

SAME-SEX SEXUAL BEHAVIOUR IN BATS

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ABSTRACT - In recent years many studies have been published on animal homosexuality. Here, we reviewed the available observations on bat homosexual behaviour, presenting some behavioural hypotheses. Same-sex sexual behaviours can be classified in 6 different groups and till now have been documented in 22 species of megabats and microbats. Further investigations are required as many more species are expected to show similar behaviours.

Key words: animal homosexuality, coercive sex, captivity, Chiroptera

RIASSUNTO - *Il comportamento omosessuale nei pipistrelli*. Negli ultimi anni si sono moltiplicati gli studi sull'omosessualità degli animali. Alcuni testi hanno riunito e sintetizzato le attuali conoscenze tentando di darne anche interpretazioni evolutive. Vengono esaminati i lavori dove gli autori attribuiscono ai chiroteri comportamenti omosessuali, fornendo possibili ipotesi motivazionali. Sono elencate 22 specie e 6 diverse tipologie. Sono necessarie ulteriori ricerche che porteranno probabilmente ad individuare un numero molto più elevato di specie con comportamenti similari.

Key words: comportamento omosessuale, omosessualità negli animali, cattività, chiroteri.

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INTRODUCTION

Homosexual behaviour in animals has been discussed since classical antiquity. Aristotle anticipated modern ethology: the earliest written mention of animal homosexuality probably dates back to 2,300 years ago, when he described copulation between same-sex pigeons, partridges and quails (Glickman 1995; Brooks 2009). Written by the Egyptian writer Horapollo Niliacus in the fourth century A.D., the Hieroglyphics of Horapollo is an anthology of "hieroglyphics", or allegorical emblems, with

speculations on "hermaphroditism" in hyenas and homosexuality in partridges (Dynes 1987; Horapollo 2007).

The first review of animal homosexuality was written by the zoologist Ferdinand Karsch-Haack (Karsch 1900); more details on the early studies are available in some more recent papers (Meyer-Holzappel 1961; Schutz 1966; Houser 1990; Brooks 2009). Books by Edward O. Wilson (1975, 1978) have stimulated great interest in homosexuality and notably in animal homosexuality (Weinrich 1990; Stein 2000), particularly in the last decade (Bagemihl

1999; Judson 2003; Balcombe 2006; Sommer and Vasey 2006; Roughgarden 2009; Poiani 2010). Also at least one children's book, "And Tango Makes Three", was produced, dealing with a homosexual couple, Roy and Silo, two Chinstrap penguins in New York's Central Park Zoo, that hatch and raise a chick named Tango (Parnell and Richardson 2005).

Recent zoological studies have provided abundant evidence for same-sex sexual behaviour among animals, not only in captivity but also in the wild (reviews in: Bagemihl 1999; Roughgarden 2004; Sommer and Vasey 2006; Bailey and Zuk, 2009). Currently, the phenomenon has been reported in more than 1500 animal species, including most vertebrate groups and also insects, spiders, crustaceans, octopi and parasitic worms, and it is well documented for 500 of them (Bagemihl 1999). Denniston (1980) concludes that "in the vertebrates, apparent homosexual behaviour increases as we ascend the taxonomic tree toward mammals ...".

Sexual behaviour in bats has been studied since the XIX century (Rollinat and Trouessart 1895a, 1895b, 1895c; 1896; 1897; Monticelli 1896). Recently, a particular copulatory behaviour has been investigated in the fruit bat *Cynopterus sphinx* (Tan et al. 2009).

The aim of this review is to summarize the current state of knowledge on same-sex sexual behaviour in bats, discussing recent reports in the historical context; existing controversies in the field are also pointed out.

A QUESTION OF TERMS

The term *homoseksuäl* (= *homosexual*) was used for the first time in two anonymous

German pamphlets published by Karoly Maria Kertbeny in 1869 (Kertbeny 2000).

In animal behaviour, there is no consensus on the terminology to be used for same sex sexual behaviours (Tab. 1).

