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Does Social Organization, Litter Size, Sexual Dimorphism, and Phylogeny  
Influence Multiple Paternity in Mammals?

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Departmental Honors Thesis  
The University of Tennessee at Chattanooga  
Biology, Geology and Environmental Science

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***Abstract:***

Animal social systems are complex and the dynamics of one component could influence the dynamics of another. The aim of this literature search research was to determine the interrelatedness between mammalian social organization and mating system, two components of social systems. The mating system was represented by multiple paternity, the number of litters with more than one father, as genetic analysis tells which individuals reproduced with who. Variables that might influence multiple paternity amongst extant mammalian species included in this study are variable social organization, male social organization, mean litter size, sexual dimorphism, and phylogenetics. Analysis was conducted using 56 mammalian species from 97 population that made up 10 orders. The overall mean percentage of multiple paternity across all the male social organizations was 0.39. Analysis revealed that two hypotheses based on the variables above that were important effectors of multiple paternity included male social organization and mean litter size. Of the male social organization units, only multimale single female groups influenced multiple paternity, Multiple paternity was negatively correlated to mean litter size, which is the opposite of what other studies have found. Variable social organization, body mass, and phylogeny were not found to be important predictors of multiple paternity. The negative correlation between litter size and multiple paternity could be explained by mate guarding or improved by analyzing using a more holistic model. The statistical power of male social organization could be improved by creating less categories of male units as either multimale or single male. Other variables of interest to multiple paternity could be social structure, breeding season length, and environmental data. This study encourages the use of quality data and more natural history studies of animals.

***Keywords:*** Mammals, behavioral ecology, social systems, social organization, mating system, multiple paternity, phylogeny, phylogenetic signal, sexual dimorphism, body mass, litter size

***Introduction:***

Animal social systems are complex and have four components, including social organization (group size and composition), mating system (who mates with who), care system (who cares for young), and social structure (who interacts with who).<sup>1</sup> Social organization can influence the other components of the social system because interactions are dependent on what individuals are present. For example, the number of adult males and females in a social unit may influence mating patterns and mating systems, which in turn could influence the care system.<sup>2</sup> Studies that examine relationships among different social system components are critical to explaining the complexity of social systems in the animal kingdom.

Historically, the mating system was determined by behavioral observations and the extent of male-female home range overlap, which has been referred to as the social mating system. For example, monogamy has been defined by exclusive home range overlap of a single adult male and female,<sup>3</sup> observation of 'pair bonds' with a preferred sexual partner,<sup>4</sup> and observation of exclusive copulation.<sup>5,6</sup> Advances in genetic analyses, initially on birds, revealed that mating systems are more complex than behavioral studies have previously shown.<sup>7,8</sup> Genetic data revealed that mating systems previously reported as monogamous based on behavioral data actually involved extra-pair mating and thus were not monogamous.<sup>9,10</sup> With these findings we can a shift away from social mating system to genetic mating systems, based on genetics rather than observations.

***Multiple Paternity:***

Within a litter or clutch, it is possible for a female to give birth to offspring that have different fathers.<sup>11</sup> This is indexed by multiple paternity (i.e., the percentage of litters or clutches

with more than one father within a population). Multiple paternity is a true measure of how many males a female reproduced with, thus indicating the genetic mating system. Multiple paternity is common in birds<sup>10</sup> and mammals<sup>9</sup>, suggesting that mating patterns are complex in these clades. High quality comparative studies should examine factors affecting multiple paternity indices rather than using mating system designations based on behavioral observations. The aim of my study was to determine if multiple paternity in mammals is influenced by social organization, litter size, sexual dimorphism, and phylogeny. These variables and their hypotheses are discussed below. I used a comparative approach to test hypotheses for variation in multiple paternity indices across mammals.

### ***Hypotheses and Predictions:***

Multiple paternity is a variable that has widespread importance in behavioral ecology research on themes such as sexual selection, sperm competition, degree of relatedness, and level of cooperation.<sup>12,13</sup> Additionally, we know that sexual selection can lead to variation in reproductive success<sup>14</sup> and extent of multiple paternity<sup>15</sup>. Because multiple paternity is widespread in research, it is important to understand variables that may affect multiple paternity, such as social organization, life history factors, sexual dimorphism, and phylogenetics. I propose four hypotheses to explain multiple paternity in mammals (Figure 1).

