

Same-sex sexual behavior in birds: expression is related to social mating system and state of development at hatching

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We report the findings of a phylogenetic comparative analysis examining patterns and frequency of occurrence of same-sex courtship and mounting behavior in birds. Our analysis has shown associations between same-sex sexual behavior and both mating system and degree of precociousness at hatching. The patterns of expression and frequency of occurrence of same-sex sexual behavior differed markedly for males and females. Patterns of same-sex sexual expression reflected the competitive sexes that actively solicit sexual interactions in heterosexual encounters. Male–male (MM) sexual behavior occurred across all mating systems, but MM mounting was significantly more prevalent in those species with facultative polygamy. The frequency of MM sexual behavior increased with degree of polygamy. Female–female (FF) sexual behavior (especially courtship) occurred most frequently in socially monogamous species and rarely occurred in species that display obligate polygamy (predominantly polygynous species). Both expression and frequency of FF sexual behavior was strongly related to the precocial state of development at hatching. FF sexual behavior is more likely to occur in species in which monogamy occurs together with the production of precocial offspring; that is, in monogamous species that are exceptions to the more common altricial mode of development. We suggest that requirement of biparental care in monogamous species may influence the greater expression of FF sexual behavior and longer term associations. Both spatial and behavioral dispersion of females and engagement in uniparental care may be important in explaining the lower incidence of FF sexual behavior in polygynous species. Social contexts where males congregate at communal leks or display areas may influence the greater expression and frequency of MM sexual behavior in polygynous species. *Key words:* altricial, animal homosexual behavior, mating systems, monogamy, polygamy, precocial, same-sex sexual behavior, social learning. [*Behav Ecol* 18:21–33 (2007)]

Although rarely addressed in the literature, sexual interactions between individuals of the same sex occur in birds, with over 130 avian species worldwide being documented as engaging in same-sex sexual, same-sex, or homosexual behaviors (Bagemihl 1999). Courtship behaviors employed for advertising to prospective mates in opposite-sex sexual interactions also occur among individuals of the same sex. Same-sex courtship activities may involve elaborate displays, synchronized dances, gift-giving ceremonies, or behaviors at specific display areas including bowers, arenas, or leks. Courtship behavior often results in same-sex mounting and even copulatory behavior, and for a subset of species, same-sex pair-bonding and long-term same-sex associations have been reported (e.g., the black swan, *Cygnus atratus*; Braithwaite 1981).

In some species, only one sex has been observed to court the same sex (e.g., female black-faced sheathbills, *Chionis minor*; Bried et al. 1999), whereas in other species both sexes participate in same-sex courtship (e.g., the galah, *Eolophus roseicapillus*; Rogers and McCulloch 1981). The same variation among species occurs for mounting: in some species, only one sex has been observed to mount the same sex (e.g., male cattle egrets, *Ardea ibis*; Fujioka and Yamagishi 1981), whereas

in other species both sexes participate in same-sex mounting (e.g., the Tasmanian native hen, *Gallinula mortierii*; Ridpath 1972). Such mounting may involve cloacal contact or attempted cloacal contact.

It seems that species may also vary in the type of same-sex sexual behavior expressed: in some species, only same-sex courtship has been documented (e.g., male regent bowerbirds, *Sericulus chrysocephalus*; Lenz 1994) or only mounting (e.g., the great crested grebe *Podiceps cristatus*; Bagemihl 1999), whereas in other species same-sex courtship and mounting co-occur (e.g., the purple swamphen, *Porphyrio porphyrio*; Jamieson and Craig 1987). Moreover, the frequency of occurrence varies greatly interspecifically.

Although the majority of individuals that engage in same-sex sexual activity usually also engage in heterosexual interactions (Mills 1991), this pattern of behavior appears to be inconsistent with traditional evolutionary theory. What adaptive value, if any, does interacting sexually with an individual of the same sex provide if the behavior does not directly contribute to an individual's fitness?

Descriptive cross-species accounts of same-sex sexual behavior exist for mammals (Dagg 1984; Tyler 1984; Vasey 1995) and birds (Bagemihl 1999) yet little, if any attention, has been directed at quantitatively examining factors that may influence its expression and maintenance across taxonomic groups. It is not known why some species exhibit only male–male (MM) or only female–female (FF) sexual behavior, whereas other species exhibit both. Nor is it known why same-sex sexual behavior is common in some species and rare

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in others. We were interested in investigating whether 1) the reproductive social organization and 2) the developmental state at hatching has any bearing on the occurrence of courtship and/or mounting behavior between members of the same sex, and we chose to investigate this in avian species.

The dominant social mating system of avian species may be broadly classified according to the degree of polygamy or, more specifically, whether a species is predominantly socially monogamous, facultatively polygamous, or obligately polygamous based on the number of potential mates acquired by one or both of the sexes and the longevity/exclusivity of the association between individuals (Owens and Hartley 1998).

Social mating system also has implications for the social structure of the species and the potential opportunity for social and/or sexual interactions among individuals. The temporal and spatial distribution/availability of the sexes, the patterns of breeding and nonbreeding dispersal, and the degree of parental care provided by each sex are all related to social mating system (Temrin and Tullberg 1995; Ligon 1999; Møller 2003; Reichard 2003). These factors influence the opportunity, expression, and frequency of sexual behavior, including courtship and copulation, mate choice, and pair-bonding among individuals of the opposite sex (Gowaty 1996), and may also influence the occurrence and frequency of sexual interactions among individuals of the same sex.

Same-sex sexual behavior has been observed for species that are primarily socially monogamous (e.g., Western gull, *Larus occidentalis*; Hunt et al. 1984) through to species that exhibit extreme polygamy (e.g., Guianan cock-of-the-rock, *Rupicola rupicola*; Trail and Koutnik 1986). Yet the sexes that express these behaviors and the frequency of same-sex sexual behavior may potentially vary with social mating system. Traditional selection theory would predict that selection may act to constrain same-sex sexual behavior, whereby same-sex sexual interactions would be less frequently observed in monogamous species in which individuals are pair bonded and a same-sex association may have a significant impact on an individual's fitness. Conversely, traditional selection theory would also predict that same-sex sexual behavior may be more frequently observed in polygamous species (i.e., in polygyny/promiscuity for males and polyandry/promiscuity for females) in which multiple sexual opportunities are possible while still affording reproductive opportunity.

State of development at hatching may also influence the development of sexual behavior, including mate choice, courtship, and copulation (Vos 1995). Early social experiences with conspecifics are important in shaping adult sexual preferences in birds (Immelmann 1972; Adkins-Regan and Krakauer 2000). Precocial and altricial species differ markedly in the acquisition of sexual preferences through imprinting (Bolhuis 1991): both precocial and altricial birds imprint sexually, but the sensitive period for sexual imprinting is preceded by a period of filial imprinting in precocial but not altricial species. Sensitive periods for sexual imprinting also vary temporally between altricial and precocial species (Oetting et al. 1995), providing opportunities for differences in social learning related to sexual preference.

A number of authors have reported that males of precocial species may sexually imprint and later mount other males, as in geese, *Anser anser* (Tyler 1984), mallard ducks, *Anas platyrhynchos* (Schutz 1965), and Japanese quails, *Coturnix coturnix japonica* (Nash and Domjan 1991).