"*Same-sex sexual behaviour*" is one among several definitions: "actions between members of the same sex that are also attributed to opposite-sex courtship or mating interactions." (Bailey and Zuk 2009). According to Weinrich (1980) "*homosexual behaviour in animals*" is "any behaviour between two members of the same sex which uses the mechanisms of sexual arousal. This definition is quite broad". For Sommer and Vasey (2006) "homosexual behaviour refers to courtship display, mounting and/or genital contact and stimulation between same-sex individuals. [...] this term does not imply some sort of life-long pattern of homosexual activity or exclusivity, nor does it denote any particular form of enduring sexual relationship, monogamous or otherwise". Bagemihl (1999) used a broader approach: "*heterosexuality* is defined as courtship, affectionate, sexual, pair-bonding, and/or parenting behaviours between animals of the opposite sex, while *homosexuality* is defined as these same activities when they occur between animals of the same sex.". Perhaps this last definition is too wide and there is the risk of including social interactions under sexual behaviour (Sommer and Vasey 2006). Another word, more in use in the past, is "*pederasty*"; this word derives from the Greek *paiderastia* = "love of boys", but in XIXth century it indicated homosexuality in general ("*pédérastie*" in Gadeau de Kerville, 1896; "*päderastie*" in Karsch, 1900). The term "*tribadism*" denotes a sort of female-female genital sex, usually known now in animals as *GG rubbing* (genito-genital) (Karsch 1900; Hohmann and Fruth 2000). *Coercive sex* (*rape*) is defined as "copulation resisted to the best of the victim's ability unless such resistance would probably result in death or serious injury to the victim or in death or

injury to individuals the victim commonly protects” (Abele and Gilchrist 1977; Thornhill and Palmer 2000). Some authors prefer to use *forced copulation* (Hilton 1982; Brennan et al. 2007). More specifically here we define coercive sex (or rape or forced copulation) as sexual contact achieved: 1. without apparent consent; 2. by the use of physical force, coercion, deception; and/or 3. when the victim is physically impaired and/or asleep or unconscious (in torpor or in hibernation).

It has long been observed that some animals appear to show behaviour resembling rape in humans, i.e. combining sexual intercourse with violent assault; these observations of forced sex among animals are not controversial but their interpretation is debated (Clutton-Brock and Parker 1995; Thornhill and Palmer 2000; Travis 2003).

As a general criterion, throughout the paper it has been chosen to use the same terms used by the author(s) of the paper where the behaviour is mentioned.

RESULTS

Same-sex sexual behaviours can be classified in 6 different groups and till now have been documented in 22 species of megabats and microbats.

1. In captivity

Studying the social behaviour of *Pteropus livingstonii* in captivity, several observations were collected on male-male and female-female sexual behaviour (Tab. 2).

“*Play*: involves prolonged gentle wrestling, holding, mounting, biting and genital interest [...] May lead to one bat being mounted by the other [...] but for males, without an erect penis. Social play (or perhaps in some cases, homosexual behaviour) of this kind has

been seen between mature females, mothers and daughters, pair of subordinate males [...]. One of two males engaged in this activity was observed to continue licking the genitals of the other [...]” (Courts 1996).

“*Copulation mount*: The male grips the female from behind, restraining her forelimbs with his (his ventral surface against her dorsal) and holds the scruff of her neck in his mouth. This has also been observed between daughter and mother - the larger daughter relentlessly in pursuit for extended periods and fighting off approaching males. This was perhaps play behaviour incorporating male-female copulations. Attempted and actual mounts were also seen during “*play*” between pairs of mature females, pairs of males, by a mature female to a male, who also groomed his genitals, and by a mother to her daughter”. “Male-male mounting behaviour in *P. rodricensis* is thought to be a way of asserting dominance. Observations of *P. livingstonii* would appear to confirm this, as male-male mounting apparently did not have a sexual function, as the mounting male was never observed to have an erect penis” (Courts 1996).

Greenhall (1965) describes homosexual behaviour in *Desmodus rotundus* (vampire bat) as an “aberrant behaviour”; the captive males were seen involved in licking and rubbing one another bodies and genitals; masturbation among young males has also been observed.

Pre-copulatory behaviour in captivity was observed in *Corynorhinus rafinesquii*: four hibernating males had been confined with an unmated female. A male used to rub his snout over the face,

Table 1 - Same-sex sexual behaviour in bats.

