- or post-copulation, or in the presence of willing sexual partners, and may only go some way towards explaining masturbation that does not culminate in orgasm. In these instances, other explanations must be employed. Moreover, as libido is a component of the proximate mechanism that mediates masturbation, the Sexual Outlet Hypothesis fails to provide an adaptive explanation for this behaviour. Nevertheless, the idea that masturbation may serve as a sexual outlet is not mutually exclusive with adaptive hypotheses.

Here, I test two functional, adaptive hypotheses for the presence of masturbation across the primate order: the Postcopulatory Selection Hypothesis and the Pathogen Avoidance Hypothesis.

5.2.2 Postcopulatory selection

There are two key means by which masturbation may enhance reproductive fitness. Both fall under the umbrella of postcopulatory selection, a form of sexual selection that influences fertilisation success once mating is achieved (Brindle, 2018). The Postcopulatory Selection Hypothesis (PSH) comprises two constituent hypotheses: the Sexual Arousal Hypothesis and the Sperm Quality Hypothesis (see Chapter 01, section 1.6).

The Sexual Arousal Hypothesis states that masturbation increases the chance of successful fertilisation by heightening sexual arousal prior to mating. The mechanisms of this may be twofold. Small male marine iguanas (*Amblyrhynchus cristatus*) – at risk of being separated from females during copulation by larger males – masturbate beforehand and store pre-prepared, viable ejaculate in specialised pouches at the tips of their hemipenes, ready to transfer to the female cloaca quickly at intromission (Wikelski & Bäurle, 1996). This may be the functional equivalent of nonejaculatory masturbation, in speeding up subsequent copulatory ejaculation. In human males (*Homo sapiens*), there is a positive correlation between duration of preejaculatory sexual arousal and subsequent ejaculate quality (Pound et al., 2002). It is likely that this is also an effective strategy in non-human primates. To date, The Sexual Arousal Hypothesis has only been invoked to explain nonejaculatory masturbation in lower-ranking male primates (Thomsen & Soltis, 2004), who may have fewer, and briefer, reproductive opportunities (before they are displaced by dominant males) and thus require faster copulatory ejaculations, and higher quality semen.

Sexual arousal, attained via masturbation, may also facilitate cryptic female choice. The vaginal transudate associated with female arousal filters out inferior sperm, whilst facilitating the transfer of high-quality sperm towards the uterus (Suarez & Pacey, 2006). Female arousal also leads to an increase in vaginal pH from 4.5 to 6.5, which is close to neutral, creating a more hospitable atmosphere for sperm (Meston, 2000). Finally, the contractions associated with female orgasm may enhance the passage of sperm through the uterine cavity, and associated secretions of prolactin are thought to capacitate sperm (Puts & Dawood, 2006; Suarez & Pacey, 2006). Females may therefore utilise masturbatory arousal and orgasm pre- or post-copulation, as a form of mate choice.

The Sperm Quality Hypothesis states that male precopulatory masturbation (to ejaculation) improves semen quality by expelling inferior sperm, thus increasing the likelihood of successful fertilisation at copulation. Both rhesus macaques (*Macaca mulatta*) and Japanese macaques show an inverse relationship between social status and masturbation rate (Dubuc et al., 2013;

Thomsen & Soltis, 2004), such that low-ranking males masturbate more frequently. In Japanese macaques, this coincides with distinctly different types of ejaculate in high- and low-ranking males. High-ranking males have large volumes of ejaculate containing low-quality spermatozoa; by contrast, low-ranking individuals have smaller volumes of ejaculate, containing highly motile, live spermatozoa (Thomsen, 2000). Anecdotal evidence suggests the strategy of producing lower-volume, higher-quality ejaculate may work for subordinate males, with DNA paternity analyses finding that six of nine infants sired over the course of a year were the offspring of low-ranking males (Thomsen, 2000).

Thus, irrespective of the precise functional pathway (sexual arousal in females and males, and/or sperm quality in males), the PSH predicts that masturbation increases the probability of successful fertilisation at copulation.

5.2.3 Pathogen avoidance

The concept that evolution may have favoured behavioural strategies that reduce the risk of sexually transmitted infections (STIs) is not new. Behavioural strategies are often the first line of defence against infection, followed by physiological and immune responses (Nunn & Altizer, 2004). While precopulatory behavioural counter-strategies, such as reducing copulation frequency or avoiding promiscuous mates, likely incur direct and indirect fitness costs, postcopulatory strategies, such as oral self-grooming or urination, need not entail such trade-offs (Nunn & Altizer, 2004). Postcopulatory strategies are observed in various mammals. Folk remedies for STI prevention in humans include postcopulatory genital washing, urination, application of topical antimicrobials, vaginal douching and urethral irrigation (Donovan, 2000). Male short-nosed fruit bats (*Cynopterus sphinx*) are fellated by females during copulation, and autofellate after copulating (Tan et al., 2009), whilst stereotyped oral-genital grooming is found in most strepsirrhine primates and certain callitrichids (Nunn & Altizer, 2004), as well as murine rodents (Hart et al., 1987). The effects of this strategy can be seen in brown rats (*Rattus norvegicus*), where postcopulatory grooming reduces the likelihood of genital infection (Hart et al., 1987). In this study, the saliva of the rats had bactericidal effects on some pathogens, but not others, suggesting that physical washing and the antibacterial properties of saliva offered independent benefits. Masturbation may represent another example of such behaviours if the ejaculate produced by males, or vaginal transudate associated with sexual arousal in females, can be used to flush out pathogens following copulation.

Precisely this strategy is utilised by male Cape ground squirrels (*Xerus inauris*), who face intense sperm competition, living in a multi-male multi-female mating system with a short (< three hour) female oestrus (Waterman, 2010). In these squirrels, masturbation rates are highest on days in which females are in oestrus. However, in direct contrast to the Postcopulatory Selection hypotheses, masturbation (with ejaculation) is more frequent after mating, with subsequent increases in frequency according to the number of previous mates a female has accepted (Waterman, 2010). This suggests that masturbation serves a different function in male Cape ground squirrels, acting as a form of genital grooming by cleansing the reproductive tract with ejaculate. Masturbation was not examined in female Cape ground squirrels. In fact, no other studies have examined female masturbation within an evolutionary framework. However, if the vaginal transudate associated with sexual arousal also helps to clean the reproductive tract, masturbation may also help females avoid infection.

The Pathogen Avoidance Hypothesis (PAH), therefore, predicts that masturbation is a form of postcopulatory genital grooming, helping to flush potentially harmful STIs from the reproductive tract.

5.2.4 Hypotheses and predictions

On the basis of the above, the purpose of this chapter is to test the PSH and PAH, with the following predictions:

According to the PSH, masturbation will be more common in species that experience higher postcopulatory selection pressure. Two indicators of postcopulatory selection pressure are species' mating system and anatomy (Brindle & Opie, 2016), with greater selection pressure occurring where females mate with multiple males and where males have a large testes to body mass ratio (Harcourt et al., 1981; Dixson & Anderson, 2004). This leads to two predictions: that masturbation will be associated with multi-male mating systems (over single-male mating systems) and larger relative testes mass.

In parallel to the PSH, according to the PAH, taxa are more likely to masturbate if they are at higher risk of infection from sexually transmitted pathogens. For a small number of well-studied species, this risk can be measured directly from records of sexually transmitted infections. However, this risk can also be assessed for a wider range of species according to the environments in which they live. Many pathogens require hot, humid conditions, or surface water, to complete their life cycles, generating consistent relationships between pathogen presence and environmental conditions. For instance, both global parasite diversity in primates, and parasitic and global infectious diseases in humans (encompassing bacterial, viral, fungal, and parasitic infections), increase towards the equator, and are closely linked to various climatic variables such as annual precipitation (Nunn *et al.*, 2005; Guernier *et al.*, 2004; respectively). This leads to two predictions: that masturbation will be associated with the presence of sexually transmitted pathogens, and with the environments where these pathogens are more common (tropical regions, and wetter, less harsh environments).

5.3 Methods

5.3.1 Data

Masturbation

Masturbation is defined as the self-stimulation of the ano-genital or breast region, carried out with an individual's own body parts or external tools. Masturbation was defined as 'present' or 'absent' for any given species. This information was taken from my database (Chapter 02), compiled from ~400 sources, including publications and questionnaire responses from primatologists and zoo-keepers. Presence/absence data were available for 105 species (37.4 % of the phylogeny, section 5.3.2) over 54 genera (79.4 % of the phylogeny). The proportion of species from each major radiation covered in the database varies, with a skew towards larger primates and apes, which are better studied. Data were available for 23.0 % of strepsirrhines, 20.0 % of tarsiers, 42.6 % of platyrrhines, 40.4 % of non-ape catarrhines, and 68.2 % of apes. Within this sample, the data coverage for males was slightly better than that for females: presence/absence data were available for females in 67.2 % of genera (n = 48 species), in comparison to 76.1 % of genera in males (n = 83 species).

Postcopulatory selection

Primate species were classified according to whether their mating system and anatomy was likely to be associated with high or low postcopulatory competition. In the first case, species with a single-male mating systems (monogamy, polygyny) were considered as having low postcopulatory competition, while species with multi-male mating systems were considered to have high postcopulatory competition (polyandry, polygynandry), following Brindle & Opie (2016). Species with intraspecific variability that routinely spans both sides of the binary grouping were discarded from the analyses. In the second case, species with larger testes mass relative to body size were identified as experiencing higher postcopulatory selection, following Harcourt et al. (1981). Mating system ('multi-male' versus 'single-male'; n = 181) and testes mass (n = 75), controlling for adult male body mass (n = 75), were therefore employed as proxies for postcopulatory selection. These data were taken from Brindle & Opie (2016).

Pathogen avoidance

Two different methods were adopted to evaluate the risk of infection from sexually transmitted pathogens: a direct approach, in which I assessed the frequency with which species were recorded to carry sexually transmitted pathogens; and an indirect approach, in which I assessed environmental correlates of pathogen abundance.

In the first approach, a measure of sexually transmitted pathogen load was gleaned from the Global Mammal Parasite Database (v2.0) (GMPD; note that here 'parasite' also refers to viral, bacterial, and fungal pathogens; Stephens et al., 2017). Data were filtered to include only sexually transmitted pathogens, and only those primate species included in the 10k Trees GenBank phylogenies. Data in which primates were only labelled to genus were also removed.