For altricial species, both males and females may display same-sex preferences in adulthood as a direct result of experience during early development. Removal of adult male birds from the rearing environment meant zebra finch chicks, *Taeniopygia guttata*, were unable to experience biparental care,

interaction with adult males, or observe interactions between male–female pairs during early development. A significant proportion of these male and female individuals exhibited same-sex preferences in adulthood (Adkins-Regan and Krakauer 2000). The sex ratio of conspecifics and later social experience has also been observed to affect sexual imprinting preferences in altricial species (Oetting et al. 1995). For these various reasons, the expression of same-sex sexual behavior may also be related to the state of development at hatching across species.

We tested our hypotheses in a phylogenetic context, using a data set of avian species of the world for which same-sex sexual behavior has been reported.

METHODS

Data collection

A survey of the literature published in scientific journals was conducted, and all reports of same-sex courtship and/or mounting behavior were tabulated. Species were included on the basis of documented evidence of same-sex sexual behavior under natural (noncaptive) conditions. We decided to include only reports of the behaviors being performed by animals in the wild because captivity may well influence the expression of sexual behavior between members of the same sex (McGraw and Hill 1999).

Many references were initially sourced from Bagemihl (1999). Apart from original research papers, Bagemihl (1999) has also systematically surveyed the multivolumed series *Birds of North America* (e.g., Poole et al. 1994), the *Handbook of the Birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic* (e.g., Cramp and Simmons 1983) and the *Birds of Africa* (e.g., Brown et al. 1982) for records of same-sex sexual behavior. We also systematically searched the contents of 13 zoological, behavioral, and ornithological journals from the international literature: *Auk* (1884–1999); *Condor* (1899–2000); *Journal of Field Ornithology* (1930–1999); *Wilson Bulletin* (1889–1999); *Australian Journal of Zoology* (1953–1987, 1995–2003); *Australian Wildlife Research* (Wildlife Research) (1974–1991, 1997–2001); *Emu* (1950–2003); *Corella* (1980–2004); *Australian Zoologist* (1914–2003); *CSIRO Wildlife Research* (1956–1973); *Australian Birds* (1982–2003); *Animal Behaviour* (1953–2003); and *Behaviour* (1953–2001). In addition, we examined citation lists of papers in which same-sex sexual behavior was reported for further candidate studies. Searches were performed on the electronic databases Biological Abstracts (1985–2005) and Web of Science (1981–2005). These databases collectively contained records for the ornithological journals *Aves* (1993–2005), *Birds of North America* (1993–2002), *Bird Behaviour* (1981–2005), *Behavioral Ecology* (1990–2005), *Behavioral Ecology and Sociobiology* (1981–2005), *British Birds* (1982–2005), *Colonial Waterbirds* (1985–1998), *Egretta* (1983–2001), *Ethology* (1986–2005), *Ethology Ecology and Evolution* (1989–2005), *Ibis* (1982–2005), *Japanese Journal of Ornithology* (1987–2005), *Journal of Avian Biology* (1994–2005), *Journal of Ethology* (1986–2005), *Larus* (1983–1999), *Ostrich* (1981–2005), *Scottish Birds* (1993–2004), *Western Birds* (1993–2005), and *Wildfowl* (1986–2003). Searches were also performed on the Searchable Ornithological Research Archive which in addition to selected aforementioned journals also contained records for *North American Bird Bander* (1976–2000), *Pacific Coast Avifauna* (1900–1974), *Studies in Avian Biology* (1978–1999), and *Ornithologia Neotropical* (1990–2002). Finally, each species record in the *Handbook of Australian, New Zealand and Antarctic Birds* (Marchant and Higgins 1990) and *Handbook of the Birds of the World* (Del Hoyo et al. 2005) was examined for documentation of same-sex sexual behavior.

Because same-sex sexual behavior has rarely been the focus of study in the ornithological literature, the occurrence of same-sex sexual behavior may be underreported due to scientific or theoretical difficulties in ascribing to it reproductive, social function or adaptive significance (Tyler 1984; Bagemihl 1999). Thus, the species list collated may represent a subset of potential species in which individuals interact sexually with the same-sex. Furthermore, we acknowledge that expression and frequency of same-sex behavior may in some instances reflect the anecdotal nature of some references to same-sex sexual behavior, the contexts in which species are studied behaviorally, and the biased way in which species are chosen to study and/or observed in the field for a variety of reasons (Clarke 1997). Nonetheless, for species in which same-sex sexual behavior has been recorded, it is instructive to attempt to compare patterns of sexual behavior with other behavioral traits. Only species in which accounts of same-sex sexual behavior could be verified with original data were included in the data set. Wherever possible, species were included only when the identification of the sex of individuals was considered reliable. Seventy-three percent of the data set comprised species classified as sexually dimorphic based on the plumage and/or weight dimorphism criteria of Owens and Hartley (1998). Of the remaining 27% of species in the data set (sexually monomorphic), sex identification was confirmed via banding and/or sex identification (i.e., laparoscopy/laparotomy/cloacal examination/DNA techniques) or other sex-specific markers/behaviors were recorded, that is, egg laying, brood patches, and cloacal protuberances. A final data set of 80 species was compiled, all of which were reported to perform same-sex courtship and/or mounting under noncaptive conditions in the published literature (Table 1).

Categories of same-sex sexual behavior, social mating system, and developmental mode

MM and FF sexual behavior

There is much confusion and subjectivity in the literature regarding what types of behavior constitute same-sex sexual activity. For the purposes of the current study, same-sex sexual behavior refers conservatively to courtship and/or mounting among individuals of the same sex, MM, or FF, regardless of the possible motivation or function of the behaviors. We recognize the existence of a wealth of further reports of same-sex affiliative behavior in the literature, broadly including allopreening, pair-bonding, and parenting activities (Bagemihl 1999). All these interrelated behavioral categories are applied loosely within the behavioral literature and considered to be, without question, integral components of opposite-sex sexual interactions (Marchant and Higgins 1990; Reynolds 1996; Zann 1996). Their context is rarely questioned, even though established links to sexual behavior often remain unclear. Although these patterns of behavior may be criticized when termed same-sex sexual, many authors have defined these associations as “isosexual,” “intrasexual,” or “homosexual” (e.g., Van Rhijn and Groothuis 1985; Huber and Martys 1993; Adkins-Regan 2002). For the sake of rigor, and to ensure the behavior examined represents sexual interactions, allopreening, pair-bonding, and parenting activities were purposefully and conservatively excluded from our analysis.

Courtship behavior, as we used the term, referred specifically to any behavioral patterns that may lead to mounting provided the same expression of behavior has also been reported in opposite-sex encounters within the same species and the behaviors were precopulatory in nature (Bastock 1967; Immelmann 1977; Marchant and Higgins 1990). Court-

ship behavior may serve other related functions such as the development and/or maintenance of pair bonds and sometimes serve dual or multiple nonsexual functions, though these instances were not included in our study (Armstrong 1965; Immelmann 1977). Mounting (pseudocopulatory) behavior describes attempted and/or achieved cloacal contact or manipulation (or insertion of the intromittent organ) and is similar in form to that reported for opposite-sex encounters for the same species (Birkhead et al. 1986; Marchant and Higgins 1990; Lombardo et al. 1994; Kaplan and Rogers 2001).

Based on these definitions, 4 dichotomous variables were constructed for species in which same-sex sexual behavior was evident; MM courtship, MM mounting, FF courtship, and FF mounting. For each variable, 0 equates to the absence of any reports of same-sex behaviors in this species and 1 equates to the presence of same-sex behaviors in this species.