### ***Hypothesis 1: Social Organization:***

Social organization often is assumed to be the same across populations within a species.<sup>16,17</sup> However, this assumption has not been supported within recent literature. Social organization is dynamic and therefore can vary between and within populations.<sup>17-20</sup> This variation is known as variable social organization and is described further within the methods. In

mammals, variable social organization has been reported in a wide range of taxa including primates,<sup>20,22</sup> marsupials,<sup>18</sup> shrews,<sup>21,23</sup> and artiodactyls.<sup>19</sup> Since social systems are interrelated<sup>1</sup>, it is logical that variability in social organization could influence mating patterns and the genetic mating system. If opportunities for multiple paternity increase with increasing variation in social organization, then **I predict** that the percentage of litters with more than one father is greatest in species with greater variable social organization.

Additionally, social organization can be represented by male social organization, which is determined by only adult males, unlike variable social organization which is determined by adult males and females. Male social organization can be multimale (with or without females) or as solitary males, thus I refer to male social organization as male social units. Indicating the male social units of a population is important because it can be used as a measure of the number of potential breeding males within a population, since that number is often unreported in studies. If male social units are more important than variable social organization, then **I predict** that the percentage of litters with more than one father is greater in species with more multi-male groups than in species with a greater percentage of single male units.

***Hypothesis 2: Litter size:***

Comparative studies in mammals support the hypothesis that multiple paternity is associated with litter size.<sup>12,13</sup> Within mammals, this association has been found to be positive as multiple paternity increase with increasing mean litter size.<sup>13</sup> Based on probability alone, large litters are more likely to have more than one father than small litters because the larger the litter the more opportunities for multiple fathers. For example, based on probability alone, a litter size of two could only have up to two fathers, but a litter size of 10 could have up to 10 fathers, and

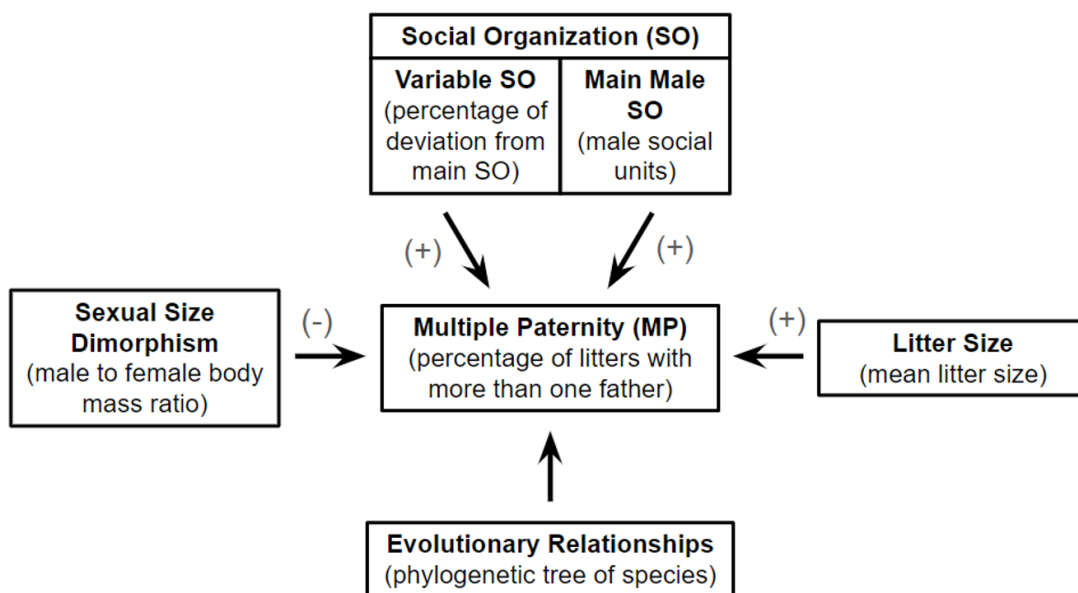
thus a greater chance of higher multiple paternity. If litter size influences multiple paternity in mammals, then **I predict** that the percentage of litters with more than one father increases with increasing mean litter size.

