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Monogamy and polyandry: their roles in neonatal survival and the inclusive fitness of the male and female parents

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ABSTRACT: Sexual selection theory postulates that males will compete with one another to inseminate the largest number of females possible. The ability of the male to be a successful polygynist allows him to pass on his genetic information to a large number of progeny. Thus, it is difficult to explain males who do not seek out more than one partner per breeding season, males who stay with a single partner for a long period of time (monogamy), and males who share a single female with several other males (polyandry). The mate-guarding hypothesis maintains that monogamy may be adaptive. A female left by one male would acquire another partner, whose sperm would then fertilize her eggs. Thus, it is in the best interest of the first male to remain with his partner if receptive females are scarce. Behavioural ecology is currently undergoing a paradigm shift, with the traditional concepts of the choosy, monogamous female and the coadapted gene complex increasingly giving way to the realization that sexual reproduction engenders conflicts, promotes polyandry, and thereby provides females with a cryptic arsenal of postcopulatory processes with which to safeguard their investment in large, costly eggs. This paper therefore revealed findings of researches about the roles of monogamy and polyandry in neonatal survival and the inclusive fitness of the male and female parents.

Keywords: Inclusive fitness, monogamy, neonates, parents, polyandry, reproduction

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INTRODUCTION

Many social groups, as they relate to sexual reproduction, have been identified in animals generally. Such social groups include monogamy, polygamy, polygyny, polyandry, polygynandry and, promiscuity (Gillespie and Myers, 2004: Myers and Armitage, 2004; Aro and Adejumo, 2010). These sexually related groups in the field of sociobiology and behavioural physiology are termed mating systems. The main reason underlying the evolution of these different mating systems is to achieve a favourable inclusive fitness which will ensure that more of their offspring survive to the reproductive age and to make sure that as many as their individual genetic traits enter the general population gene pool in order to guard against their extinction (Dawkins, 1998). Aro and Adejumo (2010) opined that the male animal with a higher capacity for production of millions of gametes within a short period will therefore benefit more if it is able to mate with as many matured females as possible. That is why polygamy and promiscuity are advanced as the more common and advantageous mating system

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among male mammalian species (Coppersmith and Lexington, 1991). The female animals on the other hand with the exemption of the fish and other aquatic creatures, produce relatively few gametes and the tendency in this case- is a phenomenon called the female choice. In this case, a female animal looks for the best quality male to mate with to ensure the continued survival of her offspring in the face of competition from other living organism (Coppersmith and Lexington, 1991). The theory of inclusive fitness brings to the fore the parental investments to neonatal survival in which both parents weigh both the costs and benefits to it in such an investment strategy (Aro and Adejumo, 2010). Polygamy (polygyny) and promiscuity have been known to reduce the attention the male would have had for its offspring, as its preoccupation in these two forms of mating system is to mate with as many females as possible to multiply its genetics traits in the population gene pool at a very rapid rate.

These two mating systems would therefore lower the male's parental investment (Rubenstein, 1980). Monogamy and eusociality on the other hand will reduce the number of offspring sired by the male but will at the same time improve its inclusive fitness since animals in social groups have been known to collaborate with their female mates to nurture the offspring to adulthood (Benshoof and Thornbill, 1979). The general view amongst researchers in the field of reproductive behaviour is that monogamy and polyandry are a rarity in mammals (Dawkins, 1998). A number of potential benefits have been suggested to explain how the increased mating costs arising from polyandry are compensated and, thus, why it may pay females to mate with more than one male even though a single ejaculate typically assures fertilization (Jennions and Petrie, 2000; Hosken and Stockley, 2003). These benefits are often classified as either non-genetic or genetic and may increase female longevity (non-genetic), offspring numbers (non-genetic and genetic) and offspring quality (genetic) (Hosken and Stockley, 2003).

While there is now increasing evidence that both types of benefits exist and contribute to the maintenance of polyandry (Hosken and Stockley, 2003), non-genetic benefits have been suggested to represent the most likely evolutionary origin of polyandry (Yasui, 1998). In resource-based mating systems, non-genetic benefits seem obvious through e.g. nutritious courtship gifts or paternal care. However, few studies show that females can also gain non-genetic benefits in non-resource-based mating systems, where males provide nothing but sperm.

