Species	Freq	Age	Rec	Researcher Observations/Summaries
Great Apes				
Bonobos (Pan paniscus)	3	1	3	Mature males frequently performed thrusts on much younger males who might actively solicit the mounting (Kano, 1980). Common also is an adult male masturbating an adolescent male lying on his back with legs spread apart. Sex serves to reduce social tension (de Waal, 1997).
Chimpanzees (Pan troglodytes)	2	2	3	Male homosex varies considerably across and within chimp populations (Bagemihl, 1999). Kollar et al. (1968) described multiple age-gap encounters (e.g., a young juvenile male interrupted copulation of an adolescent male and female, then presented to the older male, who mounted him).
Gorillas (Gorilla gorilla)	3	4	3	In all-male groups, adults are most attracted to adolescents; mounting can be initiated by either (Harcourt, 1979; Yamagiwa, 1987, 2006). Courtship and copulation occur daily (Bagemihl, 1999). Age-gap sex may help group cohesiveness (Harcourt, 1979).
Orangutans (Pongo pygmaeus)	2	2	3	Homosex is often consensual (heterosex often not), often occurs within a special friendship (Bagemihl, 1999). Example: An adolescent male that received fellatio from a young adult male became very attached to him, and followed him wherever he went (Rijksen, 1978).
Lesser Apes				
White-handed gibbons (Hylobates lar)	2	4	3	Homosex occurs sometimes in father-son pairs (Bagemihl, 1999). Edwards and Todd (1991) observed fifty- five episodes between father and adolescent son, always without tension or aggression, initiated by both; seemed to provide reassurance to the adolescent.
Siamangs (Hylobates syndactylus)	2	1	2	Father-son sex occurs (like gibbons), but is sometimes accompanied by threats, when the younger partner wants to end it before the older one does (unlike gibbons) (Bagemihl, 1999).
Old World Monkeys				
Hanuman langurs (Presbytis entellus)	3	1	3	Immature males frequently engage in mounting, often with like-aged males, but also with mature males (Sommer et al., 2006). Immature males increase their touching, mounting, and embracing of adult males as they mature (Jay, 1965). Weber (1973) found that male-male age-gap mounting was usually initiated by the immature partner, with apparent function of securing social acceptance (juveniles are no longer protected by mothers and turn to other adults; mounting and other physical contact are mechanisms to achieve social integration).
Nilgiri langurs (Presbytis johnii)	2	1	3	Dominant males (alphas) mount subordinate males (juveniles, adolescents, younger adults) in dominance displays, which the subordinates may initiate by presenting. Mounts are brief, with several thrusts but no penetration, and are part of a communication matrix that maintains troop harmony (Hohmann, 1989; Poirier, 1970).
Proboscis monkeys (Nasalis larvatus)	1	2	2	Homosexual mounting occurs in younger males (adolescents and juveniles); it tends to stem from play wrestling. It is resisted by the younger male in some cases (as females sometimes also do in heterosexual mounting). Its frequency is low, as is heterosexual sex (Bagemihl, 1999; Yeager, 1990).
Bonnet macaques	3	1	3	Males of all ages are frequently involved in a wide variety of homosex. Younger males often masturbate

Table IV: Homosexual Behavior Between Mature and Immature Males in Primates.

Table IV: (continued)

