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The effect of social groups on reproductive performance of Wistar rats

S.O. Aro[1] and D.O. Adejumo[2].
[1]*Department of Animal Production and Health, Federal University of Technology, Akure, Ondo State, Nigeria.*
[2]*Department of Animal Science, University of Ibadan, Ibadan, Nigeria.*

E-mail Address: sambolaro@yahoo.co.uk

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1 SUMMARY

Two social groups of rats (monogamous and polyandrous) were studied in a sixteen-week long experiment to evaluate their effects on reproductive and behavioral responses in the Wistar strain of rats. Thirty albino Wistar rats (20 males 10 females) with an average initial weight of 60.22 ± 4.8g were used for the study. The rats were assigned to two social groups comprising 5 males and 5 females for the monogamous group and 15 males and 5 females for the polyandrous group. The result showed that polyandry promotes a faster and statistically significant ($p<0.05$) conception and parturition rates, higher litter size (5.67 versus 4.40), higher number of pups born per female (9.40 versus 4.40) and total number of pups born (47 versus 22). The two social groups recorded reproductive success but parental investment to the survival of the neonates was better in the monogamous group. The monogamous group also had a better inclusive fitness as inferred from a greater number of offspring that survived to the weaning age and a significantly better weaning weight (94.44% versus 37.95% and 36.68g versus 31.43g), respectively. It is concluded that though polyandry results in better short-term reproductive optimality as depicted by shorter length of periods to first conception and parturition and significantly higher number of pups per females, these merits were obviated by a correspondingly poorer weaning weight, lower pre-weaning survival rate and an equally smaller number of pups weaned per female rat in this social group. Polyandrous grouping probably resulted in a faster rate of physiological conditioning of the female rats towards sexual maturity. In addition, social stress as encountered in the polyandrous group could significantly lower reproductive success of rats and probably of any mammalian species.

2 INTRODUCTION

Many social groups, as they relate to sexual reproduction, have been identified in rats and other rodents and in animals generally. Such social groups include monogamy, polygamy, polygyny, polyandry, polygynandry and, promiscuity (Gillespie & Myers, 2004: Myers & Armitage, 2004). Dawkins (1998) wrote that monogamy is relatively rare among mammals while polyandry is unknown, but that among birds, monogamy is common and polyandry is also known to occur. Wilson and Daly (1992) opined that fuller understanding of human mating behaviors (which also include monogamy, polygamy and polyandry) is better achieved by studying the mating behaviors of birds endowed with a wide range of mating behaviors and systems.

Some species of birds like the dunnocks (*Prunella nodularis)* are equipped with within species variation in their mating system as human beings to the extent of becoming

polygynandrous in which both sexes share mates among themselves (Davies, 1992).

At the extreme of these, mating behaviors in animals is eusociality, easily typified in mammals by the East African naked mole rat. Its social grouping has been stratified into the social caste system in which only the alpha male and female breed while the other males and females are engaged in altruistic work for the overall survival and success of the colony (Jarvis, 1981).

The main reason underlying the evolution of these different mating systems is to achieve a favorable 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). 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 among male mammalian species (Coppersmith & 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 organisms (Coppersmith & 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. 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 & Thorn bill, 1979).

The general view amongst researchers in the field of reproductive behaviour is that monogamy and polyandry are a rarity in mammals (Dawkins, 1998). The focus of this research was to investigate these two social groups and to unravel the costs and benefits associated therein as they relate to fertility rates, parental investment and neonatal survival using the Wistar strain of rats as the animal model.

3 MATERIALS AND METHODS

3.1 Study site: This study was carried out in the Rat House (a unit designated for all experiments on rats) of the Department of Animal Production and Health of the Federal University of Technology, Akure, Nigeria. The experimental site is located 5°12/E, 7°15/N, in the equatorial rain forest belt of Nigeria with a bimodal rainfall pattern. The research was carried out between March and July 2008.

3.2 Experimental animals: Thirty albino rats of the Wistar strain, between five to six weeks old were obtained from the Faculty of Veterinary Medicine, University of Ibadan. The rats were housed in rectangular cages constructed of solid timber frame at the four corners and wire netting on all sides. Two cages measuring 200cm x 100cm x 45 cm (length x width x height) were constructed. Each cage was partitioned into five compartments measuring 100cm x 40cm x 45cm. These cages were raised on six legs 60cm above the cemented floor.
The rats were randomly allotted to the two treatment groups i.e. the monogamous group and polyandrous group with each group housed separately in each of the two cages. The

monogamous group, made up of 5 male and 5 female rats was replicated five times with a pair of a male and a female rat occupying each of the five compartments. The polyandrous group was made up of 15 males and 5 females. This group was also replicated five times with three males and a female occupying each compartment. Each compartment was equipped with a detachable feeder and drinker to permit easy evacuation of the ort and refilling with fresh feed and water every day.