Avoidance of offspring loss caused by infanticide has been suggested as a subtle non-genetic benefit of polyandry. Males of numerous mammal species, but also of other vertebrate and of invertebrate taxa, have been observed to kill dependent young that they have not fathered (commonly seen among lions)(Van Schaik and Janson, 2000). Type of parental care is often associated with the type of mating system. This review thus attempts to bring to the fore, two mating systems: monogamy and polyandry vis-a-vis their roles in the survival of the neonates and the inclusive fitness of both the male and the female parents.

MATING SYSTEM

In sociobiology and behavioural physiology, the term mating system is used to describe the ways in which animal societies are structured in relation to sexual behaviour. The mating system specifies which males mate with which females, and under what circumstances. The following are some of the mating systems generally recognised in humans and other animals:

MONOGAMY: Single male and female pair during a breeding season

POLYGYNY: Single male may mate with more than one female during a breeding season.

POLYANDRY: Single female may mate with more than one male during a breeding season. Males mate with a single female.

PROMISCUITY: Both males and females may have more than one mate during a breeding season.

Animal Monogamy

Monogamy is one of several mating systems observed in animals. The amount of social monogamy in animals varies across taxa, with over 90% of birds engaging in social monogamy while only 7% of mammals are known to do the same (Burnham and Phelan, 2001). With birds, the locomotion method means the sharing of genetic material with non-local sources is far less difficult, and reproduction is far more successful when both the male and the female contribute food resources to the offspring. The incidence of sexual monogamy appears quite rare in other parts of the animal kingdom (Dawkins, 1998). It is becoming clear that even animals that are socially monogamous engage in extra-pair copulations. An example of this was seen when scientists studied red winged blackbirds. These birds are known for remaining in monogamous relationships during the course of mating season. During the course of the study, the researchers gave a few selected males vasectomies just before mating season. The male birds behaved like they do every season, establishing territory, finding a mate, and attempting to make baby birds. Surprisingly, the female birds whose partners were surgically altered still laid fertile eggs that hatched into nestlings which were cared for by their sterile adopted fathers (Burnham and Phelan, 2001). This showed the willingness of the female birds to go outside of the social monogamy for breeding purposes.

Varieties of monogamy in animals

Recent discoveries have led biologists to talk about the three varieties of monogamy: social monogamy, sexual monogamy, and genetic monogamy. The distinction between these three is important to the modern understanding of monogamy.

Monogamous pairs of animals are not always sexually exclusive. Many animals that form pairs to mate and raise offspring regularly engage in sexual activities with partners other than their primary mate. This is called extra-pair copulation (Ågren *et al*., 1989). Sometimes these extra-pair sexual activities lead to offspring. Genetic tests frequently show that some of the offspring raised by a monogamous pair come from the female mating with an extra-pair male partner (Solomon *et al*., 2004). "Social monogamy refers to a male and female's social living arrangement (e.g., shared use of a territory, behaviour indicative of a social pair, and/or proximity between a male and female) without inferring any sexual interactions or reproductive patterns. In humans, social monogamy equals monogamous marriage. Sexual monogamy is defined as an exclusive sexual relationship between a female and a male based on observations of sexual interactions.

Finally, the term genetic monogamy is used when DNA analyses can confirm that a female-male pair reproduces exclusively with each other. A combination of terms indicates examples where levels of relationships coincide, e.g., sociosexual and sociogenetic monogamy describe corresponding social and sexual, and social and genetic monogamous relationships, respectively." (Reichard, 2003). Whatever makes a pair of animals socially monogamous does not necessarily make them sexually or genetically monogamous. Social monogamy, sexual monogamy, and genetic monogamy can occur in different combinations. When applying these terms to people, it's important to remember that social monogamy does not always involve marriage. A married couple is almost always a socially monogamous couple. But couples who choose to cohabit without getting married can also be socially monogamous.