An overall ‘pathogen load’ was calculated per species. This was initially defined as the % prevalence of STIs, pooling across all pathogens and studies, for a given primate species. To calculate this, it was necessary to divide the total number of individuals that tested positive across all studies for that species by the total number of individuals that were tested across all studies for that species. In some cases, this required us to back-calculate a count of infected individuals per study, using the available prevalence and sample size data. For each primate species, infection counts and sample sizes were then pooled across studies to generate a new prevalence for each species (e.g., if study A recorded 1/4 positive cases, and study B recorded 3/20, I calculated prevalence as 4/24, or 0.17, in that species). At this stage, any species with sexually transmitted pathogens tested for in fewer than 10 individuals were excluded.

The resulting data sample (n = 58 species), although a reasonable size, was zero-inflated and relatively scant for species in which masturbation was absent. As such, the decision was taken to convert these proportion data into a binary pathogen occurrence of ‘presence’ (prevalence > 0) versus ‘absence’ (prevalence = 0). While it would have been more instructive to test whether primates with a higher pathogen load were more likely to masturbate, I was unable to do so for analytical reasons. Specifically, rather than examining pathogen ‘presence’ or ‘absence’, it is not possible to test for correlated evolution between a binary response variable and continuous explanatory effects within BayesTraits, and I was not confident that the sample size was large enough to run unbiased phylogenetic binary logistic regression models in R (R Core Team, 2020), particularly because the *brms* package (Bürkner, 2017) used for other analyses does not accept missing data. In contrast, the advantage of treating pathogen load as a binary variable is that the ‘Discrete’ package in BayesTraits (v3.0; Meade & Pagel, 2017) is robust to missing data. With this in mind – while it is highly unlikely that pathogens are truly absent across a species – for the purposes of these analyses, I marked them as such if all reported pathogen screens were negative in at least ten individuals. As such, the presence and absence of sexually transmitted pathogen load reported here is better interpreted as a relatively high or low sexually transmitted pathogen load, respectively.

In the second approach, given the limited availability of data on pathogen load, I assessed the environmental correlates of pathogen infection risk. In light of previous studies (e.g., Nunn *et al.*, 2005; Guernier *et al.*, 2004), I identified three potential predictors. These comprised (i) geographic region (temperate versus tropical), (ii) mean annual precipitation, and (iii) environmental harshness (i.e. the degree of climatic predictability) as proxies for pathogen load. Data on primate geographic region (n = 147 species), precipitation (n = 147 species), and environmental harshness (n = 147 species) were collected from Botero et al. (2014). Botero et al. measure precipitation as the mean annual precipitation averaged across a species geographic range, and environmental harshness as the amount of exposure to drier, less productive environments, with colder, and more variable annual temperatures (with higher scores indicating harsher environments). Only data for primate species included in the 10k Trees GenBank phylogenies were retained from the database. Analyses of the environmental correlates were restricted to only include species for which data were available for all variables within a model.

5.3.2 Phylogenies

Comparative analyses must incorporate phylogenetic information to control for the confounding effects of shared ancestry between species, given that cross-taxa data are not statistically independent (Felsenstein, 1985). The only exception to this rule is where the traits of interest are unrelated to phylogeny, i.e., they do not show a phylogenetic signal, such that closely related taxa are no more likely to show similar trait patterns than more distantly related taxa. However, I have previously confirmed that masturbation shows a strong phylogenetic signal in both females and males (Chapter 04, section 4.5), and it is therefore essential to control for phylogeny here. I therefore conducted phylogenetic analyses across a posterior distribution of 10,000 molecular phylogenies following GenBank taxonomy, from the 10kTrees project (v.3) (Arnold, Matthews, & Nunn, 2010). Where a single tree was required, I inferred a Maximum Clade Credibility tree from the distribution of 10,000 molecular phylogenies, using TreeAnnotator (Drummond & Rambaut, 2007).

5.3.3 Phylogenetic analysis

Two different phylogenetic approaches were adopted to test the PSH and PAH, depending on the format of the data available, i.e. whether the data were discrete (masturbation occurrence, mating system, pathogen load, and geographic region) or continuous (testes mass, precipitation, and environmental harshness).

Correlated evolution

Two binary traits (such as masturbation presence versus absence, and multi-male versus single-male mating systems) can produce four different combinations of observable states within a species across a phylogeny. If traits have coevolved, the rate of change between two states should depend on the background state of the other (Pagel & Meade, 2006). If the traits followed an independent pattern of evolution, the rate of change of one state should be independent of the other. By combining information on ancestral states with posterior rate distributions (i.e. transition rates between states), it is possible to discern the probable coevolutionary pathway two traits have taken (Pagel & Meade, 2006).

I assessed evidence for coevolution between (i) masturbation and mating system (multi-male versus single-male) to test the PSH; and between (ii) masturbation and geographic region (tropical versus temperate), and (iii) masturbation and pathogen occurrence (present versus absent), to test the PAH. All analyses were conducted separately for female and male primates. In addition, I checked for coevolution between mating system and pathogen occurrence, to exclude the possibility that these predictors influenced one another.

To do this, I employed reversible-jump Markov chain Monte Carlo (rjMCMC) techniques in BayesTraits v3.0 (Meade & Pagel, 2017; Pagel & Meade, 2006) to simultaneously test for coevolution between the binary variables and estimate transition rates between states. This method fits continuous-time Markov models to discrete traits, allowing them to transition to another state at any point. The rjMCMC visits each model in proportion to its posterior probability, searching for the best-fitting model to describe the coevolution of two traits across a phylogeny. I compared the fit of a dependent model of evolution, in which transition rates were free to vary, switching ‘on’ and ‘off’, to that of an independent model, where transition rates between states were constrained to be equal. Transition rates were estimated by taking the mean posterior rate estimate across all posterior models for which a given transition was active. I also calculated the proportion of iterations in which each parameter was estimated to be zero (i.e. when a transition was ‘switched off’) within the rjMCMC model.

To ensure these estimates were accurate and stable, with little run-to-run variation, each chain was run three times. All outputs were inspected to ensure marginal likelihoods were properly estimated. If the chains converged well, the model with the median log marginal likelihood was chosen (following Jordan et al., 2009). Markov chains were run for 5,000,000 iterations, after a burn-in of 500,000 samples. I employed a reversible-jump hyperprior approach, seeding from an exponential distribution of 0-0.5. Natural log marginal likelihoods of the dependent (m_D) and independent (m_I) models were estimated using a stepping-stone sampler set with 100 stones, each run for 10,000 iterations, and the default parameters of a = 0.4 and b = 1.0. Model fit was established using log Bayes Factors (BFs) = $2(m_D–m_I)$, interpreted following Kass and Raftery (1995): 0-2, minimal support; 2-6, positive support; 6-10, strong support; > 10, very strong support.

Phylogenetic logistic regressions

In order to analyse patterns of covariation between discrete and continuous traits, I built Bayesian phylogenetic binary logistic regression models using the *brms* package in R (Bürkner, 2017; R Core Team, 2020). I modelled masturbation presence as a binary response (0 = absent, 1 = present) with a single fixed effect of either testes mass (to test the PSH), or one of two environmental variables: mean annual precipitation or environmental harshness (to test the PAH). All analyses were run for female and male primates separately, resulting in four environmental models and two postcopulatory models. Phylogenetic relationships were accounted for in all models by including a variance-covariance matrix of phylogenetic distance as a random effect. Adult male body mass was included as a random effect in the postcopulatory models to control for the effects of body size on testes mass.

I ran four chains for 10,000 iterations, with a burn-in of 5,000 iterations using uninformative priors. Delta was adapted to 0.9999 and maximum tree depth set to 12. Model performance was evaluated by visually assessing trace plots as well as examining R-hat values (with those < 1.1 considered to have mixed well) and effective sample sizes (Bulk ESS should be > 100 times the number of chains, so in this case > 400).

5.4 Results

5.4.1 Postcopulatory Selection Hypothesis

I found evidence for coevolution between masturbation presence and multi-mating systems in male, but not female, primates (log BF = 2.44 and -2.40 respectively, Table 05.01), providing support for the PSH in male primates. Examination of the evolutionary transitions in males reveals that shifts from masturbation absence to presence occurred at a high rate in both single- and multi-male mating systems (*q*13 and *q*24, respectively), though more frequently in multi-male mating systems. However, masturbation was also lost frequently in single-male mating systems (*q*42), but never in multi-male mating systems (*q*31). This indicates that – while masturbation is a very labile trait in single-male mating systems – in multi-male mating systems once male masturbation has evolved, it persists (Table 05.02, Figure 05.01).

Table 05.01. Likelihood of dependent and independent models of correlated evolution between (i) masturbation and mating system, (ii) masturbation and geographic region, and (iii) masturbation and pathogen occurrence, in female and male primates. Bayes Factors were interpreted following Kass & Raftery (1995): < 2, weak evidence; 2-5, positive evidence; 5-10, strong evidence; > 10 very strong evidence. See following page.

		Dependent model	Independent model	
Coevolution analysis		**Log marginal likelihood**	**Log marginal likelihood**	**Log Bayes Factor**
Masturbation & mating system	Female	-117.45	-116.25	-2.4
	Male	-129.98	-131.2	2.44
Masturbation & latitude range	Female	-59.67	-59.22	-0.89
	Male	-74.91	-74.5	-0.82
Masturbation & pathogen occurrence	Female	-64.92	-64.31	-1.22
	Male	-74.08	-79.71	11.25

Table 05.02. Description of the rate coefficients in the model of correlated evolution between masturbation occurrence and mating system in male primates. Transition frequencies show how often a given transition occurs. Transitions shown in bold are of particular interest to the research question.