***Hypothesis 3: Sexual Size Dimorphism:***

There is a known correlation between sexual dimorphism regarding body size and the mating system in mammalian taxa such as primates, ungulates, and pinnipeds.<sup>24</sup> A common way mammals exhibit dimorphism is in body size dimorphism. In general, mammal body size dimorphism is biased towards males, since males are often larger than females.<sup>24,25</sup> This bias could be due to reasons such as intense male-male competition for reproductive access to females.<sup>24,25</sup> Male-male competition amongst mammals can be explained by males being the sex with disproportionate reproductive success.<sup>25</sup> Sexual selection will favor traits beneficial to sexual competition,<sup>25</sup> like larger body mass, leading to a high ratio of size dimorphism between males and females. There is an assumption that in monogamous species there is less sexual competition among males and thus lower size dimorphism than in polygynous species.<sup>25</sup> Taking everything into account, I infer that a limited number of large sized males have access to a female due to intense competition and since they can prevent the access of other males, this could decrease the percent of multiple paternity since a limited number of males have access to a female. If sexual size dimorphism is an indication of competition, then **I predict** a lesser percentage of litters with more than one father in species with larger adult male to female body mass ratio.

#### ***Hypothesis 4: Evolutionary Relationships:***

Extant animals may have traits due to a common ancestor. If a trait has a phylogenetic signal, it means that more closely related species will be more like each other than distantly related species. For example, body mass has been shown to have a phylogenetic signal.<sup>46,47</sup> If multiple paternity is a product of evolutionary relationships, then **I predict** there will be a phylogenetic signal related to multiple paternity amongst different taxa.



**Figure 1:** Conceptual framework of predictor variables affecting multiple paternity.

The measurement of each variable is in parenthesis.

#### ***Methods:***

#### ***Data Collection:***

I conducted a **literature search** during Fall 2022 with the Web of Science, using the keywords “multiple paternit\*” along with all the 1,314 mammalian genera<sup>26</sup>. Studies on monogamy might not include this keyword if there are species with only one father per litter. To



find papers not found in the literature search, I gathered citations from two review articles<sup>+</sup> focused on species thought to be monogamous and from this, added an additional 13 studies to my initial search. Papers from the literature search went through two levels of screening. I initially screened the titles and abstracts and rejected any deemed irrelevant. Abstracts were rejected if they were non-mammalian (i.e., studies on fish or invertebrates), studied humans, studied domestic animals, studied captive populations, or were based on observational data.

In the second screening process, I read all potentially relevant papers. Criteria for accepting papers multiple paternity data based on genetic data (not observational data) and clearly reported paternity or sibling relationship data. If a paper's figures or descriptions were unclear about paternity data, I rejected them instead of assuming potential values (i.e., graphs without exact numbers or contradictory values within the study). I accepted 120 papers from the multiple paternity search, from which I collected data on my response variable, **multiple paternity**, defined as the percentage of litters with more than one father. The value of multiple paternity was either reported by the authors or calculated based on data provided in the papers. When reported, I also recorded litter size mean and range, method of genetic analysis (programs like CERVUS and ML Relate) and the method's level of confidence (80 or 95 percent, or not reported). The total number of litters often included singletons or was not specified, but if detailed litter information was provided, I reported the total number of litters to include litters with more than two offspring. This was to provide a more accurate percentage of litters with more than one father because multiple paternity is not possible in a litter size of one, so I excluded those litters if possible.

**Variable social organization (VSO)** for each species was determined by my advisor's research collaborators.<sup>29</sup> VSO was indexed as the percent of deviation from the main social organization reported within populations. Social organization is only based on the group composition of adults, excluding juveniles. Main male social organization was based only on males (excluding females). Social organization is abbreviated based on which sex is multiple and which is single within a group; MF, MMF, MMFF, Solitary, or Sex Specific. Pairs of adult males and females is MF, multimale single female groups are MMF, multifemale single male groups are MFF, multimale multifemale groups are MMFF, if both males and females are by themselves the population is labeled solitary, and sex specific groups are males and females that have their own group composition separate from each other sex.