Socially monogamous species are scattered throughout the animal kingdom: A few insects, a few fish, a large number of birds, and a few mammals are socially monogamous. There is even a parasitic worm, *Schistosoma mansoni* that in its female male pairings in the human body is monogamous (Beltran and Boissier, 2008). The diversity of these species with social monogamy suggests that it is not inherited from a common ancestor but instead evolved independently in many different species. The occurrence of social monogamy in vertebrates is directly related to the presence or absence of oestrus; the trait in which the female is sexually excited during ovulation. Oestrus is a trait confined to placental mammals; eutherians. This explains why social monogamy is so rare in these mammals since the oestrus female will generally mate with any proximate male. Birds, which are notable for a high incidence of social monogamy, do not have the trait of oestrus (Beltran and Boissier, 2008).

Extra pair matings in "monogamous" species

In many (most) apparently monogamous species it is not uncommon for mating to occur between individuals that are not nominal mates. These are termed extra-pair matings (Owens and Hartley, 1998). Extra-pair mating is done surreptitiously when the nominal mate is not in attendance.

The advantage enjoyed by males of extra-pair matings in monogamous species has revealed that if males are successful in fertilizing eggs through extra-pair matings there will be a large benefit to his fitness because he will obtain reproductive output without having to invest in parental care (Owens and Hartley, 1998; Aro and Adejumo, 2010).

Monogamy as a best response

In species where the young are particularly vulnerable and may benefit from protection by both parents, monogamy may be an optimal strategy (Aro and Adejumo, 2010). The selection factors in favour of different mating strategies for a species of animal, however, may potentially operate on a large number of factors throughout that animal's life cycle. For instance, with many species of bear, the female will often drive a male off soon after mating, and will later guard her cubs from him similar to that of other animals after they are born. It is thought that this might be due to the fact that too many bears close to one another may deplete an area of food resources for the relatively small but growing cubs. Monogamy could be social but rarely genetic. Thierry (2006) argued that monogamy could result from conflict of interest between the sexes called sexual conflict. Organized from territorial defense and mate guarding, monogamy appears as a response of male for the control of female sexuality, but exclusive monogamy would be rare and the biological evolution would privilege the diversity of sexual behaviours

Animal Polyandry

In the field of behavioural physiology/ecology, polyandry is a type of breeding adaptation in which one female mates with many males. Another opposite breeding system to this is polygyny in which one male mates with many females (e.g., lions, deer, some primates and many systems where there is an alpha male). A common example of this can be found in the Field Cricket *Gryllus bimaculatus* of the invertebrate order Orthoptera (containing crickets, grasshoppers and groundhoppers). Females in this species will mate with any male close to them, including siblings (Alcock, 2002). Widely shown in frogs (Agile frogs, *Rana dalmatina*), polyandry was also documented in polecat (*Mustela putorius)* and other mustelids. Related to sexual conflict, Thierry (2006) found that possible explanations for polyandry include mate competition and inbreeding avoidance.

Polyandry also occurs in some primates such as marmosets, mammal groups, the marsupial genus' *Antechinus* and bandicoots, around 1% of all bird species, such as jacanas, insects such as honeybees, and fish such as pipefish. In effect polyandry will reduce the effective population size of a given closed population. Aro and Adejumo (2010) reported an average pre-weaning survival rate of 37.95% in polyandry as opposed to 94.44% in monogamy in their study with albino rats.

Types of Polyandry

There are two major types of polyandry: simultaneous and sequential. Simultaneous polyandry is when the female controls a very large territory. In this territory, the female has multiple smaller nesting territories with different males. The female mates with all males simultaneously, keeping control of the smaller territories. Another form of simultaneous polyandry, cooperative simultaneous polyandry, is when the female only has one nesting area where she mates with multiple males producing a clutch of eggs of mixed parentage with all males contributing to the eggs (Alcock, 2002). Sequential polyandry, the most common form, is where the female mates and produces a clutch of eggs with one male, then leaves the male to incubate and rear the eggs while moving on to another male in a different nesting territory. Here, the female moves from one male to another, leaving the male in full responsibility of the eggs instead of sharing the responsibility (Alcock, 2002).