Rate Coefficient	Evolutionary Transition	Transition Frequency
Gains		
$q12$	Gain of single-male mating system in absence of masturbation	Always
$q13$	**Gain of masturbation in multi-male mating system**	**Always**
$q24$	**Gain of masturbation in single-male mating system**	**Frequent**
$q34$	Gain of single-male mating system in presence of masturbation	Always
Losses		
$q21$	Loss of single-male mating system in absence of masturbation	Always
$q31$	**Loss of masturbation in multi-male mating system**	**Never**
$q42$	**Loss of masturbation in single-male mating system**	**Always**
$q43$	Loss of single-male mating system in presence of masturbation	Always

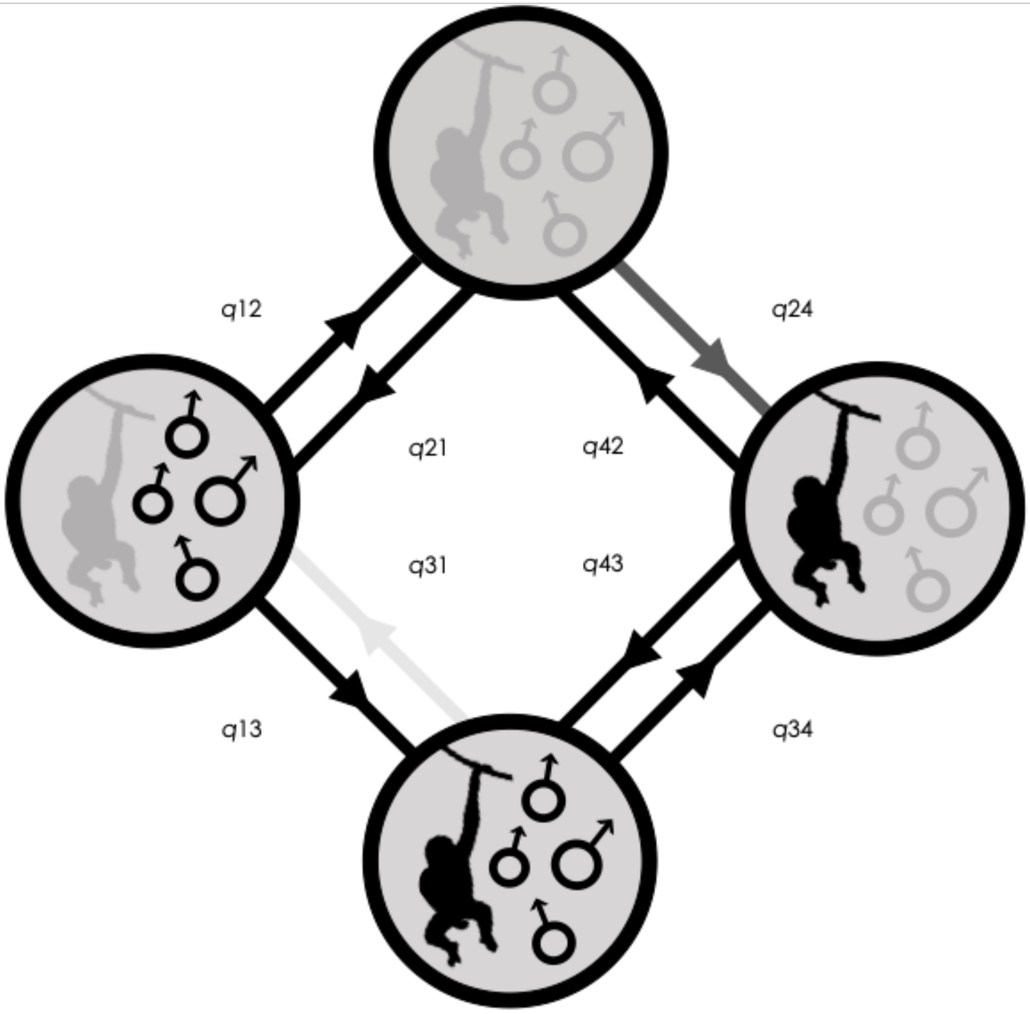

Figure 05.01. Coevolution between masturbation (present versus absent) and mating system (single- versus multi-male). Traits present in a given state are shown in black, and those absent are shown in grey. Black arrows correspond to transitions with a very low posterior probability of being zero (i.e. very common transitions), dark grey arrows to a low posterior probability of being zero (i.e. common transitions), and light grey arrows to a high posterior probability of being zero (i.e. rare transitions).

Similarly, I found moderate evidence for a positive relationship between masturbation and adult male testes mass: both female and male masturbation were more likely in those species where males exhibited relatively larger testes (Table 05.03, Figure 05.02). Thus, support was found for the PSH for both female and male primates.

Table 05.03. Model summaries of Bayesian phylogenetic binary logistic regressions between masturbation occurrence in female and male primates, and adult male testes mass. LCI and UCI are the lower and upper 80% and 95% Bayesian credible intervals of the posterior mean, respectively. Rhat is a measure of chain convergence. ESS is a measure of sampling efficiency over the bulk and tails of the distribution (i.e. the 5% and 95% quantiles). See following page.

Sex	Model	*n*	Term	Estimate	Estimate error	LCI 80%	UCI 80%	LCI 95%	UCI 95%	Rhat	Bulk ESS	Tail ESS
Female	Masturbation ~ testes mass	30	Intercept	-39.88	72.72	-91.16	-1	-184.78	8.6	1	9573	5628
			Testes mass	1.3	2.34	0.05	2.95	-0.26	5.96	1	9552	5611
Male	Masturbation ~ testes mass	47	Intercept	-5.14	15.66	-18.31	3.33	-47.05	7.81	1	3764	3388
			Testes mass	0.27	0.45	0.01	0.62	-0.12	1.44	1	5206	3292

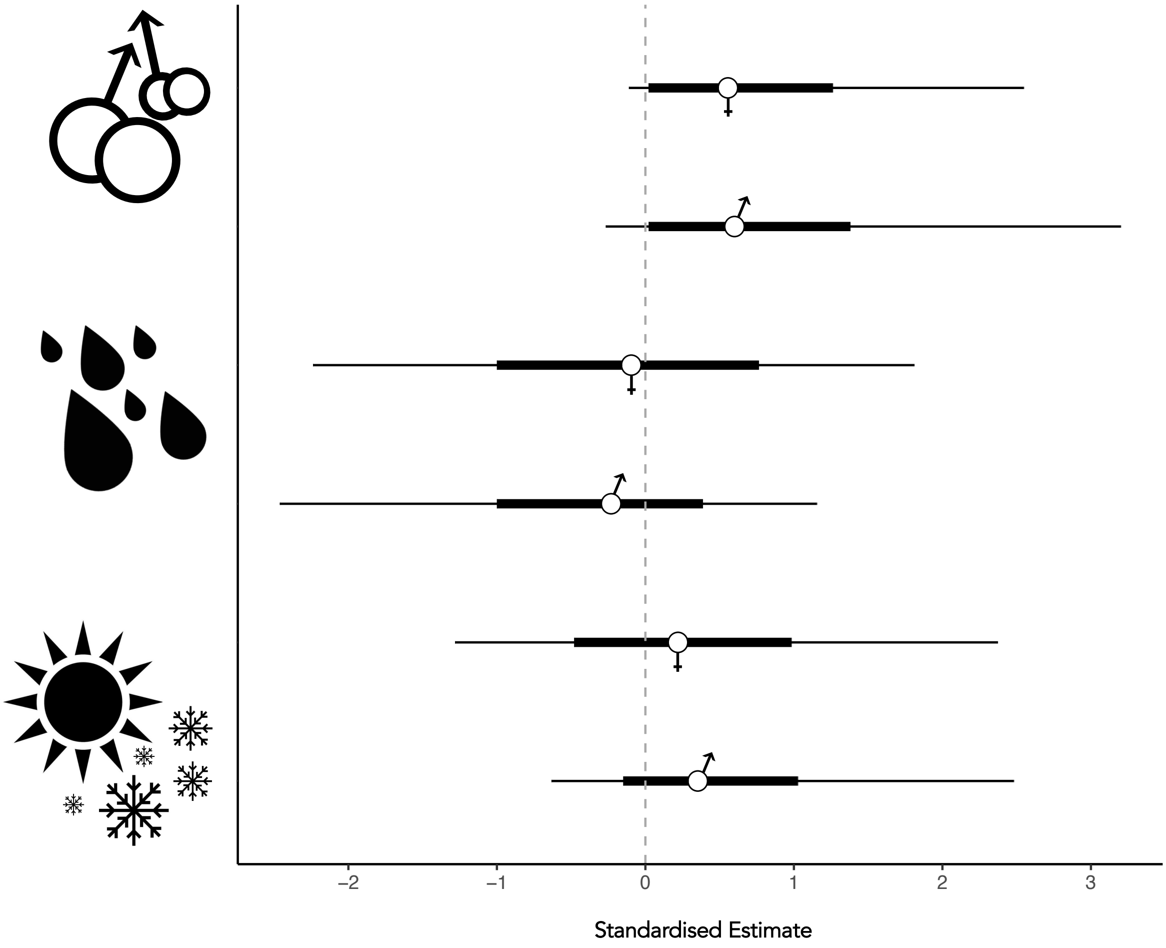

Figure 05.02. Standardised estimates (estimate/error) for masturbation presence in female and male primates with adult male testes mass, mean annual precipitation and environmental harshness. Points indicate posterior means, thick horizontal lines indicate 80% Bayesian credible intervals (BCIs), and thin horizontal lines indicate 95% BCIs. Statistical differences are considered to be substantial if the 95% BCIs do not overlap zero (dashed vertical line), and moderate if 80% BCIs do not cross zero.

5.4.2 Pathogen Avoidance Hypothesis

My analyses of masturbation and three environmental predictors of pathogen infection risk failed to find any consistent patterns. I found no evidence in support of coevolution between masturbation occurrence and geographic region in female or male primates (log BF = -0.89 and -0.82 respectively, Table 05.01). Similarly, there was no support for a relationship between masturbation and mean annual precipitation or masturbation and environmental harshness in either female or male primates (see Table 05.04, Figure 05.02).

Table 05.04. Model summaries of Bayesian phylogenetic binary logistic regressions between (i) masturbation occurrence in both female and male primates and mean annual precipitation, and (ii) masturbation occurrence in both female and male primates and environmental harshness. LCI and UCI are the lower and upper 95% Bayesian credible intervals of the posterior mean respectively. Rhat is a measure of chain convergence. ESS is a measure of sampling efficiency over the bulk and tails of the distribution (i.e. the 5% and 95% quantiles). See following page.

Sex	Model	*n*	Term	Estimate	Estimate error	LCI 80%	UCI 80%	LCI 95%	UCI 95%	Rhat	Bulk ESS	Tail ESS
Female	Masturbation ~ mean annual precipitation	28	Intercept	2.66	35.11	-26.78	-35.5	-65.17	78.72	1	7614	7495
			Mean annual precipitation	-0.02	0.21	-0.21	0.16	-0.47	0.38	1	7538	7361
	Masturbation ~ environmental harshness	28	Intercept	4.34	21.67	-11.43	21.45	-27.57	50.34	1	6410	4250
			Environmental harshness	6.2	28.26	-13.55	27.76	-36.22	67.01	1	6202	4158
Male	Masturbation ~ mean annual precipitation	48	Intercept	5.13	19.14	-7.62	19.93	-22.18	46.67	1	6343	4243
			Mean annual precipitation	-0.03	0.13	-0.13	0.05	-0.32	0.15	1	5993	4234
	Masturbation ~ environmental harshness	48	Intercept	2.9	8.61	-3.05	9.49	-7.67	20.79	1	4844	2769
			Environmental harshness	5.49	15.57	-2.32	15.97	-9.85	38.61	1	47.31	2683

In contrast, I found very strong evidence for coevolution between masturbation and pathogen occurrence in male primates, but not females (log BF = 11.25 and - 1.22 respectively, Table 05.01), providing support for the PAH in males. Examination of the evolutionary transitions in males indicates that shifts from masturbation absence to presence occurred at a high rate regardless of whether pathogens were absent (*q*13) or present (*q*24). However, masturbation was lost at a very high rate when pathogens were not present (*q*31), but never when they were present (*q*42). This indicates that masturbation is a labile trait when pathogens are not present, but once pathogens are present masturbation is retained (Table 05.05; Figure 05.03).