Species	Freq	Age	Rec	Researcher Observations/Summaries
Old World Monkeys (continued)				
(Macaca radiatá)				other males to orgasm, sometimes eating the semen. Some do only a little homosex, others a great deal (Bagemihl, 1999).
Crab-eating macaques (Macaca fascicularis)	2	1	2	Males can develop intense sexual friendships, especially between older and younger males (with affection, arousal, mounting). Homosexual mounting is both consensual (54%) and nonconsensual (46%). In the former, the mountee fully cooperates and may initiate the mounting (Bagemihl, 1999).
Crested black macaques (Macaca nigra)	5 2	4	3	Younger males often mount older ones (Bagemihl, 1999). Dixson (1977) frequently observed the oldest male in one troop presenting to younger males, who invariably responded by mounting him, often with erections. Also, ritualized "greeting" gestures (e.g., penis-grabbing), especially by younger males, are common practice (Bagemihl, 1999).
Japanese macaques (Macaca fuscata)	3	1	3	All adult and juvenile males were seen presenting to another male (aggression was rare, <3%) (Hanby & Brown, 1974). Takenoshita (1998) observed free-ranging adult-juvenile consort relationships (adults ejaculated, juveniles erected; they foraged, groomed, and attacked others together).
Pig-tailed macaques (Macaca nemestrina)	3	1	3	Age-equal and age-gap male-male mounting (juveniles, adolescents, adults) occurs frequently, is not associated with force (as heterosexual mounting sometimes is), and makes up from 8% to 67% of individual males' overall mounts (Bagemihl, 1999). Dominants invite subordinates to mount them as an elaborate display of tolerance toward subordinates (Oi, 1990) or mount subordinates as a rank maintenance mechanism (Tokuda et al., 1968).
Rhesus macaques (Macaca mulatta)	3]	3	Age-gap consort relationships occur, highly affectionate (Bagemihl, 1999). Kempf (1917) observed two juvenile males competing to be mounted by an adult male. Homosex helps juveniles get protection, integrate into group (Carpenter, 1942). Older, younger both show sexual excitement; mature-immature relationships are frequent, seem to have sexual basis (Hamilton, 1914). Redican et al. (1974) observed an immature male taking the sexual initiative with an adult male in an intensive relationship.
Stumptail macaques (Macaca arctoides)	3	1	3	Chevalier-Skolnikoff (1976) reported mutual excitement and affection in several intense friendship-based mature-immature sexual relationships. These were "rewarding" to all participants (e.g., protection for younger partner). Homosex seemed to foster greater social cohesion.
Tibetan macaques (Macaca thibetana)	3	4	3	Ogawa (1995) found that male adult-juvenile homosex occurs on a regular basis; either may initiate oral sex on the juvenile; it is never aggressive; both are excited; context is friendly. It seems to serve to reduce tension.
Savanna baboons (Papio cynocephalus)	2	1	3	All males, from juvenile to adult, greet one another via ritualized sexual behaviors. These behaviors (pre- senting, mounting, fondling) occur briefly (a few seconds), constitute "greetings," and appear to serve in part formation of coalitions (Bagemihl, 1999; Smuts & Watanabe, 1990).
Hamadryas baboons (Papio hamadryas)	2	4	3	Zuckerman (1932) observed a three-year sexual relationship between an adult and immature male. When ever the immature was threatened, the adult immediately rescued it.

Species	Freq	Age	Rec	Researcher Observations/Summaries
Old World Monkeys (con	tinued)			
Gelada baboons (Theropithecus gelada)	2	4	3	Bernstein (1975) found that mounting occurs between bachelors and immature males in the all-male group. When a bachelor successfully challenges a harem leader, he switches entirely to heterosex (the deposed leader switches to homosex).
Mona monkeys (Cercopithecus mona)	3	1	3	Glenn, Ramsier, and Benson (2006) found that homosex, with oral sex (often with orgasm), is universal in all-male groups, where males spend most of their lives. It involves all combinations from juveniles to adults; aggression is extremely rare. It seems to function to help younger males' immigration and social skills, as well as the groups' social cohesion.
Patas monkeys (Erythrocebus patas)	2	4	3	Adolescent or younger males often fondle and nuzzle the genitals and scrotum of adult males (Bagemihl, 1999).
New World Monkeys				
Squirrel monkeys (Saimiri sciureus)	2]	3	Denniston (1980) frequently observed male homosexual behavior, the commonest form being between adults and adolescents. Baldwin (1969) frequently observed sexual mounting and sometimes consortships between older adolescents and much younger juveniles (of both sexes); older adolescents, unlike younger adolescents, were gentle with their younger partners, who consequently allowed the interactions to take place (by contrast, they tended to resist the much rougher initiatives from younger adolescents).
Prosimians Verreaux's sifaka (Propithecus verreauxi)]]	1	Homosexual behavior is rare in prosimians. In this lemur species, adult males sometimes mount younger adults or adolescents, who often snap and struggle to wriggle free (Bagemihl, 1999).