General Benefits of Polyandry

There are many genetic benefits of polyandry. The first being fertility insurance. This hypothesis suggests that by mating with multiple males, the female is guaranteed to fertilize all of her eggs. The multiple partners potentially make up for one male that may not be able to fertilize the eggs. The good genes hypothesis states that the females have multiple mates because she is in search of the male that will pass along the best genes to her offspring. By finding this male, the female is increasing the survival rate of her offspring. The genetic compatibility hypothesis is one that suggests that the female finds multiple mates in order to find the most compatible genetic match for her eggs. While looking for a good match, she is also eliminating the males that are least compatible with her eggs (Alcock, 2002). The material benefits of polyandry can be seen through three hypotheses. The more resource hypothesis suggests that the more mates the female has, the more males she has to care for her clutch. The better protection hypothesis states that by having multiple partners, the female is better protected from predators. The infanticide reduction hypothesis is one that claims that since the female has multiple males, she has a lower infanticide rate because the males do not know which progeny belong to them. This prevents the males from killing other male's young. Although some infanticide occurs between females and other female's eggs, it is minimal among males (Alcock, 2002).

The effects of Monogamy and Polyandry on weight gain/body size and weight/size of the reproductive organs

Morphometric and gravimetric measurements of the male reproductive organs of livestock species have been shown to provide some of the yardsticks for assessment animals' reproductive efficiency and overall neonate fitness (Bielli *et al*., 1999; Aro and Adejumo, 2011). This is reflected in the depedency of functional capacity of the gonads for reproduction on their shapes, sizes and weights (Aro and Adejumo, 2011). Table 1 compared the weight change in monogamous and polyandrous male rats. The authors reported that total weight change for the period showed that monogamous group had a better weight change over their polyandrous group counterparts. This significant weight gain in the monogamous group might not be unconnected with the hierrarchy or dominance that was absent among males in this social group but which played itself out in the polyandrous group in which the alpha male depressed the growth rate of the subordinate males in the group (Aro and Adejumo, 2011). This observation showed that monogamy would possibly promote large sized males as opposed to polyandry.

Table 2 showed a comparison between the weight of the reproductive organs in monogamous and polyandrous male albino rats. The absolute organ weights revealed that both the combined and separate weights of the testicles were heavier in the monogamous males than in polyandrous males. The authors opined that this could be as a result of the higher live weight of the monogamous males. Thus, there seemed to be a positive correlation between the live weight and testicular weight in animals which is equally correlated to the probabilities of daughter of such sires reaching puberty at significantly ealier ages, hence an increase in the inclusive fitness of such males.

The polyandrous males had heavier epididymides between the two social groups. It was therefore observed that the testicular and epididymal sizes were inversely related in the two groups. The relatively larger epididmides in polyandrous male despite their smaller body size and testicular weight might be as a result of the frequency of copulation with the females in this group which have increased the capacity of the epididymides for sperm storage in order to meet with this exigency (Aro and Adejumo, 2011). The weight of the seminal vesicles was higher in the monogamous than in polyandrous males. The scrotal circumference and by extention testicular size has been shown to be positively correlated with seminal vesicles and that bulls with larger circumference can be expected to sire calves with moderate birth weight and above average growth rate and have male offspring with larger testicles and daughters with better milking qualities that reach puberty at an ealier age (Smith *et al*., 1989). The work of Aro and Adejumo (2011) thus revealed that monogamy could promote bigger body size, heavier seminal vesicles and bigger testes/testicles. Polyandry could result in morphological adaptation for bigger epididymides to cope with higher frequency of copulation by the males in this social group.

Table 3 showed the reproductive performance of monogamous and polyandrous group of wistar rats in a study carried out by Aro and Adejumo (2010). These figures suggest that monogamy significantly improved the reproductive parameters, indicating that the monogamous group probably had a better inclusive fitness than its polyandrous counterpart. The authors also reported that inclusive fitness is a factor of the parental investment on their neonates, which ensures better prospects for them to survive to reproductive age. The better pup weight at 5 days of age for the monogamous female group and significantly (P<0.05) superior weaning weight for the group (36.68g versus 31.43g) and the number of pups that survived to the weaning age (21 out of 22 for the monogamous compared to 17 out of 47 for the polyandrous groups) lends credence of this assertion (Aro and Adejumo, 2010).