Relative frequency of same-sex sexual behavior

Each species was scored on a categorical, ordinal scale for the relative frequency of MM and FF courtship and/or mounting after Vasey (1995). Frequency was normalized intraspecifically against the frequency in opposite-sex interactions within the same study (percent in the sample observed). A 4-point scale was employed including 0 (absent); 1 (rare), same-sex sexual behavior occurred 5% or less frequently than did opposite-sex sexual behavior or the behavior was described anecdotally and thus frequency was unable to be estimated; 2 (occasional), same-sex sexual behavior occurred 6–24% as frequently as opposite-sex sexual behavior; and 3 (frequent), same-sex sexual behavior occurred 25% or more frequently as opposite-sex sexual behavior. (Note that a 0 score was recorded when same-sex courtship or mounting had been reported but not the other).

Degree of polygamy

We categorized the dominant social mating system using the traditional classification of the degree of polygamy in mating systems derived from social interactions/bonds observed in the field, after Møller (1986) and modified by Owens and Hartley (1998). A 3-point scale was employed: 1, monogamy where polygamy was not recorded or rare in both sexes (socially monogamous); 2, facultative polygamy in one or both sexes (social monogamy co-occurring with polygyny, polyandry, promiscuity, and/or cooperative breeding systems); and 3, obligate polygamy in one or both sexes (polygyny, polyandry, and/or promiscuity). Mating system categories are admittedly broad, and much of the diversity and plasticity of avian mating systems are lost when species are collapsed in such a fashion. Despite this, broad categorization is required in comparative analysis (due to the reduced degrees of freedom (df) associated with accounting for phylogenetic relatedness), and the groupings are not meaningless as they reflect fundamental differences in the way species interact both socially and sexually (Lindénfors 2002).

State of development of young at hatching

The developmental state of young, defined as the incapability (altricial) or capability (precocial) of young to leave the nest at hatching dependent on locomotive development and foraging ability (Temrin and Tullberg 1995), was scored for each species on a 4-point categorical scale: 1, altricial (immobile, downless, remain in nest, eyes closed, fed); 2, semialtricial (immobile, downy, remain in nest, eyes open, fed); 3, semiprecocial (mobile, downy, remain in nest, fed); and 4, precocial (mobile, downy, follow parents, fed, shown food, or find own food) after Marchant and Higgins (1990).

Table 1
Survey of the expression and frequency of same-sex sexual behavior in avifaunal taxa under noncaptive conditions ($N = 80$)

Species	MMc ^a	MMm ^b	FFc ^c	FFm ^d	MMFR ^e	FFFR ^f	POLY ^g	A/P ^h	References ⁱ
<i>Struthio camelus</i>	1	0	0	0	1	0	3	4	1
<i>Centrocercus urophasianus</i>	0	1	1	1	1	1	3	4	2
<i>Biziura lobata</i>	1	0	0	0	1	0	3	4	3
<i>Cygnus atratus</i>	1	1	0	0	2	0	2	4	4
<i>Anser anser</i>	1	1	0	0	2	0	2	4	5
<i>Anser caerulescens</i>	0	1	1	0	1	1	2	4	6, 7
<i>Branta canadensis</i>	1	0	1	1	2	2	2	4	8
<i>Tadorna tadornoides</i>	0	0	1	0	0	2	1	4	9
<i>Anas platyrhynchos</i>	1	0	1	1	1	2	1	4	7, 10, 11
<i>Anas discors</i>	1	0	0	0	1	0	2	4	7
<i>Aythya affinis</i>	0	1	0	0	1	0	2	4	7
<i>Melanerpes formicivorus</i>	1	1	1	1	1	1	2	1	12
<i>Dinopium benghalense</i>	0	1	0	0	1	0	2	1	13
<i>Coracias cyanogaster</i>	0	1	0	1	1	1	2	1	14
<i>Dacelo novaeguineae</i>	0	1	0	0	1	0	2	1	15, 16
<i>Ceryle rudis</i>	0	1	0	0	1	0	2	1	7
<i>Aratinga canicularis</i>	1	0	1	0	1	1	1	1	7, 17
<i>Phaethornis superciliosus</i>	1	1	0	0	2	0	3	1	18
<i>Calypte anna</i>	1	1	0	0	2	0	3	1	19
<i>Porphyrio porphyrio</i>	1	1	1	1	1	2	2	3	20
<i>Gallinula tenebrosa</i>	0	1	0	0	1	0	2	3	21
<i>Gallinula mortierii</i>	0	1	0	1	1	1	2	3	22
<i>Tringa totanus</i>	1	1	0	0	1	0	2	4	7, 23
<i>Tringa nebularia</i>	1	1	0	0	1	0	2	4	7
<i>Tryngites subruficollis</i>	1	1	0	0	1	0	3	4	24
<i>Philomachus pugnax</i>	1	1	1	1	2	1	3	3	7, 25
<i>Chionis minor</i>	0	0	1	0	0	1	1	3	26
<i>Haematopus ostralegus</i>	1	1	1	1	1	2	2	4	27, 28
<i>Himantopus himantopus</i>	0	0	1	1	0	2	1	4	29
<i>Himantopus novaeseelandiae</i>	0	0	1	1	0	2	1	4	30
<i>Pluvialis apricaria</i>	1	0	0	0	1	0	2	4	31
<i>Larus occidentalis</i>	0	0	1	1	0	2	1	3	32
<i>Larus novaehollandiae</i>	0	1	0	0	2	0	1	3	33
<i>Larus ridibundus</i>	1	1	0	0	2	0	2	3	7, 34, 35
<i>Larus atricilla</i>	1	1	0	0	1	0	2	3	36
<i>Pagophila eburnea</i>	0	1	0	0	1	0	2	3	7
<i>Uria aalge</i>	0	1	0	0	1	0	2	2	37
<i>Alca torda</i>	0	1	0	0	3	0	2	2	38
<i>Gypaetus barbatus</i>	0	1	0	0	2	0	3	2	39
<i>Falco tinnunculus</i>	1	1	1	1	1	1	2	2	7, 40
<i>Poliiocephalus poliocephalus</i>	1	1	1	1	1	1	1	4	7, 41, 42
<i>Podiceps cristatus</i>	0	1	0	1	1	1	1	4	41
<i>Podiceps occipitalis</i>	0	1	0	0	1	0	1	4	43
<i>Phalacrocorax carbo</i>	1	0	0	0	1	0	2	1	7, 44
<i>Phalacrocorax aristotelis</i>	1	0	0	0	1	0	2	1	45
<i>Egretta garzetta</i>	0	1	0	0	2	0	2	2	7, 46
<i>Ardea cinerea</i>	0	1	0	0	2	0	2	2	47
<i>Ardea ibis</i>	0	1	0	0	2	0	2	2	48
<i>Scopus umbretta</i>	1	1	1	1	3	3	1	2	49
<i>Pygoscelis papua</i>	1	0	1	0	2	2	1	2	7
<i>Pygoscelis adeliae</i>	1	1	0	0	1	0	1	2	50
<i>Diomedea immutabilis</i>	1	1	1	0	1	2	2	2	51, 52
<i>Diomedea bulleri</i>	0	1	0	0	1	0	2	2	53
<i>Mionectes oleagineus</i>	1	0	0	0	2	0	3	1	54
<i>Perissocephalus tricolor</i>	1	1	0	0	1	0	3	1	55
<i>Rupicola rupicola</i>	1	1	0	0	3	0	3	1	56
<i>Chiroxiphia pareola</i>	1	0	0	0	1	0	3	1	57
<i>Chiroxiphia caudata</i>	1	1	0	0	1	0	3	1	7
<i>Gymnophis bicolor</i>	1	0	0	0	1	0	2	1	58
<i>Phaenostictus mcleannani</i>	1	0	0	0	1	0	2	1	59
<i>Menura novaehollandiae</i>	1	1	0	0	3	0	3	1	60
<i>Scenopoeetes dentirostris</i>	1	0	0	0	1	0	3	1	61
<i>Sericulus chrysocephalus</i>	1	0	0	0	3	0	3	1	62
<i>Ptilonorhynchus violaceus</i>	1	0	0	0	1	0	3	1	63
<i>Chlamydera maculata</i>	1	0	0	0	1	0	3	1	61
<i>Lichenostomus melanops</i>	0	1	0	0	2	0	2	1	64
<i>Notiomystis cincta</i>	0	1	0	0	1	0	2	1	65, 66
<i>Melanodryas cucullata</i>	0	1	0	0	1	0	1	1	67
<i>Pica pica</i>	1	0	1	0	1	1	2	1	68