Many of the papers in my dataset did not report **mean litter size**. To find litter size data for these species, I used data from Walker's Mammals of the World.<sup>30</sup> I correlated those mean litter sizes against the mean litter sizes reported in papers in my dataset (Supplementary Materials 1) and determined Walker's Mammals of the World to be a suitable source. If the litter size was not reported in Walker's Mammals of the World, additional primary literature was searched and used for the remaining species (n=8 species). For species that had both multiple paternity data and social organization data, I collected **body mass** for each of those species. Body mass data was collected from primary literature with the keywords "species" + "body weight / body mass / dimorphism" in Google Scholar. Criteria for body mass data collected excluded pregnant female weights whenever possible, based either on explicit statements by the authors, by excluding pregnant individuals in tables, or by avoiding data collected during obvious breeding seasons that might include pregnant females in the calculations of average female body mass. Wild populations were prioritized, but if no primary source on wild

populations existed, captive populations or lab studies were used. A weighted average of body mass was calculated for species in which multiple primary sources were available (to account for factors such as population variation) and reported as the species level body mass, from which a log transformed male to female body mass ratio was calculated.

### **Data Analysis:**

A **phylogenetic tree** of the species in my dataset was created based on 10,000 trees generated by [vertlife.org](http://vertlife.org) (that uses pseudo-posterior distribution) under the phylogeny subsets tab. The analysis was performed using Bayesian approaches to mixed regression models in the statistical software, R (results in Supplementary Materials 1, codes in Supplementary Materials 2). Each model employed to explain variation in multiple paternity was analyzed as binomial distributions in R, using mixed models to account for phylogeny and those species that had multiple populations in my dataset. All analyses for multiple paternity were conducted at the population level; however, some alternative analyses (e.g., female body mass, litter size) were conducted at the species level. Mixed models were applied in these analyses. “Intercept” analyses revealed associations of each of the individual variables and the phylogenetic tree (in matrix form). Further regressions compared proportions of multiply sired litters in the populations (with a binomial distribution) to additional variables such as male social organization (a categorical variable), female body mass (with an exponential distribution), ratio of male to female body mass (log-transformed), and mean litter size (log-transformed).” A variable’s effect on multiple paternity was considered important if the lower and upper bound of the confidence intervals did not overlap zero because there are no p-values for significance in these analyses. Multiple paternity was considered to have a phylogenetic signal if lambda value

was similar to the value of body mass in relation to phylogeny, since it is known to have a phylogenetic signal.<sup>46,47</sup>