Table IV: (continued)

Note. Freq = frequency, based mainly on Vasey's (1995) and Bagemihl's (1999) ratings (1 = incidental or rare; 2 = moderate; 3 = frequent or primary). Age = age class (dominant age pairings that occur), based mainly on Vasey's (1995) ratings (1 = mixed ages; 2 = between immatures; 3 = between adults; 4 = mature with immature). Rec = receptivity based on researchers' descriptions (1 = mostly unwilling with resistance or aggression; 2 = mix of receptive and non-receptive encounters; 3 = mostly receptive with no or little aggression). Researcher observations/summaries provide illustrations from research on typical encounters and overall nature of mature-immature male homosex.

Species Marine Mammals Dolphins and whales Boto or Amazon	Summary of Descriptions from Bagemihl (1999) or Primary Researchers Males participate in a wide variety of homosexual behavior, including various kinds of intercourse. When there is an age difference typically the older penetrates the younger. Pairs interacting sexually display a great deal of mutual affection, which Bagemihl (1999, p. 341) illustrates in a photo, in which an adult and immature partner are touching while swimming side by side.
Dolphins and whales	Males participate in a wide variety of homosexual behavior, including various kinds of intercourse. When there is an age difference typically the older penetrates the younger. Pairs interacting sexually display a great deal of mutual affection, which Bagemihl (1999,
Boto or Amazon	Males participate in a wide variety of homosexual behavior, including various kinds of intercourse. When there is an age difference typically the older penetrates the younger. Pairs interacting sexually display a great deal of mutual affection, which Bagemihl (1999,
Bottlenose dolphins (Tursiops truncates)	Homosexual behavior largely exceeds heterosexual behavior. Adolescents and younger males typically live in all-male groups, where homosexual behavior is common and exclusive. Only as full adults do they attempt to father calves via heterosexual contact Younger adolescents form homosexual pairbonds with like-age males, which often last throughout life. When there is an age difference in homosexual sex, either party may penetrate the other – adolescents have been observed penetrating adults (Bagemihl, 1999). McBride and Hebb (1948) observed adult males repeatedly interacting sexually with younger males and described an intense, affectionate bond in one pair. In an extensive ten-year field study, young immature males were found to be the most sexual (most otten with male peers, but also with all other age-sex classes); most of adult males' sexual interactions were with immature males (Mann, 2006).
Orca or killer whales (Orcinus orca)	Orcas are the largest in the dolphin family. Homosexual behavior is integral to male social life. During salmon feasting, males of a ages spend afternoons courting, being affectionate, and engaging in overt homosexual behaviors, with 90% being reciprocated. Sessions last an hour on average. Most involve adolescents and an age difference of at least five years. At least half of all males get involved.
Sperm whales (Physeter macrocephalus) Bowhead whales (Balaena mysticetus)	3–5% of males may be homosexually bonded, with couples consisting of two adults or an older and younger male. Sexual interactions leading to orgasm can take place in groups of primarily younger males. Intensive male homosexual sessions lasting up to forty minutes occur, involving mainly groups of adolescents and young adults.
Seals and Manatees	
Gray seals (Halichoerus grypus)	Male homosexual behavior is common; males of all ages mount each other on shore after molting.
Harbor seals (Phoca vitulina)	Male homosexual behavior is common, involving males of all ages, but mainly adolescents and adults.
Northern elephant seals (Mirounga angustirostris)	Adolescent and young adult males do same-sex mounting during the molting season. Adult males sometimes mount younger adoles cent or juvenile males, but the younger males usually struggle to escape.
Australian sea lions (Neopphoca cinerea) & New Zealand sea lions (Phocarctos hookeri)	Male homosexual mounting is common. All ages may be involved, but usually a younger partner mounts an older one. As mating is polygynous, many males never mate heterosexually.
West Indian manatees (Trichechus manatus)	Males can form bachelor herds. Males of all ages intensively interact homosexually, involving embracing, kissing, mouthing, caressing, genital rubbing, and frequent ejaculation.