Table 05.05. Description of the rate coefficients in the model of correlated evolution between masturbation and pathogen presence in male primates. Transition frequencies show how often a given transition occurs. Transitions shown in bold are of particular interest to the research question.

Rate Coefficient	Evolutionary Transition	Transition Frequency
Gains		
*q*12	Gain of pathogens in absence of masturbation	Never
*q*13	**Gain of masturbation in absence of pathogens**	**Always**
*q*24	**Gain of masturbation in presence of pathogens**	**Often**
*q*34	Gain of pathogens in presence of masturbation	Often
Losses		
*q*21	Loss of pathogens in absence of masturbation	Always
*q*31	**Loss of masturbation in absence of pathogens**	**Always**
*q*42	**Loss of masturbation in presence of pathogens**	**Never**
*q*43	Loss of pathogens in presence of masturbation	Always

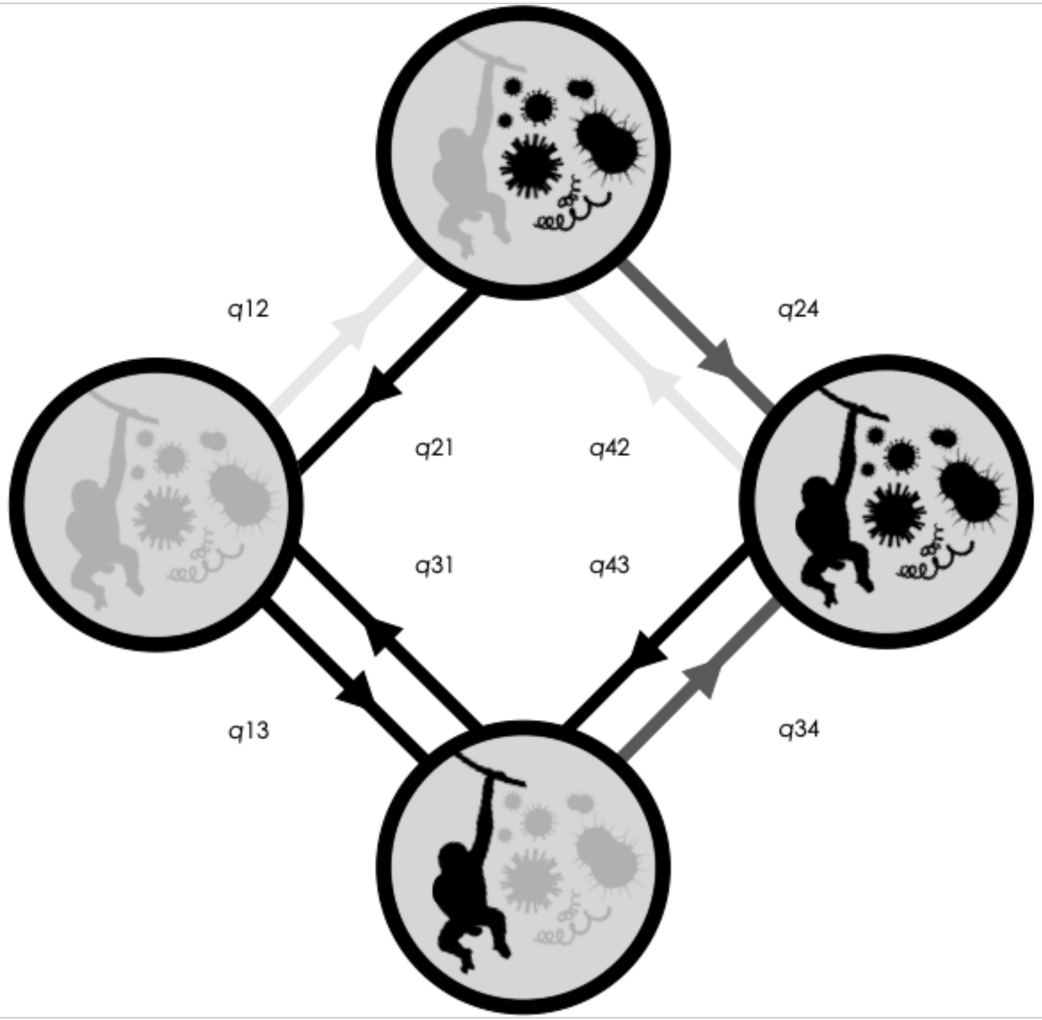

Figure 05.03. Coevolution between masturbation (present versus absent) and pathogens (present versus absent). Traits present in a given state are shown in black, and those absent are shown in grey. Black arrows correspond to pathways with a very low posterior probability of being zero (i.e. very common transitions), dark grey arrows to a low posterior probability of being zero (i.e. common transitions), and light grey arrows to a high posterior probability of being zero (i.e. rare transitions).

To ensure that the results were not an artefact of potential covariance between pathogen presence and mating system, I checked these variables for coevolution, but did not find support for this model (log BF = - 4.96, Table 05.06).

Table 05.06. Likelihood of dependent and independent models of correlated evolution between primate mating system and pathogen occurrence. Bayes Factors were interpreted following Kass & Raftery (1995): <2, weak evidence; 2-5, positive evidence; 5-10, strong evidence; >10 very strong evidence.

	Dependent model	Independent model	
Coevolution analysis	**Log marginal likelihood**	**Log marginal likelihood**	**Log Bayes Factor**
Mating system & pathogen occurrence	-128.89	-126.41	-4.96

5.5 Discussion

In this chapter I have tested functional, adaptive hypotheses for the evolution of masturbation within a comparative phylogenetic framework for the first time. My analyses indicate that both postcopulatory selection and sexually transmitted infections exert selective pressure over masturbation in primates, though the degree of support for this differs in females and males, as well as between the different measures of selective pressure (results summarised in Table 05.07). Below, I discuss support for the PSH (section 5.5.1) and the PAH (section 5.5.2), before considering the relationship between pathogen avoidance, masturbation, and oral-genital grooming (section 5.5.3). I conclude with a brief discussion of the limitations of this analysis, and priorities for future directions (section 5.5.4).

Table 05.07. Summary of test results from Chapter 05.

Hypothesis	Predictor	Support Female	 Male	Table
Postcopulatory selection	Mating system	-	X	05.01
	Testes mass	X	X	05.03
Pathogen avoidance	Pathogen load	-	X	05.01
	Geographic region	-	-	05.01
	Precipitation	-	-	05.04
	Environmental harshness	-	-	05.04

5.5.1 Postcopulatory Selection Hypothesis

In males, I found strong support for the PSH, with masturbation covarying with both mating system and testes mass, as predicted. Male masturbation presence is unstable in single-male mating systems, but evolves and is maintained when primates live in multi-male mating systems. I also detected a moderate positive association between masturbation and adult male testes mass in both female and male primates. These results confirm that previous findings in males (Dixson & Anderson, 2004) remain robust when examined with an increased sample size and within a rigorous Bayesian phylogenetic framework. However, support for the PSH does not allow us to distinguish the relative importance of the two constituent hypotheses that underpin the PSH, namely, the Sexual Arousal Hypothesis and the Sperm Quality Hypothesis (section 5.2.2).

5.5.2 Pathogen Avoidance Hypothesis

I also found strong support for the PAH in males, with masturbation coevolving with pathogen presence. Similar to the results for male masturbation and mating system, when pathogens are absent, male masturbation presence is labile, but when they are present, masturbation evolves and is retained.

There may be several explanations for why masturbation would coevolve with pathogen presence in males but not in females. One of the key functions of seminal plasma is to provide antibacterial defence for sperm once it reaches the female reproductive tract (Edstrom et al., 2008), but these bactericidal properties also protect hosts from STIs (Schulze et al., 2020). In males, ejaculate is forcefully expelled through the urethra, whereas during female arousal, vaginal transudate passes gradually through the vaginal wall, coalescing to form a film which is eventually secreted (Levin, 2003). Since the urethra is the primary site of infection for many STIs (Donovan, 2000), the powerful expulsion of bactericidal ejaculate through the urethral opening is likely to be a far more effective means of avoiding infection than the slow secretion of transudate from the vaginal canal, which does not necessarily cleanse the urethra. Furthermore, unlike in males, the PSH and PAH may be mutually exclusive in females. Under normal conditions, when a female is not aroused, vaginal pH is moderately acidic, in order to defend against infection (Meston, 2000). However, according to the PSH, one mechanism of cryptic female choice is that, during arousal, vaginal pH increases to become more neutral. While this creates a more hospitable environment for sperm, allowing females to differentially favour certain males, it is also less hostile towards pathogens, leaving females vulnerable to infection (Meston, 2000).

5.5.3 Masturbation and oral-genital grooming: alternative solutions to the same problem?

These results are consistent with the idea that primates might have evolved behavioural strategies, in this case masturbation, to reduce the risk of STIs.

However, a previous study exploring the relationship between pathogen-avoidance behaviour and STI risk failed to find a relationship. Specifically, Nunn (2003) found no evidence that those species at greater risk of infection (i.e. primates that mate with multiple partners, as defined by relative testes mass and oestrus duration) were more likely to employ two postcopulatory behavioural strategies to cleanse the reproductive tract: oral-genital grooming and urination (Nunn, 2003). Instead, while most strepsirrhines and callitrichids show stereotypic oral-genital grooming and urination after copulation, such behaviour is rarely seen in larger primates (catarrhines and non-callitrichid platyrrhines), who are less physically able to reach their genitals orally. This may indicate that these traits are not environmentally driven, but reflect derived phenotypes. Interestingly, strepsirrhines and callitrichids also engage in scent-marking behaviours, including urination and ano-genital rubbing (Nunn & Altizer, 2004), while masturbation is rare in these clades. It therefore seems possible that the presence of scent-marking (through urination and ano-genital rubbing) in strepsirrhines and callitrichids predisposed them to orally groom their genitals and urinate in order to mitigate STI risk, rather than to masturbate. In contrast, in the absence of scent-marking, larger primates may use masturbation to reduce the risk of STIs.