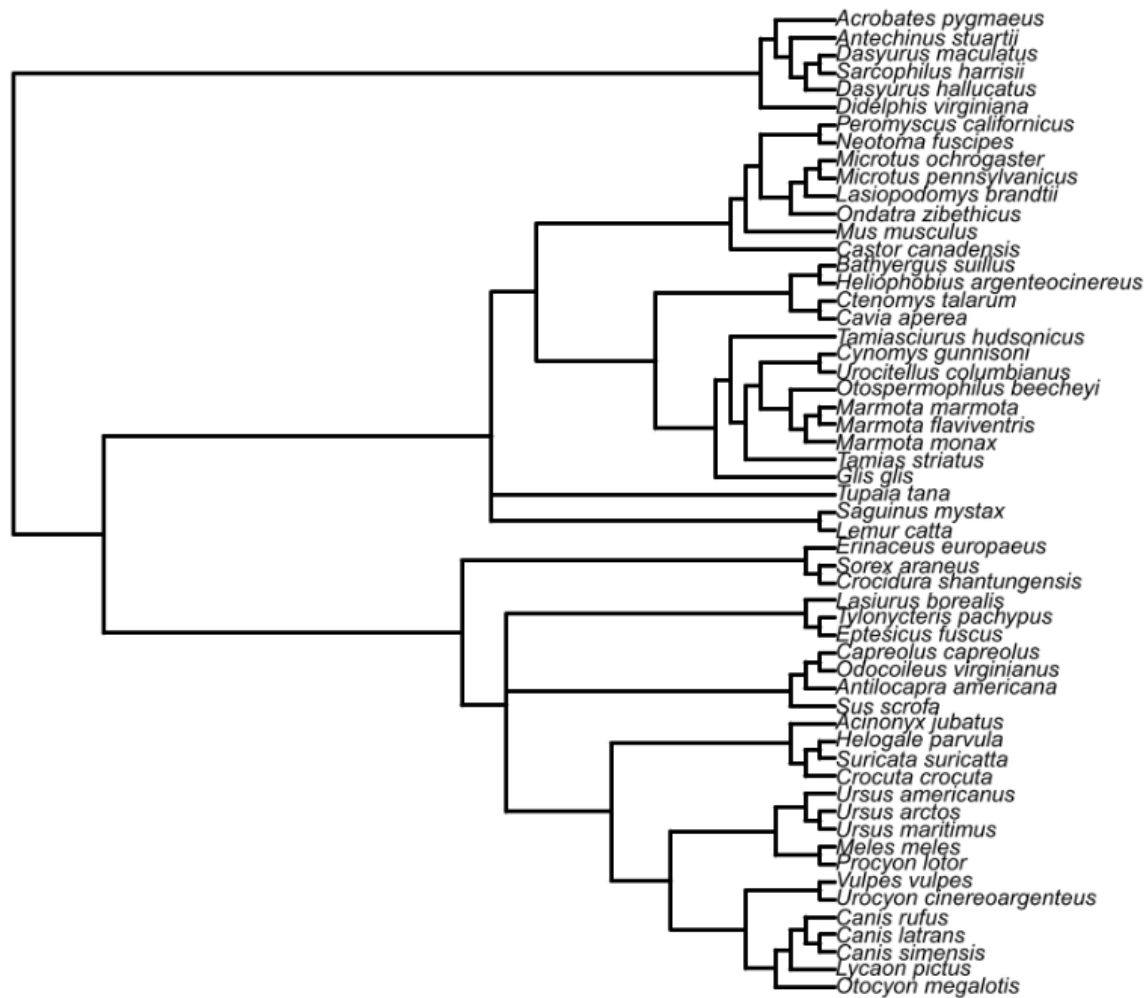
### ***Results:***

The literature search from Web of Science yielded 321 publications, and with the two additional studies,<sup>27,28</sup> resulted in 93 species with multiple paternity data. Of these 93 species, 56 species in 10 therian orders had both multiple paternity data and social organization data. These 56 species were used for the analysis and consisted of 97 populations (2 of which were the same population studied at two different years by different publications, which was therefore treated as 4 populations; Appendix 1) (Table 1). The phylogenetic tree for the 56 species is shown in Figure 2. Each species has data on the proportion of litters with multiple paternity, mean litter size, male to female body mass ratio, deviation from main social organization, and male social unit summarized by order in Table 1. Species level and population level data is available in Appendix 1. The overall mean percentage of multiple paternity across all the mammalian male social units was 0.39 (Table 4).

### **Is there a phylogenetic signal for body mass and multiple paternity?**

Body mass has been shown to be correlated to phylogeny<sup>46,47</sup>, so the body mass data of the 56 species was analyzed in relation to their trimmed phylogenetic tree. This value was then used to determine if multiple paternity had a phylogenetic signal as well. The lambda value for body mass was 0.81, which fell between the lower and upper bounds (0.47-0.97). This lambda value indicates the value of correlation with the phylogenetic tree since body mass is known to correlate with phylogeny. The lambda value for multiple paternity was 0.31, which fell between the lower and upper bounds (0.29-0.67). Since 0.31 is not close to 0.81, the lambda values

indicate that multiple paternity was weakly associated with the phylogenetic tree. Based on these observations, phylogenetic signal is statistically removed in subsequent analyses.



**Figure 2:** Trimmed consensus phylogenetic tree of the 56 species included in this study.

**Table 1: Summary of data across mammalian orders in this study.** In parenthesis under order and male social units, is the number of species (n). The average multiple paternity, mean litter size, body mass ratio (males to females), and deviation from main social organization (SO) is the average of all species in that order. In parentheses is the range of the values in the given column for that order.