Table V: Homosexual Behavior Between Mature and Immature Males in Subprimate Mammals

Table V: (continued)

Species	Summary of Descriptions from Bagemihl (1999) or Primary Researchers
Marine Mammals (Seals an	d Manatees) (continued)
Walruses (Odobemus rosmarus)	Males are segregated during the nonbreeding summer months. Here, homosexual courtship, affection, and sex are common. Typi- cally, a younger male will display to an older one, and each may mount the other. Groups of younger males may crowd an adult male, making body contact. An adult may sing a courtship song to a group of younger males or a specific younger male compan- ion that accompanies him. Younger and older males also pursue each other during the breeding season. Homosexual behavior is very common if not universal among male Walruses, even during the breeding season, where up to a third of mounting is between younger males or between an adult and a younger male.
Hoofed Mammals	
Deer and Moose White-tailed deer (Odocoileus virginianus)	Males are sex-segregated most of year. Mounting sometimes occurs between two adults, two yearlings, or an older-younger pair, where the younger mounts the older one (Bagemihl, 1999). Most commonly, it is young males that mount others. Mounting is not based on dominance; no specific function is apparent. Mountees generally do not oppose being mounted if age-discrepant, but do so more if two immature males are involved (Bartos & Holeckova, 2006).
Wapiti (Cervus elaphus)	They are sex-segregated most of year. Mounting occasionally occurs between two adult or adult-yearling males. Male pairs may form companionships, either older-younger or age-equal.
Père David's deer (Elaphurus davidianus)	Males sometimes mount each other, with the younger mounting the older one.
Moose (Alces alces)	They are often solitary. Yearling males sometimes mount adult males. Sometimes adult males associate with younger male compan- ions called satellites.
Antelopes and Gazelles	· · · · · · · · · · · · · · · · · · ·
Pronghorns (Antilocapra americana)	Some males get territories and breed. The rest live in bachelor herds, where homosexual mounting occurs to a moderate degree. Males of all ages participate, but adult males usually direct their attentions to adolescents. Mounting is preceded by courting. Most males (70%) never breed.
Blackbuck (Antilope cervicapra)	Males with territories mate with females. The rest live in bachelor herds, where most engage in mounting. This follows friendly sparring. Adult males often perform courtship displays to adolescent males before mounting them. Blackbuck males are predominately homosexual, leaving the group only once or twice in their lives attempting to breed.
Grant's gazelles (Gazella granti)	They live in mixed or all-male groups. Homosexual behavior is rare. Adult males usually attack other males trying to mount them.
Wild Sheep, Goats, Buffa	lo
Bighorn sheep (Ovis canadensis) & Thinhorn sheep (Ovis dalli)	Males live in homosexual societies in sex-segregated bands. Only during the rutting season do they meet females. Older males court younger, smaller males and mount them. The mountee facilitates by assuming lordosis. Interactions are non-aggressive; the younger male is usually willing. So pervasive is this, that females will mimic younger males to attract older males. Geist (1975) views older-younger male homosex as an adaptation, allowing the younger males to live in the group.
Musk-oxen (Ovibos moschatus)	They are in mixed or all-male groups. Adult males court and mount adolescent and juvenile males. Younger males do the same with each other. Mountees sometimes resist (as females do), but sometimes assent. About 40% of courting and 10% of mounting are homosexual.