Table 1, continued

Species	MMc ^a	MMm ^b	FFc ^c	FFm ^d	MMFR ^e	FFFR ^f	POLY ^g	A/P ^h	References ⁱ
<i>Corvus monedula</i>	0	0	1	0	0	1	2	1	69
<i>Ptiloris victorae</i>	1	0	0	0	3	0	3	1	70
<i>Ptiloris magnificus</i>	1	0	0	0	1	0	3	1	63
<i>Sialia sialis</i>	1	0	0	0	1	0	2	1	71
<i>Tachycineta bicolor</i>	0	1	0	0	1	0	2	1	72
<i>Riparia riparia</i>	0	1	0	0	2	0	2	1	7
<i>Hirundo pyrrhonota</i>	0	1	0	0	1	0	2	1	73
<i>Pseudonigrita arnaudi</i>	0	1	0	0	1	0	2	1	74
<i>Euplectes orix</i>	1	0	0	0	2	0	3	1	75
<i>Fringilla coelebs</i>	1	0	1	0	1	1	1	1	7
<i>Xanthocephalus xanthocephalus</i>	0	1	0	0	1	0	3	1	76

Species taxonomy based on Sibley & Munroe (1990, 1993).

^a Occurrence of MM courtship.

^b Occurrence of MM mounting.

^c Occurrence of FF courtship.

^d Occurrence of FF mounting.

^e Frequency of MM sexual behavior.

^f Frequency of FF sexual behavior.

^g Degree of polygamy.

^h State of young at hatching, altricial-precocial.

ⁱ References for data on same-sex sexual behavior: (1) Sauer (1972); (2) Scott (1942); (3) Lowe (1966); (4) Braithwaite (1981); (5) Huber & Martys (1993); (6) Diamond (1989); (7) Bagemihl (1999); (8) Collias & Jahn (1959); (9) Riggert (1977); (10) Lebret (1961); (11) Bossema & Roemers (1985); (12) MacRoberts & MacRoberts (1976); (13) Neelakantan (1962); (14) Moynihan (1990); (15) Legge (1990); (16) Legge (2004); (17) Buchanan (1966); (18) Stiles & Wolf (1979); (19) Stiles (1982); (20) Jamieson & Craig (1987); (21) Garnett (1978); (22) Ridpath (1972); (23) Hale & Ashcroft (1982); (24) Myers (1989); (25) Hogan-Warburg (1966); (26) Bried et al. (1999); (27) Heg & Van Treuren (1998); (28) Makkink (1942); (29) Kitagawa (1988); (30) Reed (1993); (31) Nethersole-Thompson & Nethersole-Thompson (1961); (32) Hunt et al. (1984); (33) Mills (1994); (34) Van Rhijn & Groothuis (1985); (35) Van Rhijn & Groothuis (1987); (36) Noble & Wurm (1943); (37) Hatchwell (1988); (38) Wagner (1996); (39) Bertran & Margalida (2003); (40) Olsen (1985); (41) O'Donnell (1990); (42) Fjeldsa (1983); (43) Nuechterli & Storer (1989); (44) Kortlandt (1995); (45) Snow BK (1963); (46) Fujioka (1988); (47) Ramo (1993); (48) Fujioka & Yamagishi (1981); (49) Campbell (1993); (50) Davis et al. (1998); (51) Frings & Frings (1961); (52) Fisher (1971); (53) Warham (1967); (54) Westcott & Smith (1994); (55) Snow (1972); (56) Trail & Koutnik (1986); (57) Snow DW (1963); (58) Willis (1967); (59) Willis (1973); (60) Lill (1979); (61) Marshall (1954); (62) Lenz (1994); (63) Strahan (1996); (64) Franklin et al. (1995); (65) Castro (2001); (66) Ewen & Armstrong (2002); (67) Lansley (2003); (68) Baeyens (1979); (69) Roell (1979); (70) Frith & Cooper (1996); (71) Pinkowski (1977); (72) Lombardo et al. (1994); (73) Emlen (1954); (74) Collias & Collias (1980); (75) Craig (1974); (76) Longcore (1967).

Statistical analyses

Ordinary linear modeling techniques assume that the residuals are independent and normally distributed with zero mean. However, in situations where the errors are not normally distributed, linear models can be generalized to cases where the residuals come from some other distribution in the exponential family (such as Binomial, Poisson, etc.), producing generalized linear models (GLMs; McCullagh and Nelder 1989). We used GLMs to examine the relationship between the occurrence and frequency of same-sex sexual behaviors (assuming statistical independence) and our independent variables (degree of polygamy and state of development of young) and to perform comparisons among differing degrees of polygamy and developmental state of young. We assumed the Poisson distribution for categorical dependent variables (frequency of same-sex sexual behavior) and the binomial distribution for dichotomous dependent variables (same-sex courtship, same-sex mounting). Significant differences among levels of our independent variables were assessed via the Wald statistic (compared with z or t distribution dependent on sample size) (Harrell 2001).

Usual statistical methods assume that each data point is an independent sample. However, closely related species may not be statistically independent as they share a common evolutionary history (Harvey and Pagel 1991). Recent studies suggest that this lack of independence is an important property of virtually all cross-species data sets (Freckleton et al. 2002; Blomberg et al. 2003), although correlations due to phylogeny may be fewer for behavioral data (Blomberg et al. 2003). Cur-

rent popular approaches to the analysis of such data have mainly used Felsenstein's (1985) phylogenetically independent contrasts (or equivalently, generalized least squares linear modeling methods; Garland and Ives 2000; Rohlf 2001). These techniques are appropriate if the residuals are normally distributed. When the residuals are not independent and/or normally distributed and GLMs are the method of choice, GLMs are most often fitted using generalized estimating equation (GEE) methods (Liang and Zeger 1986; Hardin and Hilbe 2003). GEE methods employ a GLM approach, incorporating the phylogenetic relatedness among species as a correlation matrix, to specify dependence among observations in the model. Paradis and Claude (2002) first introduced GEE methods for phylogenetic comparative analyses. Traits analyzed via this procedure may be continuous, categorical, or dichotomous, and two or more traits may be analyzed simultaneously.