5.5.4 Limitations and future directions

Environmental proxies

While there was strong support for the PAH when examining pathogen load, no support was found when indirect measures of STI risk were used, namely geographic region, annual rainfall, and environmental harshness. The most likely reason for this is that the environmental predictors were poor indicators of actual STI risk. Although there is good evidence that such environmental variables are correlated with the diversity of a wide range of pathogens (e.g. Nunn et al., 2005; Guernier et al., 2004), there are no corresponding data limited specifically to pathogens that are sexually transmitted. Since these are passed on via direct contact between individuals (Gewirtzman et al., 2011), the environmental measures employed as proxies may not have adequately captured regional variation in sexually transmitted infection pressure.

Pathogen load

Although I found strong support for coevolution between male masturbation and pathogen pressure, categorising pathogen load as 'present' or 'absent' in a given species is highly reductive. In reality, pathogen load falls along a broad continuum. It would be useful to unpick this further and examine whether primates with a higher pathogen load are more likely to masturbate than those with a lower pathogen load. This was not possible with the limited sample size and restricted means of statistical analysis, but it is hoped that in future an increase in the number of primate species tested, and the number of pathogens assessed, along with an increase in masturbation data, will enable this question to be addressed in a far more nuanced light.

5.6 Chapter summary

Chapter 05 investigated the adaptive significance of primate masturbation, examining *why* it evolved. Two adaptive hypotheses were tested: the Postcopulatory Selection Hypothesis (PSH) and the Pathogen Avoidance Hypothesis (PAH). In support of the PSH, Bayesian phylogenetic analyses found that masturbation in both sexes shows a positive relationship with a large relative testes mass, and male masturbation appears to have coevolved with multi-male multi-female mating systems. While in support of the PAH, the same analyses indicate that male masturbation has coevolved with pathogen presence. The analyses presented in this chapter indicate that both female and male masturbation may be influenced by high postcopulatory selection, and that male, but not female, masturbation may also be related to pathogen load. Together, these results highlight the potential adaptive value of masturbation within the primate order.

CHAPTER 06

GENERAL DISCUSSION

6.1 Summary of findings

Given that masturbation occurs throughout the animal kingdom, there has been remarkably little research into its natural history, evolution, and potential functions. Of all animals, masturbation seems to be especially common in the primates. This, coupled with the fact that they are one of the most well-studied taxonomic groups, makes primates an ideal order within which to begin a systematic study of masturbation.

6.1.1 The database

In order to study masturbation across the primate order, it was first necessary to collate and categorise the limited information that was already available in the academic literature. A literature search provided 246 publications, and formed the basis of all future work. However, there were still significant 'gaps' in the database, with information missing for many important clades, particularly those which tend to be more difficult to observe, such as nocturnal, small-bodied species, and those that spend more time high in the canopy. Academic literature was therefore supplemented with information gleaned from questionnaires, targeted towards primatologists and others who had extensive experience with taxa for which the published literature provided little or no information. These questionnaire responses added a further 150 sources to the database, bringing the total number of sources to 396. Together, these sources generated a total of 569 separate reports, covering both female and male primates.

6.1.2 The natural history of masturbation

To understand the underlying biological processes behind a trait, it is important to first understand the forms which that trait can take, i.e. it's natural history. However, to date, there has been no systematic, cross-taxa comparison of the forms and context of masturbation in any group of animals. Chapter 03 examined the natural history of masturbation across the primate order, utilising the database compiled in Chapter 02 to examine its distribution, as well as the diverse forms it takes (*how* primates masturbate), and the environmental context within which it occurs (*where* primates masturbate). The data indicate that masturbation is never observed in tarsiers or female strepsirrhines, and is rare in male strepsirrhines, while being relatively common in platyrrhines, and very common in catarrhines, of both sexes. Masturbatory form was found to be highly diverse, with primates employing a wide range of behaviours. Importantly, masturbation was found to be common in the wild, as well as in captivity, in opposition to the Pathology Hypothesis, which states that masturbation is a pathological condition only found in captive individuals.

6.1.3 The evolution of masturbation

Understanding the evolutionary history of a trait is an important step in helping to uncover its ultimate function. Chapter 04 first examined whether masturbation shows an association with phylogeny in female and male primates (i.e. do more closely related species show more similar trait patterns?), before reconstructing its ancestral state at eight key nodes across the primate order to address the question of *when* masturbation evolved. Analyses showed that both female and male masturbation show a strong phylogenetic signal, indicating that species with more recent shared ancestry are more likely to show the same pattern of masturbation occurrence.

Ancestral state reconstructions, using Bayesian phylogenetic methods, showed similar patterns for females and males, with masturbation likely first appearing in ancestral (non-tarsier) haplorrhines and being retained in ancestral catarrhines, and all subsequent nodes. Reconstructions were more equivocal for ancestral platyrrhines, although it is likely that they masturbated too. Similarly, reconstructions were less clear for ancestral strepsirrhines, although it looks likely that females did not masturbate. Notably, reconstructions of the root of the tree were inconclusive, likely reflecting the relative paucity of data on strepsirrhines.

6.1.4 The adaptive function of masturbation

To fully understand the ultimate function of a trait, it is important to investigate its potential adaptive significance, in addition to its evolutionary history. To examine *why* masturbation evolved, Chapter 05 tested two adaptive hypotheses using a Bayesian framework: the Postcopulatory Selection Hypothesis, which predicts that masturbation increases the probability of fertilisation at copulation, and the Pathogen Avoidance Hypothesis, which predicts that masturbation reduces the risk of infection by sexually transmitted pathogens. Evidence was found in support of both hypotheses. In the case of the Postcopulatory Selection Hypothesis, both female and male masturbation show a positive relationship with a relatively large testes mass, and male masturbation appears to have coevolved with multi-male mating systems. In the case of the Pathogen Avoidance Hypothesis, male masturbation appears to have coevolved with pathogen presence.

6.2 Findings in context

Taken together, these findings begin to illuminate the natural history, evolution, and potential functions of autosexual behaviour in the primate order. Masturbation is a phylogenetically ancient, widely distributed, and diverse behaviour. Functionally, masturbation may allow a female to exert cryptic choice for fertilisation by a preferred male, while in males, masturbation may help both to increase the probability of fertilisation and to avoid sexually transmitted infections.

In terms of the *proximate* causes that lead to masturbation (following Tinbergen's framework, see Chapter 01; Tinbergen, 1963), the data presented in Chapter 03 indicate that it is not simply a pathological behaviour that occurs as a consequence of captivity (the Pathology Hypothesis), since it is also common in wild primates of both sexes. However, it is possible that masturbation is a sexual outlet for taxa with neuroendocrinological specialisations for high sexual arousal (i.e. those with multi-male multi-female mating systems; Dixson & Anderson, 2004). While this Byproduct Hypothesis cannot account for all cases of masturbation – such as those that occur immediately pre- or post-copulation, or in the presence of willing partners – there is no reason why it may not be the *proximate* cause of masturbation at other times.

One of the most striking patterns revealed is that masturbation appears to be rare, or non-existent, in many strepsirrhines, but common in most catarrhines. The *ultimate* cause of this can be explained in different ways, according to the level of inquiry adopted (following Tinbergen's framework, see Chapter 01; Tinbergen, 1963). First, when the *evolution* of masturbation was examined (Chapter 04), it was found that it likely first evolved as a regular behaviour in ancestral (non-tarsier) haplorrhines, and may have been absent in ancestral strepsirrhines. The second approach is to examine the *adaptive significance* of masturbation, as in Chapter 05. In these analyses, it was found that both postcopulatory selection and sexually transmitted infections exert selective pressure over masturbation in primates, but why would this mean that masturbation is more common in catarrhines than other groups? First, multi-male multi-female mating systems seem to be less common among strepsirrhines, which may lead to lower postcopulatory selection pressure. Second, as identified in Chapter 05, strepsirrhines, and certain platyrrhines, orally groom their genitals and scent-mark with urine (Nunn & Altizer, 2004). It may be that, given that these behavioural phenotypes are already present in these taxa, and may already play a role in reducing the risk of infection by sexually transmitted pathogens, there is no need for masturbation to be employed as an additional form of pathogen avoidance. By contrast, oral-genital grooming and scent-marking are not common catarrhine behaviours. If masturbation had already evolved in this group alongside increased postcopulatory selection pressure, it may have been 'repurposed' to also serve as a means of reducing the risk of sexually transmitted infection in male catarrhines. In other words, in catarrhines, masturbation may have originated in response to high postcopulatory selection, but may have subsequently been exapted for pathogen avoidance (and maintained via the combined influence of postcopulatory selection and selection for pathogen avoidance). Thus, strepsirrhines, and some platyrrhines, may reduce STI risk by grooming their genitals orally and by urinating, while other platyrrhines, and catarrhines, may reduce STI risk through masturbation.

6.3 Limitations & future directions

6.3.1 Missing data

Although the database collated in this study provides the widest possible coverage of masturbation in the primate order, there are still significant gaps in the data reflecting a complete lack of reports for certain taxa. Species for which data are missing are predominantly members of the Strepsirrhini, but there are also notable gaps within the Platyrrhini, and even some genera of Catarrhini (for example, there are no data for the genus *Colobus*). Collating data on these species is vital if we are to build a complete picture of masturbation across the primate order. As it stands, information on catarrhines predominates the database, which has likely biased the outcomes of the analyses presented here. For example, the natural history of masturbation presented in Chapter 03 is heavily influenced by patterns in (non-tarsier) haplorrhines, and the catarrhines in particular. The availability of more data across more species would facilitate analyses of inter-specific differences, providing a more detailed picture of the natural history of masturbation within the primate order. Greater species coverage would also be beneficial to understanding the evolutionary history of masturbation. For example, with more information on masturbation occurrence in extant strepsirrhines, it would be possible to reconstruct the phenotype of ancestral strepsirrhines with more confidence, which, in turn, may shed light on the ancestral state of all primates.

6.3.2 Systematic research protocols

In this study, data on the natural history of masturbation were compiled and categorised according to the descriptors used in the original articles, without being 'standardised' before inclusion in the database (Chapter 02). This approach was adopted in part so that the data could be examined in the greatest level of detail provided, but also to gain a better understanding of the range of autosexual behaviours displayed by primates, while avoiding potentially biasing the database with prior assumptions. Given this approach, it is possible to make several recommendations as to how future research protocols should aim to collect data on masturbation in a systematic way, in primates and other animals.

At the very minimum, masturbation should be included in research ethograms, so that its presence or absence can be charted in a wider range of species. The inclusion of masturbation in behavioural catalogues would facilitate the collection of data on research campaigns during which researchers looked out for masturbation, but it was not observed. If research effort on a given species was high, but no autosexual behaviours were observed, a species could be described as non-masturbatory with greater confidence.