Table V:	(continued)
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Species	Summary of Descriptions from Bagemihl (1999) or Primary Researchers
Hoofed Mammals (Wild Sh	eep, Goats, Buffalo) (continued)
Mountain goats (Oreamnos americanus)	They are often sex-segregated. Adult males court younger males, using the species-typical approach used in courting females. Typi- cally, the yearling male reacts aggressively. Almost one-fifth of courtships during the breeding season occur between adult and yearling males.
American bison males (Bison bison)	Male bison spend most of their time alone or in bachelor herds. In these herds, homosexual mounting, including full penetration, is prevalent, especially among younger males (i.e., adolescents), and exceeds heterosexual mounting in frequency. The mounted animal often facilitates the mounting. Younger males also sometimes form tending bonds with other males, involving following, defending, and mounting or being mounted by their partners (Bagemihl, 1999). Homosexual behavior is not based on dominance, but may serve a bonding function (Vervaecke & Rodin, 2006).
Other Hoofed Mammals	
Giraffes (Giraffa camelopardalis)	They are often in all-male groups. Sparring between males is almost always gentle, begins as calves and juveniles, and is most common among adolescents. Participants are often of different sizes, with the smaller, younger one usually initiating. Mounting sometimes accompanies sparring, and mostly involves older adolescents mounting younger ones. These behaviors are not associated with dominance. Homosexual behavior occurs mainly among the young (Pratt & Anderson, 1985).
African elephants (Loxodonta africana) & Asiatic elephants (Elephas maximus)	African and Asiatic male elephants often form all-male herds. Breeding males associate only temporarily with females. Male homosexual mounting occurs regularly, especially among younger males. In African elephants, homosexual mounting may be preceded by extensive affectionate interaction, and both adult and younger males participate. Males also form long-lasting bonds called companionships, mainly between older and younger "attendants"—heterosexual couples do not form long-lasting bonds. The attendant male and adult male often help each other in various ways, and they are constant companions. Sometimes an older male will have two attendant males. In Asiatic male elephants, almost a fifth have a male companion.
Other Mammals Dwarf cavies (Microscavia australis)	Dwarf cavies are small rodents that live in colonies of twenty to fifty individuals. Adult males are sexually attracted to juveniles of both sexes. A typical homosexual encounter begins with an adult male and juvenile male sitting together quietly, often in front of the juvenile's mother, who is not visibly bothered. The two males then engage in affectionate contact, which eventually escalates to sexual behavior. Adult males often have favorite younger males, and will actively seek them out while ignoring other juvenile males. More than half of adult male-juvenile sexual interactions are same-sex. Most males are homosexually involved. Occasionally, an adult male will have an adolescent male companion, who feeds with him and is physically affectionate with him. The adult may allow the adolescent to mount a female he is courting. Adult males in two other species, mocó or rock cavies (Kerodon rupestris) and préa (Galea spixii), sometimes also court juvenile males.
Feral cats (Felis catus)	In an extensive field study, a quarter of males did homosexual mounting, but only occasionally. It always occurred in the presence of estrus females. Mounters were adults, and mountees were adolescents, smaller in size, comparable to adult female size. Mount- ers bit the backs of mountees' necks, as they do when mounting females. Older-younger male homosexual mounting appears to be an outlet for heterosexual mountings that were recently frustrated (Yamane, 2006).

Note. The descriptions are based mostly on Bagemihl's (1999) summaries. Only when based on other authors instead or as well, citations are given.

Species	Summary of Descriptions from Bagemihl (1999)
Aquatic and shore birds Canada geese (Branta canadensis)	18 % of adult males form homosexual bonds with partners, who may be other adults or juveniles.
Ruffs (Philomachus pugnax)	About half of males are involved predominantly in same-sex sex. Certain adult males acquire a territory called a lek, where they display to potential sex partners, male as well as female. Male visitors may be those without leks or younger males, who have not yet developed adult plumage. The younger males rarely are heterosexually involved, but instead do mounting with each other and with adult lek residents.
Perching and song birds	
Guianan cock-of-the-rock (Rupicola rupicola)	Male homosexual mounting between two adolescents and between an adult and adolescent is routine, accounting for about half of all copulations and involving about 40 % of the total male population and 64 % of the adolescent male population. Cer- tain adult males acquire leks, which females and young males visit to see whether they want to mate. In a typical homosexual encounter, while an adult male is displaying his colorful plumage, an adolescent male will land nearby. The adult keeps his back to the adolescent, showing off his plumage and inviting the adolescent to mount him. The adolescent climbs onto the adult's back, achieves genital contact, and then mounts several times in succession. Adolescents usually visit the display courts of numerous other adult males and may have relations with up to seven adults in a season, including some adults without leks. Adult males who avoid heterosexual contacts are the ones most often mounted by adolescent males
Swallow-tailed manakins (Chiroxiphia caudata)	Several adult males will form long-term associations and display together on their leks to attract both females and adolescent males. When a young male arrives, the adult males perform a group courtship ritual, in which they take turns jumping up and hovering in front of him. The young male sits motionless as he watches the spectacle. Same-sex sexual behavior likely makes up a sizable proportion of all sexual activity.
Blue-backed manakins (Chiroxiphia pareola)	Pairs of adult males behave similarly to swallow-tailed manakins, displaying to a third male, which is sometimes an adolescent, performing leapfrogging and cartwheels to impress the other male.
Bicolored antbirds (Gymnopithys bicolor)	Male homosexual pair-bonds make up 4–6% of all pair-bonds; partners may be two adults or an older and younger bird. The bonds are initiated by courtship-feeds, in which one offers the other a spider or an insect. The receiving male, unlike a female, then passes it back. Once paired, they become constant companions.
Red bishop birds (Euplectes orix)	In their nesting territories, adult males court both females and males, the latter being younger males who look like females in terms of their plumage coloring. When a younger male approaches, the adult male performs a distinct bumble-flight and displays his plum- age to attract the oncomer.
Orange bishop birds (Euplectes franciscanus)	In captivity, both adult and younger males attempt to mount young males, who usually reject the attempt or react indifferently at most.
Red-shouldered widowbirds (Euplectes axillaris)	Adult males sometimes court younger males.