The derivation of the correct df for statistical hypothesis tests is an issue in phylogenetic GEE models. The problem arises because there is only one single cluster of observations in a phylogenetic GEE model (i.e., one phylogeny), whereas GEE models are usually fitted to data from multiple clusters. Paradis and Claude (2002) proposed a heuristic method to approximate the appropriate df using the phylogeny, based on the ratio of the distance of nodes to tips to the distance from the root to tips. Their method performed well in simulations. We used the method of Paradis and Claude (2002) in order to examine how the phylogenetic correlations among species affected our conclusions from the analyses that treated species as independent.

A matrix of fixed correlations specifying dependence among species observations was derived from shared branch lengths (fixed branch lengths = 1) based on the phylogenetic topology of Sibley and Ahlquist (1990) above the family level. Relationships among genera and among species within genera were based on Sibley and Ahlquist (1990) where possible, supplemented with a composite of several phylogenies (Strauch 1985; Livezey 1986; Sheldon 1987; Christidis and Schodde 1992; Sheldon and Winkler 1993; Björklund 1994; Crochet et al. 2000) and the taxonomy of Sibley and Monroe (1990) ($N = 80$, phylogenetic $df = 30.49$) (see Appendix 1, electronic Supplementary data). The resultant matrices were again fitted, specifying Poisson or binomial distributions. Significant differences among parameter estimates for each category of the degree of polygamy and developmental state of young at hatching were again assessed via the Wald statistic. Analyses were performed using R (R Development Core Team 2005) with the Analyses of Phylogenetics and Evolution (APE 1.3-1) package (Paradis et al. 2004).

Assigning branch lengths equal to 1 assumes that all speciation events are present in the phylogeny and that traits change only at speciation events. In order to explore the effect of different branch length assumptions on our analysis, we reanalyzed our data using Grafen's (1989) branch lengths ($\rho = 1$), which sets the node height proportional to the number of taxa above it in the phylogenetic tree (phylogenetic $df = 10.49$). There was a high concordance in the results obtained between the 2 techniques (i.e., 97% of significance tests produced the same result). The only difference maintained by the analysis using Grafen's branch lengths that the equal branch length approach did not maintain was a significantly higher frequency of FF sexual behavior in precocial species compared with altricial species. Differences maintained by the equal branch length approach that were not maintained by the analysis with Grafen's branch lengths were a significantly higher frequency of FF sexual behavior in facultative polygamy than obligate polygamy and a higher occurrence of FF mounting in monogamy than facultative polygamy. We thus chose to report the results for unit branch lengths, as the differences between the 2 approaches did not alter the overall interpretation of results.

RESULTS

MM sexual behavior and social mating system

MM sexual behavior was reported more often than FF sexual interactions. The probability of occurrence of MM courtship

was significantly higher in species exhibiting obligate polygamy compared with monogamy or facultative polygamy (Table 2, species data; Figure 1a). MM mounting was also significantly higher in species exhibiting facultative polygamy compared with those exhibiting monogamy or obligate polygamy (Table 2, species data; Figure 1b). The frequency of MM sexual behavior increased with degree of polygamy. Frequency of occurrence of MM sexual behavior (predominantly courtship) was significantly higher in obligate polygamy compared with monogamy (Table 2, species data; Figure 1c).

When the data were corrected for phylogenetic relatedness, a number of relationships became nonsignificant. The significant differences remaining were a significantly greater occurrence of MM mounting in facultative polygamy compared with monogamy and significantly greater frequency of occurrence of MM sexual behavior in obligate polygamy compared with monogamy and facultative polygamy (Table 2, contrast data).

FF sexual behavior and social mating system

FF sexual behavior occurred predominantly in socially monogamous species. The occurrence of FF courtship was significantly lower in species exhibiting both facultative and obligate polygamy compared with monogamy (Table 2, species data; Figure 1d). Similarly, expression of FF mounting was significantly lower in species exhibiting both facultative and obligate polygamy compared with monogamy (Table 2, species data; Figure 1e).

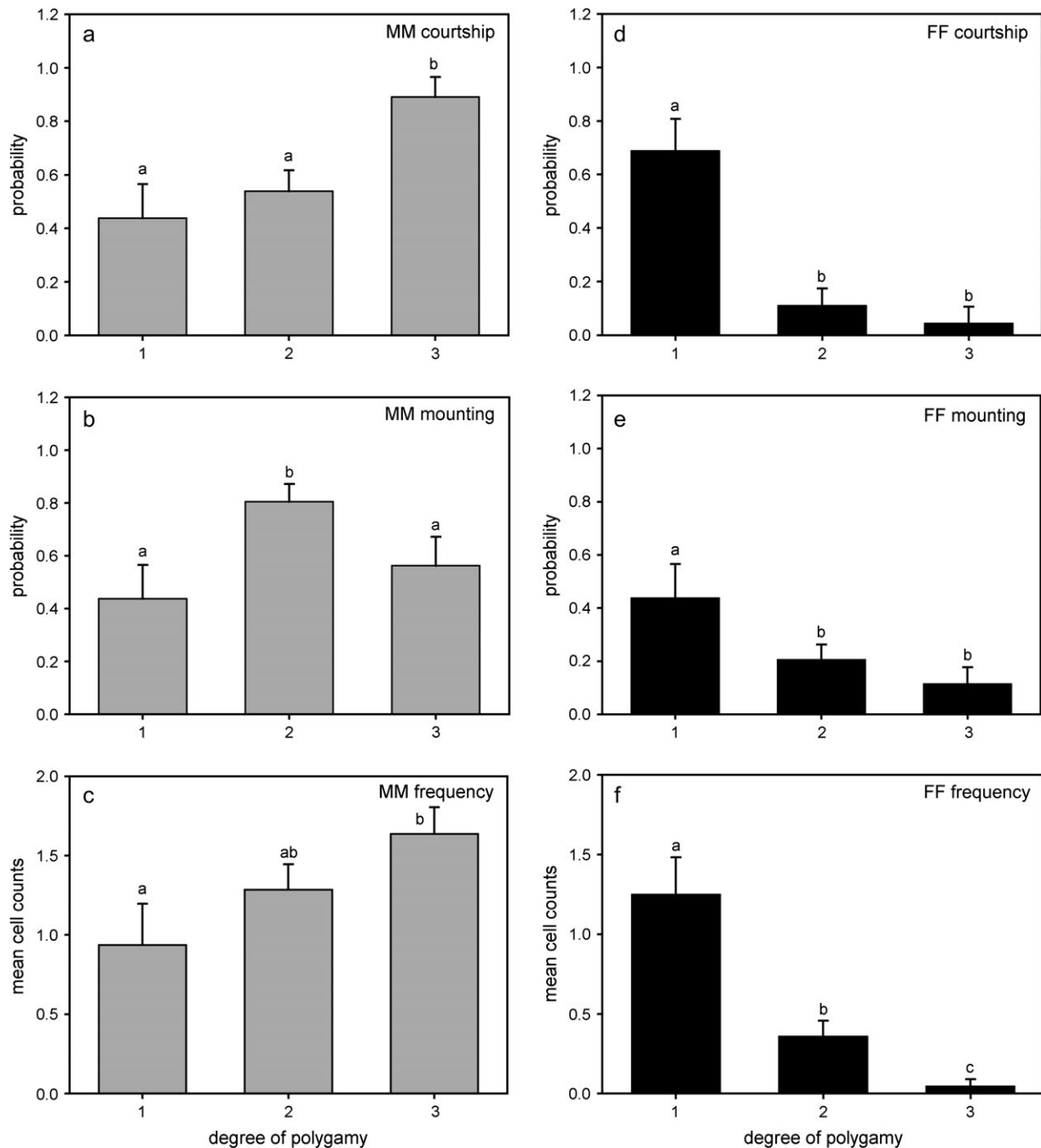
The frequency of FF sexual behavior decreased as the degree of polygamy increased (opposite to the frequency of MM sexual behavior). The frequency of FF sexual behavior was significantly lower in species exhibiting facultative polygamy compared with monogamy. Obligate polygamous species exhibited significantly lower frequencies of FF sexual behavior than both monogamous and facultative polygamous species (Table 2, species data; Figure 1f).