Mutual homosexual grooming and licking	Nelson 1964, 1965; Greenhall 1965; Courts 1996
Homosexual masturbation	Greenhall 1965
Homosexual play	Neuweiler 1969; Courts 1996
Homosexual mounting	Rollinat and Trouessart 1895, 1896; Reed 1946; Vesey-Fitzgerald 1949; Neuweiler 1969; Barclay and Thomas 1979; Thomas et al. 1979; Crucitti 1981; Gebhard 1995; Courts 1996; Crucitti <i>in litteris</i>)
Coercive sex – Rape – Forced copulation	Pearson et al. 1952; Barclay and Thomas 1979; Thomas et al. 1979; Gebhard 1995; Judson 2003
Cross species homosexual sex (<i>Myotis daubentoni</i> and <i>M. nattereri</i>)	Vesey-Fitzgerald 1949

Table 2 - Bat species observed while engaging in homosexual activities.

	IN CAPTIVITY
<i>Pteropus livingstonii</i>	Courts 1996
<i>Pteropus rodricensis</i>	Courts 1996
<i>Desmodus rotundus</i>	Greenhall 1965
	IN THE WILD
<i>Pteropus poliocephalus</i>	Nelson 1964, 1965
<i>Pteropus giganteus</i>	Neuweiler 1969
<i>Corynorhinus rafinesquii</i>	Pearson et al. 1952
<i>Miniopterus schreibersii</i>	Crucitti <i>in litteris</i>
<i>Eptesicus serotinus</i>	Rollinat and Trouessart 1895; Vesey-Fitzgerald 1949
<i>Myotis bechsteinii</i>	Vesey-Fitzgerald 1949
<i>Myotis capaccinii</i>	Crucitti 1981
<i>Myotis daubentonii</i>	Vesey-Fitzgerald 1949
<i>Myotis lucifugus</i>	Barclay and Thomas 1979; Thomas et al. 1979
<i>Myotis myotis</i>	Rollinat and Trouessart 1896
<i>Myotis mystacinus</i>	Vesey-Fitzgerald 1949
<i>Myotis nattereri</i>	Vesey-Fitzgerald 1949
<i>Nyctalus noctula</i>	Vesey-Fitzgerald 1949; Gebhard 1995
<i>Nyctalus leisleri</i>	
<i>Pipistrellus pipistrellus</i>	
<i>Plecotus auritus</i>	
<i>Barbastella barbastellus</i>	Vesey-Fitzgerald 1949
<i>Rhinolophus ferrumequinum</i>	
<i>Rhinolophus hipposideros</i>	

neck, forearms and ventral surface of the female; in one occasion he mounted on the female's back; several time the female flew off and "he would embrace and nose the first bat that he encountered regardless of sex. Even torpid males would receive from him as much as a minute of nosing before he continued his search." (Pearson et al. 1952). Following the previously mentioned definitions, this behaviour can be regarded as "coercive sex or rape or forced copulation".

A male *Eptesicus serotinus* was observed while trying to mount other males in captivity; one male approached another with his penis erect and mounted him from behind, grasping him above the neck and thrusting his penis between the other male's legs (Rollinat and Trouessart 1895c). This mating attempt occurred during hibernation (February), when the males were put in a warm room. The same behaviour was seen in *Myotis myotis*, again during the arousal from hibernation and following location in a warm room (Rollinat and Trouessart 1896).

2. In the wild

Among the reproductive calls of *Pteropus poliocephalus* Nelson (1964) identified a "precopulation call": "This pulsed grating call is continuously uttered by the partners of hetero- or homosexual grooming, in which the wing membranes are wrapped around the partners, and the chest, neck, and wing membranes of the other are bitten and licked" ; males may have an erection (Nelson 1965). This species lives in sex-segregated camps during the non-breeding period, before conception

(from early September until early December). In some way it is seasonally bisexual and both sexes show this form of *mutual homosexual grooming*, more common in males. *Pteropus giganteus* males often mount one another (with erections and thrusting) while play-wrestling (Neuweiler 1969). In *Myotis lucifugus* males often mount other males (as well as females) during the late fall and winter, when many of the mounted individuals are torpid. These coercive copulations usually include ejaculation and the mounted animal often makes a typical "copulation call", consisting of a long squawk (Barclay and Thomas 1979; Thomas et al. 1979). A similar behaviour was seen in hibernacula of *Nyctalus noctula*; sexual active males, woken up from lethargy on a warm day, were involved in mating with active and lethargic females. "Several times attempts were made to copulate with lethargic males. These then behaved like females, calling out loudly and presenting their buccal glands with opened mouth" (Gebhard 1995).