Table VI: Homosexual Behavior Between Mature and Immature Males in Birds

Table VI: (continued)

Species	Summary of Descriptions from Bagemihl (1999)
Aquatic and shore birds	
Black-billed magpies (Pica pica)	Homosexual behavior involving adult males with adolescent or juvenile males occurs occasionally. A typical courtship begins with one male ritually begging the other, followed by the second hopping around the first. Afterward, the two might form a pair-bond, in which they stay near one another, preen one another, and cooperate in evicting intruders.
Gray-breasted jays (Aphelocoma ultramarina)	Adult males have been observed to courtship-feed younger males.
Victoria's riflebirds (Ptiloris victoriae)	Adult males sometimes court younger males, using spectacular displays that are also used in heterosexual interactions. Male-male courtships occur frequently, although mounting is rarer and is likely to drive the mountee away.
Regent bowerbirds (Sericulus chrysocephalus)	Males build bowers, tunnels of twigs decorated with a variety of colors (e.g., from berries). Adult males display in their bowers to both females and younger males, sometimes ritually offering gifts to their guests. Juvenile males also build bowers and court males and females. When an adult male arrives, the juvenile male behaves in a ritual manner to attract the adult into the bower. Adult males spend 15% of their time displaying to other males, and juvenile males spend 28% of their time doing the same.
Satin bowerbirds (Ptilonorhynchus violaceus)	Adult males have been observed to court younger males.
Superb lyrebirds (Menura novaehollandiae)	Adult males often court adolescent males upon encountering them alone or in groups. The adult may closely follow the adolescent, even for hours, periodically performing a wing display accompanied by serenading the younger male with a variety of vocal- izations. Adults will occasionally mount the adolescents, but genital contact may not occur because the younger male does not facilitate the interaction. Adolescent males also court and mount one another, behavior that is usually mutual. Occasionally an adult and adolescent male will engage in a mutual display to one another. Adult males approach groups of adolescents fairly often during breeding season and twice as often outside of it. They spend more than half their time away from their display mounds as- sociating with adolescent males. Most males are bisexual, courting both females and adolescent males. Adolescent males appear to be exclusively homosexual in their behavior and often form companionships with like-aged males. Male and female lyrebirds live largely separate lives aside from brief encounters during breeding season.
Other birds	
Anna's hummingbirds (Calypie anna)	Both females and juvenile males visit an adult male's territory to feed on his supply of currant and blossoms. If a juvenile male visits, the adult male will perform a dive display several times, in which he climbs 150 feet, dives toward the visitor, and makes loud shrieking sounds. After the display, the visitor will usually fly off, with the adult in pursuit, singing at him. If the adult succeeds in attempting to mount the younger male, the latter usually strongly resists, and the adult may attempt to use force. About 25% of sex in this species is between males.
Acorn woodpeckers (Melanerpes formicivorus)	A ritualized group display occurs involving courtship and sex. At dusk, the members of a group gather and begin mounting one another in all combinations. Males mount females and other males, females mount males and other females, young woodpeckers mount older ones, and older woodpeckers mount younger ones. Reciprocal mounting is common. This mounting display is a regular feature in this species, occurring daily all year around.