<b>Orders (species)</b>	<b>Avg. Multiple Paternity</b>	<b>Avg. Mean Litter Size</b>	<b>Avg. Body Mass Ratio</b>	<b>Avg. Dev. from MainSO</b>	<b>Male Social Units (species)</b>
<b>Artiodactyla (4)</b>	<b>0.29</b> (0.15-0.44)	<b>2.88</b> (2.00-5.43)	<b>1.19</b> (1.11-1.32)	<b>25.24</b> (0.0-57.1)	<b>Solitary (2), MF (1), SexSpecificGroup(1)</b>
<b>Carnivora (16)</b>	<b>0.31</b> (0.0-0.86)	<b>3.27</b> (1.43-6.00)	<b>1.23</b> (0.89-2.10)	<b>16.77</b> (0.0-58.3)	<b>Solitary (4), MF (3), MMF (1), MMFF (8)</b>
<b>Chiroptera (3)</b>	<b>0.64</b> (0.46-0.82)	<b>2.38</b> (2.00-3.13)	<b>0.88</b> (0.83-0.95)	<b>5.38</b> (0.0-16.1)	<b>Solitary (2), MFF (1)</b>
<b>Dasyuromorpha (4)</b>	<b>0.74</b> (0.44-0.93)	<b>5.03</b> (3.11-7.04)	<b>1.44</b> (1.11-1.94)	<b>3.13</b> (0.0-12.5)	<b>Solitary (3), MMFF (1)</b>
<b>Didelphimorphia (1)</b>	<b>0.41</b>	<b>8.71</b>	<b>1.20</b>	<b>29.41</b>	<b>Solitary (1)</b>
<b>Diprotodontia (1)</b>	<b>0.75</b>	<b>3.13</b>	<b>1.07</b>	<b>0.00</b>	<b>MMFF (1)</b>
<b>Eulipotyphla (3)</b>	<b>0.36</b> (0.28-0.40)	<b>4.73</b> (3.00-6.20)	<b>1.04</b> (1.03-1.07)	<b>17.03</b> (0.0-35.3)	<b>Solitary (3)</b>
<b>Primates (2)</b>	<b>0.21</b> (0.20-0.21)	<b>2.00</b> (2.00)	<b>0.97</b> (0.95-0.99)	<b>20.40</b> (2.7-38.1)	<b>MMFF (2)</b>
<b>Rodentia (21)</b>	<b>0.42</b> (0.0-1.00)	<b>4.22</b> (1.50-7.50)	<b>1.13</b> (0.64-1.55)	<b>16.72</b> (0.0-64.6)	<b>Solitary (10), MF (3), MFF (3), MMFF (5)</b>
<b>Scandentia (1)</b>	<b>0.67</b>	<b>2.00</b>	<b>1.00</b>	<b>7.14</b>	<b>MF (1)</b>

### Is multiple paternity associated with variable social organization?

The value of variable social organization in species was represented by their deviation from the species' main social organization (Dev. from MainSO, table 2). The deviation from main social organization did not predict multiple paternity, since the confidence interval passed zero (estimate = 0.00, CI: 0.01, 0.02; Tabel 2).

Predictor	Estimate	Margin of Error	Lower Confidence Interval	Upper Confidence Interval
Dev. from MainSO	0.00	0.01	-0.02	0.02

**Table 2:** Results for variable social organization, represented by deviation from main social organization, in relation to multiple paternity.

### Is multiple paternity influenced by mean litter size and type of male social unit?

Mean litter size did predict multiple paternity since the confidence intervals did not pass zero, and was negatively associated with mean litter size, as the estimate is a negative value (estimate: -3.55, CI: -5.35, -1.88; Table 3). All male social units were compared to MF, so MF does not appear in Table 3 while all other male social units do. The male social unit MMF was the only important male social unit in relation to multiple paternity as the confidence interval did not pass zero (estimate: 3.90, CI: 0.58, 7.37; Table 3). A summary of multiple paternity in each main male social unit showed that the greatest percentage of multiple paternity occurred in MMF (Table 4).