When the data for females were corrected for phylogenetic relatedness, most of these significant relationships were maintained. The expression of FF courtship was significantly lower in species exhibiting both facultative and obligate polygamy compared with monogamy. The frequency of FF mounting was significantly lower in species exhibiting facultative polygamy compared with monogamy. The frequency of FF sexual behavior decreased significantly as the degree of polygamy increased. Obligate polygamous species exhibited significantly lower frequencies of FF sexual behavior than both monogamous and facultative polygamous species (Table 2, contrast data).

Table 2
Wald statistics for same-sex sexual behavior parameter estimates employing species level (raw) data (z) and contrast data (t), assessing differences among levels of the independent variable the degree of polygamy

	MMc	MMm	MMFR	FFc	FFm	FFFR
Species data (Wald, z)						
1 versus 2	0.26	2.28*	1.08	-3.18*	-2.08*	-3.67*
1 versus 3	2.62*	0.38	1.81*	-3.37*	-2.29*	-3.23*
2 versus 3	2.80*	-2.08*	1.12	-1.21	-0.82	-1.99*
Contrast data (Wald t)						
1 versus 2	0.82	2.31*	1.31	-3.22*	-2.07*	-3.95*
1 versus 3	1.06	1.41	3.87*	-3.90*	-1.71	-2.68*
2 versus 3	0.52	-0.89	3.90*	-1.75	-0.21	-2.02*

1 = monogamy; 2 = facultative polygamy; 3 = obligate polygamy. Dependent variables include male-male courtship (MMc), male-male mounting (MMm), the frequency of male-male sexual behavior (MMFR), female-female courtship (FFc), female-female mounting (FFm), and the frequency of female-female sexual behavior (FFFR). *denotes significant difference between levels, $P < 0.05$.

**Figure 1**

Transformed linear combinations of species level (raw data) parameter estimates of (a) MM courtship, (b) MM mounting (probability scores), and (c) the frequency of MM sexual behavior (mean expected cell counts) and (d) FF courtship, (e) FF mounting (probability scores), and (f) the frequency of FF sexual behavior (mean expected cell counts) with social mating system of the avian species (Degree of polygamy: 1 = monogamy, 2 = facultative polygamy, 3 = obligate polygamy). Mean \pm standard error. For each dependent variable at the species level (raw data) where significant differences were observed among groups, similar letters denote statistically similar probabilities/mean cell counts.

MM sexual behavior and state of development of young at hatching

Expression of MM sexual behavior was equally distributed across categories of developmental state at hatching. No significant differences among developmental state categories were observed in neither the expression of MM courtship nor the frequency of MM sexual behavior (Figure 2a,c). However, the occurrence of MM mounting was significantly higher

in semialtricial species compared with altricial species (Table 3, species data; Figure 2b).

When the data were corrected for phylogenetic relatedness, the significantly greater occurrence of MM mounting in semi-altricial compared with altricial species was maintained. In addition, there were significantly greater occurrences of MM mounting in semiprecocial and precocial species when compared with altricial species (Table 3, contrast data).

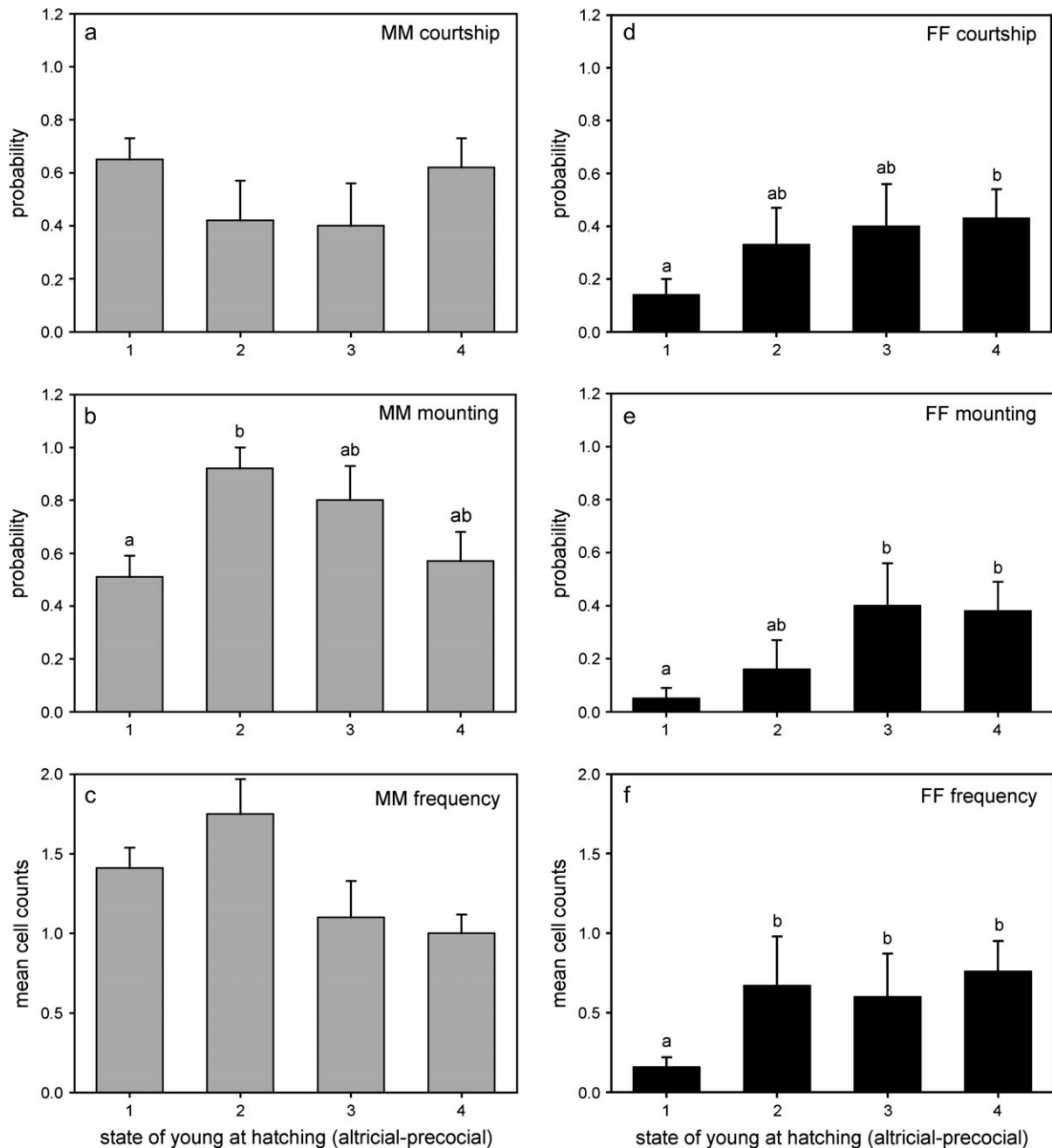


Figure 2

Transformed linear combinations of species level (raw data) parameter estimates of (a) MM courtship, (b) MM mounting (probability scores), and (c) the frequency of MM sexual behavior (mean expected cell counts) and (d) FF courtship, (e) FF mounting (probability scores), and (f) the frequency of FF sexual behavior (mean expected cell counts) with the state of development of young at hatching of the avian species (1 = altricial, 2 = semialtricial, 3 = semiprecocial, and 4 = precocial). Mean \pm standard error. For each dependent variable at the species level (raw data) where significant differences were observed among groups, similar letters denote statistically similar probabilities/mean cell counts.