If masturbation was observed, researchers should include contextual information regarding both the environment in which it occurred (for example, was it in the wild, a semi-free ranging setting, or captivity?), and the individual characteristics of the individual masturbating (for example, sex, age, and dominance-rank, if applicable). Ideally, researchers would document whether it occurred pre- or post-copulation, and if so, by how long (in minutes), as this would help disentangle hypotheses that account for masturbation pre-copulation (i.e. the Postcopulatory Selection Hypothesis), and those that account for masturbation post-copulation (i.e. the Pathogen Avoidance Hypothesis). Similarly, if masturbation was observed in male primates, it is important to report whether ejaculation occurred as this would help differentiate between the Sexual Arousal Hypothesis, and the Sperm Quality Hypothesis.

If it is possible to collect further detail on the form of masturbation, this should also be reported in clear, unambiguous terminology, and the body parts and/or tools involved should be reported in detail.

6.3.3 Fossil calibration

An obvious limitation with taking a phylogenetic approach to reconstruct a behavioural trait is that it is (usually) not possible to ground truth the results. However, rare, circumstantial, evidence is present in the recent archaeological record. For example, scientists at the university of Tübingen discovered what they believe to be a 28,000 year old dildo in the Hohle Fels Cave in South Germany (Amos, 2005; Figure 06.01), while a collection of phallus-shaped instruments recovered across France from the Upper-Palaeolithic have been suggested to constitute masturbatory devices, as well as important ritual items (Angulo & García-Díez, 2009, Figure 06.01). Nevertheless, aside from these relatively modern, human artefacts, it is difficult to imagine a scenario in which the act of masturbation, or evidence of masturbation, would be fossilised.

Figure 06.01. Examples of masturbatory devices found in the archaeological record. (A) A 28,000 year-old dildo, measuring 20 cm long x 3 cm wide. (B) A collection of phallic masturbatory devices from the Upper-Palaeolithic (38,000 – 11,000 years BCE). Images adapted from (A) The Urgeschichtliches Museum Blaubeuren, Germany website (https://www.urmu.de/de/Forschung - Archaeologie/Eiszeitkunst/Phallus) and (B) Angulo & García-Díez, 2009.

6.4 Outlook

6.4.1 The importance of females

While the data presented here suggest that female masturbation is less common than male masturbation, it is important to note that this is likely influenced by the fact that there is far less information available on females. This may in part reflect the fact that female sexual arousal tends to be less conspicuous than male sexual arousal, but it is also likely to reflect a broader trend in biology: a deplorable paucity of information on female sexual behaviour and morphology. Given this lack of data, it is easy to put females to the side, in favour of research on males, which tends to bring with it larger sample sizes and a useful back catalogue of previous scientific endeavour. Fortunately, however, attitudes are shifting, and research into the evolution of female sexual morphology (and to some extent, behaviour) is on the rise. If we are to gain a deeper understanding of how and why masturbation evolved, it is vital that females share the spotlight.

6.4.2 You're an animal!

As part of the natural repertoire of human sexual behaviour, masturbation has an important role to play in wider public health (e.g., Sarnoff & Sarnoff, 1979; Levin, 2007; Zimmer & Imhoff, 2020). In terms of the public health implications of this study, the finding that masturbation is widespread throughout the primate order, practiced by wild-living members of both sexes, and all age-groups, is a strong counter-argument to those who condemn human masturbation as 'unnatural' – an attitude that is still held and disseminated, often in connection with religious convictions. However, even if those who disapprove of masturbation would accept the fact that it is 'natural', they are likely to simply change direction by arguing that humans, far from striving to live 'naturally', should aim to be civil and cultivated, rather than 'animalistic'.

It is therefore unlikely that entrenched conservatism will be susceptible to a rational discourse about natural behaviours (cf. Sommer, 2006). This is unfortunate, because acolytes of these schools of thought, who nevertheless find it difficult to resist the urge to masturbate, may suffer guilt, psychological distress, and difficulties in sexual performance as a result (Patton 1986). This is not to say that human societies should indiscriminately accept all behaviours that are also present in other animals, given that many involve conflict, aggression, and killing. In non-human primates, for example, these include infanticide, cannibalism, sexual coercion, and violence between neighbouring groups (Sommer, 2006; Minocher & Sommer, 2016). Still, as a typically solitary activity, masturbation has far less destructive potential. Indeed, it's suppression may do more harm than good (Patton, 1986).

There is still a long way to go before societal taboos around masturbation disappear. Historical opinions that masturbation is an "*unnatural sin*", and the "*preposterous entertainment*" of the depraved, are not yet constrained to the past (Laqueur, 2003, p. 64 & 37, respectively). However, slowly, the tide is beginning to turn. Today, masturbation is accepted by many as a healthy, 'natural', aspect of sexuality. The research presented in this thesis certainly supports this view.

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APPENDIX I

Example questionnaire circulated by V. Sommer & A. Parish (1992)

Dr. Volker Sommer / Amy Parish, Department of Anthropology,
University of California, Davis CA 95616, USA
Phone / FAX 001-916-758-1154

November 27th, 1992

TO:

QUESTIONNAIRE : MASTURBATION IN NONHUMAN PRIMATES

Dear Colleague,

Your assistance in conducting a review on "Masturbation in Nonhuman Primates : Distribution, Mechanisms and Functions" would be greatly appreciated! The questionaire supplements data extracted from about 250 research articles. Please spell out information which is not covered by particular questions. If you have data on more than one species, please copy the sheets. You might feel free to you give copies to other interested primatologists. To save postage, you may return the questionnaire as a printed matter. All respondents will be acknowledged and receive a reprint of the (hopefully) resulting publication.

In case you are planning to dig through your records (with the consequent danger of not returning the questionnaire at all because of lack of time), please answer only the most obvious questions out of your memory.

In order to gather broad qualitative data, we define masturbation rather loosely as "any form of autosexual stimulation." Please do <u>not</u> report instances of pressing / rubbing / thrusting against conspecifics of the same or the opposite sex, although we are aware of the likely continuum between autosexual and hetero- or homosexual activities.

Thank you for your cooperation. Sincerely yours.

[redacted]
Volker Sommer

[redacted]
Amy Parish

Time required : about 15 min.

"Not observed" is important information too !!!

NEGATIVE-EVIDENCE-QUICK-REPLY

1 I have NOT observed evidence of masturbation in males or females
during my work with (species) ____________________
which lasted for a period of ____________________
in captivity (lab/zoo) ____________________
in the field (site) ____________________
in groups of following composition ____________________

2 I am convinced, that masturbation in this species
( ) does not occur
( ) might occur, if observed more closely

3 Has anyone else from your study site ever observed masturbation ?
( ) I don't know
( ) No
( ) Yes ____________________

POSITIVE EVIDENCE

RESEARCH BACKGROUND

4 I HAVE observed masturbation
☐ in females
☐ in males
of the following species
latin name ______________________
common name _____________________
while carrying out observations in
☐ captivity ____________________
☐ the field ____________________

5 My experience with the species
spans about __________ years /
__________ months and comprises
about _______ hours of observation.

6 My observations are published
☐ no
☐ yes ____________________

SPECIES CHARACTERISTICS

7 Natural grouping pattern
☐ unknown
☐ one-male-one-female units (monogamy)
☐ one-male-multi-female (polygyny)
  ☐ small units (< 6 individuals)
  ☐ large units (6+ individuals)
☐ multi-male-multi-female (polygynandry)
  ☐ small units (< 6 individuals)
  ☐ large units (6+ individuals)
☐ multi-male-one-female (polyandry)
☐ solitary foragers
☐ other ______________________

8 Mating season
☐ unknown
☐ no
☐ yes _________________________

9 Mating calls
☐ no
☐ by females
☐ by males

10 Mounts with thrusting occur between
☐ male-female (= mating)
☐ female-female
☐ male-male
☐ female-male

11 Penile erections
☐ common
☐ only during sexual interactions

12 Ejaculation typically
☐ during first mount
☐ after several mounts
☐ unknown

13 Female orgasm
☐ unknown
☐ no
☐ apparently / yes ___________________________

SOCIAL PROFILE OF MASTURBATORS	Female				Male			
	adult	sub-ad.	juven.	infant	adult	sub-ad.	juven.	infant
14 Age-sex class in which masturbation was observed	AF	SF	JF	IF	AM	SM	JM	IM
	( )	( )	( )	( )	( )	( )	( )	( )
15 How many individuals were seen masturbating?	AF	SF	JF	IF	AM	SM	JM	IM
- one	( )	( )	( )	( )	( )	( )	( )	( )
- up to 3	( )	( )	( )	( )	( )	( )	( )	( )
- up to 5	( )	( )	( )	( )	( )	( )	( )	( )
- up to 10	( )	( )	( )	( )	( )	( )	( )	( )
- more than 10	( )	( )	( )	( )	( )	( )	( )	( )
16 How often was masturbation observed in a typical individual ?	AF	SF	JF	IF	AM	SM	JM	IM
- once	( )	( )	( )	( )	( )	( )	( )	( )
- up to 3 times	( )	( )	( )	( )	( )	( )	( )	( )
- up to 5 times	( )	( )	( )	( )	( )	( )	( )	( )
- up to 10 times	( )	( )	( )	( )	( )	( )	( )	( )
- more than 10 times	( )	( )	( )	( )	( )	( )	( )	( )
17 Duration of masturbation	AF	SF	JF	IF	AM	SM	JM	IM
- unknown	( )	( )	( )	( )	( )	( )	( )	( )
- short (< 1 min)	( )	( )	( )	( )	( )	( )	( )	( )
- 1-2 min	( )	( )	( )	( )	( )	( )	( )	( )
- > 2 min	( )	( )	( )	( )	( )	( )	( )	( )
18 Individual copulated during life history stage when masturbating?	AF	SF	JF	IF	AM	SM	JM	IM
- unknown	( )	( )	( )	( )	( )	( )	( )	( )
- no	( )	( )	( )	( )	( )	( )	( )	( )
- unlikely	( )	( )	( )	( )	( )	( )	( )	( )
- likely	( )	( )	( )	( )	( )	( )	( )	( )
- yes	( )	( )	( )	( )	( )	( )	( )	( )
19 Dominance rank in social group	AF	SF	JF	IF	AM	SM	JM	IM
- unknown	( )	( )	( )	( )	( )	( )	( )	( )
- high	( )	( )	( )	( )	( )	( )	( )	( )
- medium	( )	( )	( )	( )	( )	( )	( )	( )
- low	( )	( )	( )	( )	( )	( )	( )	( )