According to Vesey-Fitzgerald (1949) homosexual behaviours were observed in all British bat species (twelve in 1949): "Homosexuality is common in the spring in all species, and, since the males are in full possession of their powers, I suspect throughout the summer... I have even seen homosexuality between Natterer's and Daubenton's bats (*Myotis nattereri* and *M. daubentoni*)".

In two different situations Crucitti (1981) saw *Myotis capaccinii* males in the same position of male-female heterosexual mounting, one gripping the back of the other's fur. A similar be-

haviour was also observed in *Miniop-
terus schreibersii* (Crucitti, *in litteris*).

DISCUSSION

In general, it is difficult to collect information on same-sex sexual behaviour (Dagg 1984), because being rather rare, it can be easily overlooked by researchers. Moreover, some authors may be either reluctant to refer to or not concerned with homosexual events. Referring to bats, their nocturnal activity and the difficulty to distinguish the sex of mating individuals make this task even harder. Denniston (1980) reported that "frequent homosexual activity has been described for all species of mammals of which careful observations have been made". As most animals have only been observed in the wild for a limited amount of time, more field studies will consequently increase our knowledge of homosexuality in the animal kingdom and the number of species reported with homosexual behaviours.

Some general questions are:

a) "Captivity and domestication" vs. "natural conditions": same-sex sexual behaviour is more frequent in captive than in wild populations, maybe because males and females are grouped together by sex or in different ways than in the wild; captive animals can form bonds atypical of natural situations.

b) Why does homosexual behaviour occur? Referring to insects, Gadeau de Kerville (1896) distinguished two categories: "pédéderastie par nécessité" (pederasty by necessity) and "pédéderastie par goût" (pederasty by taste/choice); the former occurs when a

male insect has the imperious need to copulate but no females are available; the latter refers to coupling between males in the presence of available females. Captivity probably caused the number of cases of homosexuality to increase but "il n'en est pas moins absolument certain" (nevertheless it is absolutely certain) that couplings between male insects also occur in a state of complete freedom; such occurrence also takes place among vertebrates (Gadeau de Kerville 1896). Homosexual behaviour is usually observed in solitary mammals under two conditions: 1) reproductive fitness is maintained through homosexual behaviour when the availability of one sex, usually females, is limited; 2) animals kept in intensive housing conditions perform homosexual behaviour to dissipate stress and wield dominance (Feige et al. 2007).

c) What causes same-sex sexual behaviour? Several explications have been proposed: social play; physical contact (non-play); dominance-assertion; aggression and intrasexual conflict; social tension regulation; sexual excitement; social relationship; alloparental care; practice for adult heterosexual copulation; poor discrimination (Bagemihl 1999; Sommer and Vasey 2006).

Current knowledge about same-sex sexual behaviour in bats does not allow to answer any of the previous questions.

Even less known is the meaning of *cross species sex*; sometimes animals harass other animals (from the same or closely-related species) for sex. As an example, an Antarctic fur seal was observed while attempting to have sex with a king penguin on Marion Island

(De Bruyn 2008). Either the seal's predatory impulse had been redirected into sexual arousal or it was a sexual manifestation of the play instinct of seals. Unfortunately, it is not possible to extrapolate these hypotheses to explain the inter-specific same-sex events recorded by Vesey-Fitzgerald (1949).

More observations are needed to better classify and understand these different behavioural patterns, keeping in mind that any account of homosexuality in animal is in some way the account of human interpretations of these phenomena (Bagemihl 1999).

Reviewing the available records on homosexual behaviour among non-human animals, it appears that this behaviour is not exclusive over their whole lifespan (Cvorovic 2006; Sommer and Vasey 2006; *contra* Poiani 2010). Accordingly, at first sight this behaviour violates the fundamental principle of procreation (Sommer and Vasey 2006). Nonetheless, homosexual behaviour is a component of the behavioural repertoire of several species and it might have evolutionary implications for social, sexual and reproductive strategies which are still not fully understood, e.g. by removing some individuals from the pool of animals available for mating (Bailey and Zuk 2009). According to Roughgarden, given the pervasive presence of homosexuality throughout the animal kingdom, same-sex partnering must be an adaptive trait that has been carefully preserved by natural selection (Roughgarden 2009). In these terms, scientific research on this behaviour is still at the beginning (Bagemihl 1999).

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