FF sexual behavior and state of development of young at hatching

The occurrence of FF courtship was significantly higher in precocial than altricial species (Table 3, species data; Figure 2d). The expression of FF mounting was significantly higher in semiprecocial and precocial species compared with altricial species (Table 3, species data; Figure 2e).

The frequency of FF sexual behavior was significantly higher in precocial, semiprecocial, and semialtricial

compared with altricial species (Table 3, species data; Figure 2f).

When the data for females were corrected for phylogenetic relatedness, a subset of relationships were maintained. The expression of FF courtship was significantly greater in semiprecocial and semialtricial than altricial species. FF mounting was significantly higher in precocial, semiprecocial, and semialtricial species compared with altricial species. The frequency of FF sexual behavior was significantly higher in semiprecocial

Table 3

Wald statistics for same-sex sexual behavior parameter estimates employing species level (raw) data (z) and contrast data (t), assessing differences among levels of the independent variable the state of development of young

	MMc	MMm	MMFR	FFc	FFm	FFFR
Species data (Wald, z)						
1 versus 2	-1.40	2.14*	0.85	1.49	1.18	2.62*
1 versus 3	-1.39	1.56	-0.74	1.80	2.53*	2.27*
1 versus 4	-0.23	0.43	-1.32	2.40*	2.78*	3.23*
2 versus 3	-0.08	-0.77	-1.25	0.32	1.19	-0.19
2 versus 4	1.11	-1.86	-1.81	0.54	1.26	0.31
3 versus 4	1.13	-1.21	-0.26	0.15	-0.10	0.50
Contrast data (Wald t)						
1 versus 2	-1.78	4.13*	2.20*	2.24*	2.33*	1.95
1 versus 3	-1.06	2.41*	-0.45	4.03*	3.67*	2.11*
1 versus 4	0.06	4.20*	-0.64	1.66	3.48*	1.88
2 versus 3	0.49	-1.87	-2.81*	1.69	1.08	0.71
2 versus 4	1.68	-1.95	-3.07*	-0.87	0.56	0.11
3 versus 4	1.03	0.27	-0.24	-2.76*	-0.75	-0.69

1 = altricial; 2 = semialtricial; 3 = semiprecocial, and 4 = precocial. Dependent variables include male-male courtship (MMc), male-male mounting (MMm), the frequency of male-male sexual behavior (MMFR), female-female courtship (FFc), female-female mounting (FFm), and the frequency of female-female sexual behavior (FFFR). *denotes significant difference between levels, $P < 0.05$.

species compared with altricial species (Table 3, contrast data).

DISCUSSION

Our analyses suggest that consistent patterns exist between the expression/frequency of same-sex sexual behavior and social mating systems in avian taxa and that the interplay among these variables differs in males and females. Expression of FF sexual behavior, that is, mounting and especially FF courtship, was highest in monogamous species and significantly lower in species exhibiting facultative and obligate polygamy. As the degree of polygamy increased, the frequency of FF sexual behavior decreased, being especially low in species exhibiting obligate polygamy. The opposite trend was found for males. Although the occurrence of MM courtship and the frequency of MM sexual behavior (courtship and/or mounting) were distributed across all mating systems, both were lower in monogamous systems. The frequency of MM sexual behavior increased significantly with the degree of polygamy. Most relationships for FF sexual behavior with social mating system were maintained after phylogenetic correction. Conversely, some relationships for males were maintained, whereas others became nonsignificant suggesting some patterns were an artifact of phylogenetic relatedness. MM mounting remained significantly higher in species displaying facultative polygamy, and the frequency of MM sexual behavior remained significantly greater in obligate polygamy compared with monogamy and facultative polygamy after controlling for the effects of phylogeny. Most species within the obligate polygamy category exhibited MM courtship, yet few exhibited MM mounting. Many of the species within this category are the closely related bowerbirds and birds of paradise, which may explain variation in significant relationships observed after phylogenetic consideration.

In socially monogamous systems, both sexes benefit from socioreproductive exclusivity (Reichard 2003) and the frequency of pair-specific display, coordinated displays, courtship, sexual solicitation, and mounting are more often bidirectional and occur before, during, and after pairing (Bastock 1967; Wachtmeister 2001). Under these conditions, both males and

females also court and mount individuals of the same sex, although the expression and frequency of occurrence is greater for females. For a number of monogamous species, longer term FF bonding and FF coparenting of offspring from male-female (MF) extrapair copulations occur (e.g., *Larus novaehollandiae*; Mills 1991).

Why was FF sexual behavior observed more frequently in monogamous species when traditional selection theory would predict otherwise? Adaptive hypotheses offered argue that FF pairings may arise in species in which biparental care is required for survival of offspring and when opportunities for male-female pairing are limited demographically and/or behaviorally (Conover 1984). A pattern has been observed in many representatives of Laridae in which supernormal clutches (associated with FF pairing, courtship, mounting, and coparenting) are more frequent when the population exhibits a female-biased sex ratio (Hatch 1993; Bagemihl 1999; Nisbet and Hatch 1999). Perhaps, the most compelling evidence in support of this sex ratio bias hypothesis for FF pairs is available from formal hypothesis testing conducted on colonies of the ring-billed gull, *Larus delawarensis*, and the Californian gull, *Larus californicus*. These studies experimentally manipulated the sex ratio to produce a female bias by removing males. The frequency of supernormal clutches of 4-6 eggs (a measure or index of FF pairings) was greater in colonies from which males had been removed than it was in control colonies (Conover and Hunt 1984). It may be advantageous for females to pair with other females and coparent while seeking extrapair reproductive opportunity with paired males (to obtain fertilized eggs). Mills (1991) found that although FF pairs in silver gulls, *L. novaehollandiae*, have a lower overall lifetime reproductive success than MF pairs (0.85 FF vs. 1.91 MF, mean number of offspring fledged in lifetime), over 50% of females in populations do not breed at all. The effects of demographic biases may hold promise in terms of adaptive explanations for the formation and maintenance of FF associations within these monogamous species, especially when opportunities for MF extrapair copulation exist outside the pair bond (Birkhead and Møller 1995).

The frequency of MM sexual behavior was lower in monogamous species, and increased as the degree of polygamy

increased, as would be predicted within a traditional adaptive framework. This pattern is opposite to the pattern for females. Unlike FF sexual behavior though, which is predominantly restricted to monogamous species and almost absent in polygamous species, MM sexual behavior does occur across all species. Some species that are primarily socially monogamous (within the context of other polygamous associations) do display MM sexual behavior, form long-term MM pairs, and may even coparent (e.g., *A. anser*; Huber and Martys 1993; *C. atratus*, Braithwaite 1981). In the black swan, *C. atratus*, males may temporarily associate with a female, mate, and then break the bond once the eggs have been laid or they may usurp nests or steal eggs from MF clutches. These male pairs perform parenting duties, including incubation and caring for cygnets (Braithwaite 1981).