(field observers : go to next section)

CAPTIVE OBSERVATIONS : CONDITIONS OF INDIVIDUALS OBSERVED MASTURBATING

Female	Male	20 Enclosure
( )	( )	indoor
( )	( )	indoor / outdoor
( )	( )	outdoor

Female	Male	21 Public access
( )	( )	no
( )	( )	yes

Female	Male	22 Housed
( )	( )	singly
( )	( )	socially

Female	Male	23 During infancy
( )	( )	reared with mother in a social group
( )	( )	reared by humans
( )	( )	bottle reared
( )	( )	sex-segregated
( )	( )	socially isolated

Female	Male	24 Individual was
( )	( )	gonadally intact
( )		ovariectomized
( )		estrogen treated
	( )	castrated
	( )	testosterone treated

Female	Male	25 Behavior influenced by
( )	( )	chemical substances
( )	( )	manipulation of brain
( )	( )	none of above

CONTEXT OF MASTURBATION

Female	Male	26 If masturbator lived socially, members of the following age-sex classes were present (if known, fill brackets with particular numbers)
( )	( )	unknown
( )	( )	variable
( )	( )	adult females
( )	( )	subad. / juv. females
( )	( )	infant females
( )	( )	adult males
( )	( )	subad. / juv. males
( )	( )	infant male

Female	Male	27 Opposite sex could be contacted
( )	( )	tactilly
( )	( )	visually
( )	( )	auditorily
( )	( )	olfactorily
( )	( )	none of above (isolated)

Female	Male	28 If living in social group, members of opposite sex were sexually
( )	( )	attractive
( )	( )	proceptive
( )	( )	receptive
( )	( )	none of above

Female	Male	29 For masturbators who mated : The correlation between the two sexual activities can best be described as
( )	( )	little mating/little mast.
( )	( )	little mating / much mast.
( )	( )	much mating / little mast.
( )	( )	much mating / much mast.

Female	Male	30 Typical contexts, when masturbation occurred ?
( )	( )	unknown
( )	( )	no
( )	( )	yes ____________________

Female	Male	31 In the course of a day, masturbation occurred most frequently during
( )	( )	early morning
( )	( )	morning
( )	( )	noon
( )	( )	afternoon
( )	( )	late afternoon
( )	( )	night
( )	( )	no pattern
( )	( )	unknown

Female	Male	32 In the course of a year, masturbation occurred most frequently
( )	( )	during mating season
( )	( )	outside mating season
( )	( )	during rainy season
( )	( )	during dry season
( )	( )	no pattern
( )	( )	unknown

QUALITATIVE DESCRIPTION OF FEMALE MASTURBATION

33 Stimulated body parts
☐ anus
☐ clitoris
☐ vagina
☐ breast-nipples
☐ other

34 Stimulation was achieved
☐ with hand
☐ with foot
☐ with mouth
☐ with tail
☐ with inanimate object
☐ by inserting object ______________
into (body part) ______________
☐ by rubbing / pressing / thrusting against substrate
☐ other ______________

35 Masturbation resulted in an orgasm
☐ unknown
☐ no
☐ sometimes
☐ often

36 Reproductive status of adult masturbators
☐ unknown
☐ menstruating
☐ follicular phase
☐ luteal phase
☐ during mid-cycle estrus
☐ pregnancy
☐ lactation

37 Accompanying gestures
☐ unknown
☐ hip-grasp
☐ present
☐ pelvic thrusts
☐ other ______________

38 Special facial expressions
☐ unknown
☐ no
☐ yes ______________

39 Vocalization
☐ unknown
☐ no
☐ yes ______________

40 Conspicuous condition of sex-organ
☐ unknown
☐ clitoris darkening
☐ clitoris enlarged
☐ other ______________

41 Excitement (______________) during typical instance of masturbation was
☐ little
☐ moderate
☐ high

42 My assumption is, that female masturbation occurred because :

____

QUALITATIVE DESCRIPTION OF MALE MASTURBATION

43 Stimulated body parts
( ) anus
( ) penis
( ) testes
( ) other

44 Stimulation was achieved
( ) with hand
( ) with foot
( ) with mouth
( ) with tail
( ) with inanimate object
( ) by inserting object ____________________
into (body part) ____________________
( ) by rubbing/pressing/thrusting against substrate
( ) other ________________________________

45 Ejaculation occurred
( ) unknown
( ) never
( ) sometimes
( ) often

46 Semen was eaten
( ) unknown
( ) never
( ) sometimes
( ) often

47 Accompanying gestures
( ) unknown
( ) hip-grasp
( ) present
( ) pelvic thrusts
( ) other ____________________________

48 Special facial expressions
( ) unknown
( ) no
( ) yes ______________________________

49 Vocalization
( ) unknown
( ) no
( ) yes___________________________________

50 Conspicuous condition of sex-organ
( ) unknown
( ) penis flaccid
( ) penis erect
( ) other _____________________________

51 Excitement (__________________) during typical instance of masturbation was
( ) little
( ) moderate
( ) high

52 My assumption is, that male masturbation occurred because :

____

53 COMMENTS

____

Date _________________________ Signature

Fold and return to

Dr. V. Sommer
Anthro Dept. UCD
Davis CA 95616
USA

APPENDIX II

Example questionnaire circulated by R. Thomsen (1997)

#543

30.3.98 4

(30) ✓

QUESTIONNAIRE: MASTURBATION (M) IN MALE PRIMATES

Dear Resarcher, your help in conducting a review on male masturbation in primates would be greatly appreciated!
If you have data of more than one species or from the same species from different study sites, please copy the sheets. You might feel free to give copies to other interested primatologists. All respondents will be acknowledged and receive a reprint of the (perhaps) resulting publication. In order to gather broad qualitative data, I define male masturbation as: "rhythmically rubbing or just stimulating the erect penis with one or both hands or feet no matter wether ejaculation takes place or not". Thank you very much for your cooperation.

Sincerely yours, Ruth Thomsen

16.1.98

If possible, please answer with „yes" or „no"
If there is a question to which you can't give answer to, please use „?"

A BASIC INFORMATION: I recognized masturbatory behaviour in:

(1) species: BRACHYTELES ARACHNOIDES
(2a) study site: ESTAÇÃO BIOLÓGICA DE CARATINGA, MINAS GERAIS, BRASIL
(2b) 100% wild living: X provisioned:...... monkey park....... zoo:......... laboratory:.........
(3) social organization: MULTI-MALE, MULTI-FEMALE
(4) consortship: a) stable:.......... b) non-stable:.......... c) other: X
(5) adult SR (no. of ad. males: ad. females in a troop): a) sure: 13:19 * b) estimated:..........
(6) your time of observation at this species: 16 YEARS * DURING PERIOD OF DATA BELOW

B MALE MASTURBATION:

(1) Type of M (how did the observed male(s) masturbate?):
a) rhytmically.......... b) just playing with the erect penis X c) both X
(2) Do you know the age of male(s) observed masturbating? a) yes: X ....years b) no:.......
(3) *estimated* frequency of M of all males together from your study-troop: How often did you recognize M per day? * (1-3 times) ** (4-10) *** (>11) [✓ ? (I can't estimate)]
a) in the mating-period: X by non-troop-males:.......... by troop-males X
b) in the non-mating-period: X by non-troop-males:.......... by troop-males X
c) no information about mating-period is available:..........
d) species without clear mating-period:..........
(4) have you ever observed masturbation of a male staying in a consortship? N/A
(5) ejaculation was observed:
a) in the mating-period: X
b) in the non-mating-period: X
c) species without clear mating period..........
(6) ejaculation was not observed..........
(7) the masturbating male(s) ate the ejaculate: a) never:.......... b) sometimes X c) always ~~X~~

C DO YOU HAVE ANY IDEA IN WHICH CONTEXT THE MALE(S) MASTURBATE? (for instance before or after any aggressional behaviour, regarding an estrous female or copulation of other individuals, before feeding on ripe fruits...)

1 time ~~[illegible]~~ after a failed attempt to mate; other times during rest periods ✓

D ANY NOTES FROM YOU ON MALE MASTURBATION?

....

(please use the backside of this sheet to continue) »»»

Your name and address: Karen B. Strier, Dept of Anthropology, UW-Madison
kbstrier@facstaff.wisc.edu → Observations from: Laiena R.T. Dib romeudib@bhnet.com.b

Please send to: Ruth Thomsen, LM-University of Munich, Dep. of Zoology, at: Nigawa-Takamaru 2-22-31, 665 Takarazuka, Japan (it is my field-site address from 7-10-97 until 30-9-98). e-mail: merz@pluto.dti.ne.jp

K. B. Strier
UW - Madison
Department of Anthropology
1180 Observatory Drive
Madison, [illegible] 53706 U.S.A.

APPENDIX III

Example questionnaire circulated by R. Thomsen (1997)

#553

(142)

(54) 142

QUESTIONNAIRE (2. Version)
MASTURBATION IN MALE PRIMATES

Dear resarcher, your help in conducting a review on male masturbation in primates would be greatly appreciated! If you have data of more than one species or from the same species from different study sites, please copy the sheets. You might feel free to give copies to other interested primatologists. All respondents will be acknowledged and receive a reprint of the resulting publication. In order to gather broad qualitative data, I define male masturbation as: "rhythmically rubbing or just stimulating the erect penis with one or both hands or feet no matter wether ejaculation takes place or not". Thank you very much for your cooperation.

6/ 1998, Sincerely yours, Ruth Thomsen

If possible, please answer with **yes** or **no**.

If there is a question to which you can`t give answer to, please use **??**

A BASIC INFORMATION

I saw masturbation in:

(1) species:......Saimiri......
(2a) name and location of your study site:....NIH Lab Colony, NIH Animal Center
(2b) 100% wild living:....provisioned:......monkey park........zoo:..................laboratory:.....Yes.................
(3a) breeding system:..captive caged..............(3b) unknown:......................................
(4) your time of observation at this species (roughly):....15 years......................................

I never saw masturbation in:

(1) species:..
(2a) name and location of your study site:..
(2b) 100% wild living:....provisioned:.........monkey park........zoo:..................laboratory:.........................
(3a) breeding system:...(3b) unknown:...
(4) your time of observation at this species (roughly):..

B MALE MASTURBATION

(1) How did the observed male(s) masturbate?
a) rhythmically...................b) just playing with the erect penis................c)both...Yes....d) I don´t know:......
(2) Do you know the age of male(s) observed masturbating? a) yes:....9-15.. years b) no:.................................
(3) When did you see masturbation?
a) in the mating-period:.......Yes.....
c) no information about mating-period is available:...
d) species without clear mating-period:...
(5a) **masturbation with ejaculation** was observed:
a) in the mating-period:...........Yes......................
b) in the non-mating-period:...................................
c) species without clear mating period.........................
(5b) **masturbation was never with ejaculation**:.........Yes............................
(6) the masturbating male(s) ate the ejaculate: a) never:...............b) sometimes.....Yes....c) always........................