Variables	Estimate	Margin of Error	Lower Confidence Interval	Upper Confidence Interval
<b>Mean Litter Size</b>	<b>-3.55</b>	<b>0.88</b>	<b>-5.35</b>	<b>-1.88</b>
MFF	-0.78	1.00	-2.75	1.16
<b>MMF</b>	<b>3.90</b>	<b>1.75</b>	<b>0.58</b>	<b>7.37</b>
MMFF	0.55	0.69	-0.80	1.92
SexSpecificGroup	-0.58	1.53	-3.70	2.42
Solitary	-0.19	0.68	-1.51	1.17

**Table 3:** Results for mean litter size and male social units in relation to multiple paternity. Significant associations are bolded.

Social Organization (species)	Mean Multiple Paternity
<b>MF (8)</b>	0.375
<b>MMF (1)</b>	0.857
<b>MMFF (17)</b>	0.420
<b>SexSpecificGroup (1)</b>	0.296
<b>Solitary (25)</b>	0.377
<b>Total (56)</b>	0.390

**Table 4:** Mean multiple paternity for each male social unit. Species number in parentheses (n).



### Is multiple paternity influenced by degree of sexual size dimorphism?

The measure of sexual size dimorphism is represented by male to female body mass ratio. The body mass ratios did not predict multiple paternity since the confidence interval passed zero (estimate = -1.80, CI: -6.57, 3.10; Table 5).

Predictor	Estimate	Margin of Error	Lower Confidence Interval	Upper Confidence Interval
Body Mass Ratio	-1.80	2.50	-6.57	3.10

**Table 5:** Results for sexual dimorphism, represented by body mass ratio of males to females, in relation to multiple paternity.

#### *Discussion:*

Evolutionary relationships, variable social organization, and sexual size dimorphism comparisons were not found to be important effectors of the occurrence of multiple paternity. Litter size and one type of male social organization (MMF) were found to be important effectors of the occurrence of multiple paternity.

Litter size and multiple paternity were expected to have a relationship with one another, but the negative trend between them was surprising. This is because multiple paternity and mean litter size has been reported as positively correlated, albeit weakly so, in mammals<sup>13</sup> and reptiles.<sup>31</sup> This negative trend could be explained by the mate guarding hypothesis, where males (typically) defend females for exclusive breeding rights,<sup>2</sup> reducing the number of other males available to sire a female's litter. Within a population, successful mate guarding could lead to a lower percentage of multiple paternity if there is a reduced number of available males to a female. Multiple paternity could also be affected by the number of females that a male is defending as the more females a male tries to mate guard the less effective mate guarding might

become. The male body condition would determine how successful a male is at mate guarding or a male's social status might affect who has mating rights with who. One subsequent way studies could determine the success of mate guarding could be by recording the number of females with litters per social unit as a more successful male at mate guarding might have more females he is reproducing with. Alternatively, this negative trend between mean litter size and multiple paternity could be further analyzed using a more holistic model that includes all variables affecting multiple paternity simultaneously (Figure 1), as opposed to the comparison of multiple paternity with mean litter size and male social organization (Table 3).

Regarding male social organization, I hypothesized that multiple paternity would be greatest in multimale multifemale groups, such as MMFF. Since MMF was the only male social unit as an important effector of multiple paternity, this hypothesis was supported because it was a multimale group, but it was not a multifemale group as it is a single female group. MMF supported my hypothesis that multimale groups were important, but that fact that MMF was important and MMFF was not, I was surprised because only male groups with a single female, not multiple females, was important to multiple paternity. It is logical that in a multimale single female group, multiple males could mate with a single female and thus increase the percentage of offspring with multiple paternity in a litter. In contrast, among multimale multifemale groups, the number of individuals in a group might be too great, providing so many mating opportunities that there is no longer an effect on the occurrence of multiple paternity. It is important to note however, that MMF had a small sample size ( $n=1$  species), which is too small to analyze for statistical significance. Sample size could be improved by decreasing the categories of social units by combining all multimale groups (MMF, MMFF) into one category and all single male (MF, M) groups into another, to increase statistical power.

As for the non-important comparisons, variable social organization was not found to affect multiple paternity and did not support my initial hypothesis that greater multiple paternity would occur in species with greater variable social organization. Variable social organization could not be important to multiple paternity if the mating system is not affected by social organization, or possibly because other social systems, such as social structure, are affecting the social organization and/or mating system instead. Social structures include hierarchies among animals, which may give some individuals in a group exclusive breeding rights<sup>2</sup> that could in turn effect the percentage of multiple paternity within litters.