Most species displaying facultative polygamy are also socially monogamous with varying degrees of polygamy and cooperative breeding arrangements, although MF extrapair copulations are predominantly male solicited (e.g., *Alca torda*; Wagner 1996). Under these types of social organization, expression of same-sex courtship and especially of mounting was more common in males than in females.

Species in the data set displaying obligate polygamy mainly exhibit male polygyny as their dominant mating strategy (91%). Strong sexual selection, through female choice and males advertising for additional mates, translates to males being the dominant actors in solicitation, courtship, and mounting attempts (Cunningham and Birkhead 1998). These species exhibit predominantly MM courtship, and to a lesser degree mounting, and rarely display FF courtship and/or mounting. Similarly, little evidence is found in the literature on same-sex pair-bonding, exclusivity, or maintenance of same-sex associations under these social conditions. When dealing with such data sets though, there is the possibility that observer's attention may be focused on displaying males, and thus interactions among females may be overlooked when males are the focal sex (e.g., displaying males on leks, bowers, and arenas).

For these polygynous species, males may engage in same-sex sexual behavior while still affording MF reproductive opportunities. Male-biased social contexts may also explain the expression of MM mounting and especially courtship. Examples of male biased social contexts for polygynous species in the data set include males residing in all-male groups at juvenile stages of life history (e.g., lyrebird, *Menura novaehollandiae*; Lill 1979); males visiting male display areas (e.g., regent bowerbird, *S. chrysocephalus*; Lenz 1994); males visiting leks (e.g., Guianan cock-of-the-rock, *R. rupicola*; Trail and Koutnik 1986); or males congregating and courting at communal leks (e.g., buff breasted sandpiper, *Tryngites subruficollis*; Myers 1989). MM sexual interactions may occur to facilitate social alliances and inclusion, allowing resource exchange required for reproduction (Roughgarden 2004; Roughgarden et al. 2006), reinforce dominance hierarchies (Fujioka and Yamagishi 1981), arise as a competitive strategy for opposite sex mating opportunity (Wagner 2003), or as a mechanism in juvenile males (as is the case in many of the bowerbirds) to facilitate learning of courtship displays from adult males (Collis and Borgia 1993).

In species with obligate polygamy, FF sexual behavior is rarely observed and the frequency very low. Most species in the obligate polygamy category in the current study were polygynous, in which females tend to be dispersed spatially and/or behaviorally during the breeding season, nest solitarily, and provide uniparental care in terms of incubation, food provisioning, and post hatching defense (e.g., regent bowerbird, *S. chrysocephalus*; Lenz 1994). Perhaps, these social conditions reduce the opportunity for interactions with other females and/or the need for associating with other individuals to pro-

vide care of offspring. Alternatively, there is always the possibility that dispersal makes it less likely that observers will detect same-sex interactions among females. It is also interesting to note that obligately polygamous species that display variations of polyandry as a reproductive strategy are largely absent from the data set, with the exception of *Struthio camelus* (predominantly polygynandrous; Kimwele and Graves 2003), and that in this species FF sexual behavior has not been observed although we would perhaps predict otherwise.

An alternative interpretation of patterns consistent with selection theory may be that the sex that actively solicits in heterosexual interactions, that is, the competitive sex, is the one participating in same-sex sexual behavior. For polygynous species, this role is played by males and for polyandrous species females. For monogamous species, both sexes may solicit. Thus, MM interactions would be predicted to occur more frequently in polygynous species (as observed in our data set) and FF interactions to occur more frequently in polyandrous species. In the absence of polyandrous species in the data set (only one example was found in the literature), FF interactions would be expected to occur more frequently in monogamous species when compared with those that are polygamous (predominantly polygynous). This was confirmed in our analyses. Whether FF sexual interactions do not occur in polyandrous species or remain to be observed and documented warrants future consideration.

In terms of the state of development of young at hatching, FF sexual behavior was more frequently expressed in precocial or semiprecocial species compared with altricial species. Although some relationships varied after phylogenetic consideration, due to closely related taxa in a subset of obligately polygamous species, most patterns were maintained (Table 3). The expression of FF courtship was greater in semiprecocial and semialtricial than altricial species. Expression of FF mounting was greater in precocial, semiprecocial, and semialtricial species compared to altricial species. The frequency of FF sexual behavior was higher in semiprecocial species than altricial species. Indeed some 60% of species in the data set that display social monogamy and FF sexual behavior produce precocial or semiprecocial young. This would seem to be at odds with overall patterns in birds because, as a generalization, socially monogamous species tend to produce altricial young and species under variations of polygamy are more usually associated with the production of precocial young (Temrin and Tullberg 1995). Thus, FF sexual behavior is more likely to occur in species in which monogamy coincides with the production of precocial offspring (i.e., in monogamous species that are exceptions to the predominant altricial mode of development). Social cues and interactions with female targets very early in development and/or reinforced by later experience may influence the development and hence the expression of FF sexual behavior for some individuals in these species. To date, no data exist for the role of filial and sexual imprinting on the development of FF preferences in precocial species, although a number of studies have reported the development of male sexual preferences for males in precocial species as a direct consequence of sexual imprinting (Schutz 1965; Lorenz 1966; Nash and Domjan 1991). However, our results would suggest that the focus on MM interactions in precocial species may be somewhat misdirected because FF interactions are more common under field conditions. For FF sexual behavior, it seems important to examine differences between precocial and altricial species in the early development of the acquisition of sexual preferences. Perhaps, filial imprinting in precocial species or the temporal difference in sexual imprinting between precocial and altricial species is influential.

We have demonstrated in this study that, although same-sex courtship and mounting behavior appears to be uncommon

in birds, enough variation is present to permit examination of same-sex sexual behavior in relation to mating system and developmental state at hatching and to document social conditions under which it is more likely to occur for both males and females. The frequency of MM sexual behavior increased with degree of polygamy, although occurred across all mating systems. FF sexual behavior occurred predominantly in socially monogamous species. FF sexual behavior was also more likely to occur in species in which monogamy occurs together with the production of precocial offspring; that is, in monogamous species that are exceptions to the more common altricial mode of development. The social context conferred by a particular mating system and mode of development are likely contributing factors to the expression and frequency of same-sex sexual behavior. In some cases, same-sex sexual behavior may serve social and/or sexual functions not necessarily related to reproduction, confer indirect fitness benefits, and/or be adaptively neutral, co-occurring within the context of reproductive opportunity. Attempting to ascribe adaptive function and fitness benefits to all sexual interactions may be misdirected. Many individuals who engage in same-sex sexual interactions also participate in heterosexual interactions (Bagemihl 1999). Equally, many populations include nonbreeding individuals; a proportion of which may engage in heterosexual courtship and copulation yet never reproduce during their life history (Collias and Jahn 1959; Mills 1991). Our findings highlight a need to re-examine both same-sex and opposite-sex sexual behavior in a context broader than currently provided by traditional selection theory, which interprets the “function” of sexual behavior predominantly in terms of direct reproductive fitness.

SUPPLEMENTARY MATERIAL

Supplementary Material can be found at <http://www.beheco.oxfordjournals.org/>.

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