C ANY NOTES FROM YOU ABOUT MALE MASTURBATION IN PRIMATES?

....
....
....
....

Your name and address:......Deborah Bernhards
LCE, NICHD, NIH
Bethesda, MD

THANK YOU!

Joseph

Please send to: Ruth Thomsen, LM-University of Munich, Dep. of Zoology, Luisenstrasse 14, 80333 Munich, GERMANY

APPENDIX IV

Example questionnaire circulated by M. Brindle & V. Sommer (2018 - 2021)

Auto-Sexual Behaviour in Primates

Matilda Brindle & **Prof. Volker Sommer**
Department of Anthropology,
University College London,
14 Taviton Street,
London,
WC1H 0BW

Dear Colleague,

We are conducting a review on auto-sexual behaviour (masturbation) across the Primate order and would greatly appreciate insights you can offer from your own work – hence this questionnaire.

Replies will supplement data from around 350 research articles and previous questionnaires. We are particularly interested in data - positive or negative - on strepsirrhines, platyrrhines and tarsiers as these are under-represented in our database. It is important for us to establish whether this is because masturbation is extremely rare or non-existent in these taxa, or because it is simply not reported to the same extent as in the catarrhines.

If you are unsure of the reply to any of the questions, please leave the answer box empty. If you do not feel you have time to complete the full questionnaire, please fill out the 'quick questionnaire' at the start.

Please feel free to pass this questionnaire on to any other primatologists who may be able to provide us with information. Respondents will be acknowledged in our database and resulting publications.

Thank you for your kind assistance.

Sincerely yours,

Matilda Brindle
(MSc, NERC DTP PhD Candidate)
[redacted]
matilda-jane.brindle.14@ucl.ac.uk

Volker Sommer
[redacted]
v.sommer@ucl.ac.uk

Auto-Sexual Behaviour in Primates

Overview

Working definition for masturbation: 'any form of auto-sexual stimulation'.

Note: we do not consider pressing, rubbing or thrusting against conspecifics of either sex – this is considered 'allo-sexual' rather than 'auto-sexual' behaviour.

Your name ______________________________

Study species (common & Latin name)______________________________

Duration of study ______________________________

Study site (e.g. lab, zoo, semi-free ranging, wild) ______________________________

Name and location of study site ______________________________

Group composition ______________________________

Quick Questionnaire: Negative Evidence

1. I **HAVE NOT** observed evidence of masturbation in males or females of this species.

☐

Quick Questionnaire: Positive Evidence

2. I **HAVE** observed masturbation in this species.

☐ Yes, in females

☐ Yes, in males

3. In which age groups did masturbation occur?

	Adult	**Subadult**	**Juvenile**	**Infant**
Female	☐	☐	☐	☐
Male	☐	☐	☐	☐

4. Was a masturbatory orgasm observed?

☐ Yes, in females

☐ Yes, in males

5. Please provide a brief qualitative description.

____

____

____

6. My observations are published.

☐ Yes (reference) ______________________________

____

____

☐ No

Extended Questionnaire: Positive Evidence

Living Conditions and Environment

7. If captive, were your study subjects provided with environmental enrichment?

☐ Yes (please specify) ____________________
☐ No

8. Had your study subjects undergone any experimental manipulation? (E.g. social isolation, drug treatment, neurological treatment, behavioural training).

☐ Yes (please specify) ____________________
☐ No

9. How would you rate the habitat your study subject lived in (1 = plentiful, 5 = extremely harsh). Please provide a brief description.

☐ 1 ☐ 2 ☐ 3 ☐ 4 ☐ 5

____
____
____

10. Were your study subjects provisioned?

☐ Yes (please specify) ____________________
☐ No

11. Were your study subjects exposed to members of the public?

☐ Yes
☐ No

Context of Masturbation

12. Was there a trigger to masturbation? (E.g. group conflict, excitement, frustration).

☐ Yes (please specify) ____________________
☐ No

13. Was it possible for masturbating individuals to contact the opposite sex?

☐ Physically
☐ Visually
☐ Auditorily
☐ Olfactorily
☐ No contact (isolated)

14. Was masturbation directed at another individual?

☐ Yes (please specify) ____________________
☐ No

15. What was the sexual status of the females in the group?

☐ Attractive ☐ Proceptive ☐ Receptive ☐ None

16. Did masturbation occur in association with copulation?

☐ Yes, pre-copulation (please specify how long prior to copulation) ____________________
☐ Yes, post-copulation (please specify how long after copulation) ____________________
☐ No

17. Masturbation occurred most frequently:

☐ During mating season
☐ Outside of mating season
☐ During rainy season
☐ During dry season

18. Did your study group breed seasonally (>67% of births occur within a peak 3 month period)?

☐ Yes
☐ No

19. What mating system best describes that of your study group?

☐ Polygynandry
☐ Polyandry
☐ Polygyny
☐ Monogamy

20. Where did masturbating individuals fit within the dominance hierarchy?

☐ High
☐ Middle
☐ Low

21. Roughly how many/what percentage of the group were observed to masturbate?

Females ____________________

Males ____________________

22. How often was masturbation observed in a typical individual per day/week?

Females		**Males**	
Adult	____________	Adult	____________
Subadult	____________	Subadult	____________
Juvenile	____________	Juvenile	____________
Infant	____________	Infant	____________

Qualitative Description of Masturbation

23. Typical duration of masturbation:

☐ < 1 minute

☐ 1-2 minutes

☐ 2-3 minutes

☐ >3 minutes

24. How often did masturbation culminate in an orgasm?

Females	**Males**
☐ Frequently	☐ Frequently
☐ Sometimes	☐ Sometimes
☐ Never	☐ Never

25. If males were observed to ejaculate, was this ingested?

☐ Yes

☐ No

26. Which parts of the body were stimulated? (E.g. penis, clitoris, anus, nipples etc.).

____

27. What was used to stimulate these body parts? (E.g. fingers, foot, tail, the ground, fruit).

____

28. How did stimulation occur? (E.g. rub, thrust, suck, stroke).

____

29. What was the condition of the genitalia of masturbating individuals? (E.g. penis erect, vaginal tumescence, enlarged clitoris, darkened genitalia).

____

30. Was masturbation accompanied by any gestures?

☐ Yes (please specify) ____
☐ No

31. Was masturbation accompanied by any facial expressions?

☐ Yes (please specify) ____
☐ No

32. Was masturbation accompanied by vocalisations?

☐ Yes (please specify) ____
☐ No

33. Excitement during masturbation was typically:

☐ High
☐ Moderate
☐ Little

34. My assumption is, masturbation occurred because:

____
____
____

Thank you for your participation. Please add additional information below.

APPENDIX V

Acknowledgements & reference list for data sources (Chapter 02)

This research would not have been possible without the kind assistance of colleagues who responded to questionnaires or provided additional information: P. A. Adoyo, W. Angst, G. Anzenberger, S. Bearder, S. Benning, D. Bernhards, C. Bettridge, M. Böer, R. Boonratana, C. Borries, A. I. Y. Boug, M. Bowler, R. W. Byrne, F. Colmenares, M. Crofoot, R. Curran, G. Davis, L. J. Digby, H. Donkin, G. Ellison, G. Epple, C. Fichtel, B. Fruth, S. Fujita, J. Ganzhorn, A. Georgiev, M. S. Gerald, L. Germani, N. Hidayatik, G. Hanya, S. Harcourt, M. Hauser, S. Hayakawa, S. Heiduck, J. Henke-von der Malsburg, E. W. Heymann, D. Hill, G. Hohmann, M. Huck, J. Jaffe, P. M. Kappeler, C. Knogge, A. Korstjens, M. Krebs, I. Küderling, A. Kumar, B. Kunz, J. A. Kunz, J. Küster, N. Kutsukake, E. Loser, K. Maynard, T. McKinney, A. Meder, L. Miller, B. Moorman, A. Nekaris, O. Nevo, U. Nieschalk, R. Noë, B. Noë-Slijter, M. A. Norconk, K. Okamoto, A. Paul, L. Peckre, S. Perry, O. Petit, J. Phillips-Conroy, P. Piegnot, S. Preuschoft, U. Radespiel, M. Ramsay, M. Razafindrasamba, U. Reichard, D. Rendall, K. Rudolph, S. Rūmenas, D. Sajuthi, J. B. Silk, J. Soltis, C. B. Stanford, K. Stewart, K. A. Strier, H. Sugiura, H. Swam, T. Tamaka, B. Thierry, L. L. Tórrez- Herrera, V. Torti, M. A. van Noordwijk, C. van Schaik, A.-S. Warkentin, K. Watanabe, I. Weiche, A. Weldon, G. C. Westergaard, L. White, J. M. Whitehead, D. Wrogemann, J. Yamagiwa, C. P. Yeager, D. Zimmer, E. Zimmermann, D. Zumpe. Early elements of the database were curated by Amy Parish and Uta Skamel.

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APPENDIX VI

Publications

Brindle, M., Ferguson-Gow, H., Williamson, J., Thomsen, R., Cowlishaw, G., & Sommer, V. (in prep). Primate masturbation is functionally related to postcopulatory sexual selection and pathogen avoidance.

Brindle, M., Thomsen, R., Cowlishaw, G., & Sommer, V. (*in prep*). An overview of primate masturbation: how, when, and why.

Sommer, V., Thomsen, R., & **Brindle, M.** (in press). Masturbation in primates. In T. Shackelford (Ed.) *The Cambridge handbook of evolutionary perspectives on sexual psychology*. Cambridge University Press

Havercamp, K., **Brindle, M.**, Sommer, V., & Hirata, S. (in press). Spontaneous nocturnal erections and masturbation in captive male chimpanzees (*Pan troglodytes*). *Behaviour*

Williamson, J., Teh, E., Jucker, T., **Brindle, M.**, Bush, E., Chung, A. Y. C., Parrett, J., Coomes, D., Lewis, O. T., Rossiter, S. J., & Slade, E. M. (2022). Local-scale temperature gradients driven by human disturbance shape the physiological and morphological traits of dung beetle communities in a Bornean oil-palm-forest mosaic. *Functional Ecology, early view.*

Gilbert, J. D., **Brindle, M.,** & Faulkes, C. G. (2022). Anecdotal observation of a sexual encounter between two male naked mole-rats. *Behaviour, 1,* 1-13.

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