Sexual size dimorphism was not important in affecting multiple paternity and did not support my hypothesis that multiple paternity would decrease with increasing ratio of male to female body mass. Sexual selection may not be a major driver of multiple paternity in these 56 therian mammal species, or the metric of body mass may not capture the effects of sexual selection. Sexual dimorphism can also be expressed as morphological differences like skull size<sup>32,33</sup> or anogenital distance.<sup>34,35</sup> There are also alternative mating tactics, such as sneaker males or sperm competition, that cheat the exclusivity of large dominant breeders. Alternative mating tactics are often reported in invertebrates and fish<sup>36</sup> but have also been reported in some mammals.<sup>37,38</sup> Lastly, no phylogenetic signal was detected related to the frequency of multiple paternity litters. This could be due to a small sample size (n=56 species) out of the more than 6,000 extant mammalian species.<sup>26</sup> In researching why phylogeny was not important, I learned that behavioral traits often show less phylogenetic signal than other traits, such a body size.<sup>39</sup> Behavioral traits might not be defined by evolutionary relationships alone, perhaps due to the complexity of animal behavior and behavior might be learned traits rather than inherited traits through genetics.

Regarding the interrelatedness of animal social systems framework,<sup>1</sup> this study's results did not fully support the hypothesis that social systems are interrelated. My variables of male social organization and variable social organization are within the framework of social organization, which could influence the mating system, as represented by multiple paternity. On one hand, it seemed that male social organization may be an important effector of multiple paternity, but on the other hand, variable social organization was not. This is one of the first studies that tests the relationship between social systems, but it only weakly supports the idea that all aspects of the social system framework are interrelated. More studies need to be conducted on the interaction among social systems to reach a determine their degree of interrelatedness in various animal clades. The metrics employed in this study may not capture the interrelatedness of the social systems, and as mentioned above, this study could be changed to improve its statistical power.

In the future, it would be beneficial to use different forms of analysis, such as a multivariate model that simultaneously analyzes all variables affecting multiple paternity. Exploring different levels of analysis could also provide new insights, e.g., examining differences between species and population level studies, or looking for trends across all mammals, rather than within individual orders, as has been done with sexual size dimorphism.<sup>24</sup>. There could be other variables that may influence the degree of multiple paternity, including environmental variation or mating season length. Environmental data such as rainfall is an indicator of food availability, which could influence animal social systems. Breeding season length may determine how many males mate with a female during her oestrus period. During a short breeding season, there is greater overlap in the timing of oestrus among females within a

population, which likely limits the ability of males to monopolize a female for exclusive copulation.<sup>40</sup>

The results of the present study highlight the need for more field studies that collect natural history data on mammals. In the wake of climate change, animals adjust their behavior<sup>41</sup> and face high extinction rates.<sup>42</sup> Behavioral ecology studies can help inform conservation efforts by bettering our understanding of animals' life histories, including their social systems. It would be advantageous to study animal populations while they exist and under the most natural conditions possible before populations are dramatically affected by climate change.

My study included 56 mammalian species, which is only a small fraction of the more than 6,000 extant mammalian species.<sup>26</sup> A larger sample size would increase the statistical power of an analysis such as this one, but there is a limited number of studies on wild populations, and an even more limited number of species with primary sources providing reliable information on their social systems. For example, I had 93 species with mating system data, but only 56 of those also had social organization data. For the species I included in my final dataset, I only accepted high quality data. Though this resulted in a smaller dataset, but I continue to prefer the use of high-quality data over larger less accurate datasets.<sup>43</sup> This is because quality data has helped inform that the genetic mating system is different from the observed mating system and complex.<sup>7,8,9,10</sup> Also quality data helped clarify the assumption that all populations of a species shared the same social organization by showing there is variation in social organization across populations. I suggest future studies include social systems data in their models of multiple paternity, but this requires long-term studies, since interactions and relationships among individuals are complex and vary across time. Not only does the field of behavioral ecology need more natural history studies, but we also need more long-term studies<sup>44,45</sup> to provide complex

data on social structure. The continued use of genetic data in studies can also inform the mating system with measurements like multiple paternity.

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