Table 1: Weight Change (g) of Monogamous and Polyandrous Males Albino Rats

Parameters	Monogamous group	Polyandrous group	+SEM
Initial weight	65.12	64.22	1.40
Final weight	257.32[a]	232.38[b]	5.98
Total weight change for the period	192.20[a]	168.16[b]	3.36
Daily weight change for the period	1.72	1.50	0.12

[a, b] = Means in the row but with different superscripts are significantly different (P<0.05)

Source: Aro and Adejumo (2011)

Table 2: Absolute Body and Organ Weight (g) of Monogamous and Polyandrous Male Albino Rats

Parameters	Monogamous group	Polyandrous group	+SEM
Number of males	5.00	5.00	0.00
Body weight	257.32[a]	232.38[b]	5.98
Weight of left testis	1.00	0.83	0.25
Weight of right testis	1.10	0.74	0.18
Combined testicular weight	2.10	1.58	0.38
Weight of left epididymis	0.40	0.56	0.10
Weight of right epididymis	0.43	0.57	0.06
Combined epididymal weight	0.83	1.13	0.11
Weight of seminal vesicle	1.33	0.86	0.12

[a, b] = Means in the row but with different superscripts are significantly different (P<0.05)

Source: Aro and Adejumo (2011)

Table 3: Reproductive performance of monogamous and polyandrous groups of Wistar rats

Reproductive Parameters	Monogamous group	Polyandrous group	±SEM
Average number of days to 1st conception	109.00[a]	99.33[b]	12.19
Average number of days to 1st parturition	130.00[a]	120.33[b]	12.19
Average parity for the trial period(16 weeks)	1.00	1.67	0.41
Litter size for the trial period (16 weeks)	4.40	5.67	1.12
Average birth weight (g)	5.33	5.82	0.10
Pups weight at day 5(g)	9.31	9.42	0.07
Weight gained/ pups for the 1st 5 days (g)	3.77	3.60	0.17
Average number of pups born/female	4.40[b]	9.40[a]	3.14
Total Number of pups for the trial period(16 weeks)	22.00	47.00	-
Total number of pups weaned	21.00	17.00	-
Average number of pups weaned/female	4.16[a]	3.57[b]	0.75
% pre-weaning survival	94.44[a]	37.95[b]	7.28
Average weaning weight (g)	36.68[a]	31.43[b]	0.69

a.b= means in the same row with different superscripts are significantly ($P<0.05$) different

Source: Aro and Adejumo (2010)

CONCLUSION

Monogamy is exceptionally rare in mammals. The mate-assistance hypothesis suggests that males who make a parental investment in their young are usually monogamous. Although fewer than ten percent of male mammals give substantial parental care, most of these exceptional males are monogamous. Males who make a large parental investment increase the likelihood that their offspring will survive and pass on their genetic information, thus it serves the same genetic purpose as the paternal animal not making an investment in his offspring, trying to fertilize as many females as possible, and having many litters with low survival rates. Females often mate with several males (polyandry) before producing offspring. Even when males provide no material benefits, polyandry can enhance offspring survival. This enhancement is widely attributed to genetic benefits that arise whenever paternity is biased towards males that sire more viable offspring. By mating with many males, females may increase the probability of their eggs becoming fertilized by the sperm of genetically superior or compatible male. Thus, certain genes or gene combinations should result in polyandrous females producing offspring of higher fitness than monandrous females. "Good sperm" hypothesis predicts that sperm that are more successful in competition for fertilising the eggs are also more effective in producing viable offspring. Polyandry can also be an efficient strategy for increasing offspring survival, probably via the avoidance of male infanticide. In a closed system however, these gains could be obviated by social conflicts which may ensue among the competing male for the attention of the female and this may distract her attention from adequate mothering care of the neonates thus reducing the survival of the neonates to the reproductive stage and possibly her own inclusive fitness. Since maternal effects cannot be entirely excluded, therefore more studies are required to validate the maternal effects and parental investment as they affect the offsprings survival.

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