The perforations in the wire netting allowed the faecal pellets to fall to the ground directly thus reducing the risk of infestation with intestinal parasites. The rats were supplied *ad libitum* with feed and water. The rats were kept in these cages for one week to acclimatize with their new environment before the commencement of data collection.

3.3 Data collection: Data were collected on reproductive parameters like average number of days to first conception and parturition, litter size, birth weight, percentage pre-weaning survival of pups and average weaning weight of the pups. Behavioral studies (Dawkins, 1998) of the rats in the two treatments of the groups were also carried out in order to ascertain the peri-natal and maternal behaviour of the females, paternal behaviour of the males to the neonates and parental and neonatal investment on the survival of the young.

3.4 Data analysis: Data on reproductive and behavioral studies were subjected to statistical analysis by testing the difference between two means of independent samples (T-test) using S.A.S (1999) statistical package.

4 RESULTS AND DISCUSSION

4.1 Reproductive Performance: Results of the reproductive performance of the two social groups of rats is presented in Table 1. The average number of days to first conception was significantly shorter ($p<0.05$) in the polyandrous group (99.33 versus 109.00days in the monogamous group). The polyandrous group, by corollary, also had their first litter at a comparatively shorter time interval (120.33 days as opposed to 130.00 days for the monogamous group). The import of this is that polyandrous social grouping probably resulted in a faster rate of physiological conditioning of the female rats towards sexual maturity. It could also have been caused by the combined effect of pheromones and tactile stimulation of the females through more exposure to allogrooming by the males in the polyandrous group. Solomon (1991) conducted similar research on two groups of Prairie Voles differing in age and concluded that the proportion of pairs producing a litter within 60 days was influenced significantly by the age at pairing.

Table 1: 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.

The number of parity per group for the duration of trial averaged 1.00 for the monogamous and 1.67 for the polyandrous group. This clearly showed that some of the females in the polyandrous group gave

birth more than once while those in the monogamous group gave birth only once during the entire period. The females in the monogamous group were able to nurture their offspring without undue molestation and precocious mating advances from the only male in the pair. The polyandrous group was different in that the males' preoccupation was to mate with the only female, which actively commenced on the second day of parturition.

The resumption of post-partum oestrous in rats is supported by the work of Parker (1990) that female rats experience post-partum oestrous 18 hours after giving birth. These precocious mating activities by the males probably left the females deranged as they were caught between meeting the sexual demands of the sexually aggressive males and nursing their pups. Puffer *et al.* (2004) suggested that it is better to place the expecting doe into a separate cage about 5-7 days prior to the commencement of parturition in order to foreclose these males' sexual advances. The frequency of nursing (feeding) and retrieval of the pups was also largely curtailed by the activities of the males, which took turns to mate with the only female. The very short oestrous cycle in rats that comes every four days did not help matters either as the increased sexual engagement by the males continued unabated throughout the lactation period. Because of this, many of the pups in the polyandrous group became unthrifty and died before attaining the weaning age at day 21 after parturition. These observations were in consonance with the work of Owen (1996).

The litter size of the monogamous group averaged 4.40 pups while that of the polyandrous group was 5.67 pups. This revealed that the polyandrous group was more fecund than the monogamous group. The reason for this could be increased harvest of sperm cells by the females of the polyandrous group from their sexually aggressive males than in the monogamous group where one male did the mating. Reddy (2003) reported that some species of rats might engage in polyandry in order to secure more sperms to fertilize their eggs. According to Rubenstein (1980), the polyandrous group could be described as the better reproductive optimizer as adjudged by their higher litter size.

The average birth weights per pups were 5.53 and 5.82g for the monogamous and polyandrous groups, respectively. The polyandrous group gave higher but statistically insignificant birth weight than the monogamous group. Their birth weights were in the range reported previously (Parker, 1990; Nowak, 1999 and Grzimek, 2003).

The weight change for the first 5 days of life for the pups revealed that pups of the monogamous group gained better than those in the polyandrous group (3.77 versus 3.60g). This might have been because of better parental investment in the monogamous group (Kohl *et al*, 2001). The females of this group suckled, insulated from cold and retrieved their pups unmolested by their males. The males of this group even contributed to the survival of the neonates by helping the dam to retrieve the pups and sandwiching them between their bodies and those of the mother rats to keep them warm. This observation is however at variance with the views of Parker (1990) and Grzimek (2003), who concluded that males of *Rattus norvegicus and Rattus rattus* do not care for their pups. Their observation was however based on observations of these animals in the wild as opposed to the laboratory -controlled conditions of this trial.

The average number of pups born per female was 4.40 for the monogamous group and 9.40 for the polyandrous group, while the total numbers of pups for the sixteen weeks experimental period were 22 and 47 for the respective social groups. This clearly points to the high reproductive prolificacy of the polyandrous group. The average number of pups born per female in the polyandrous group surpassed 8 pups per birth for *Rattus norvegicus* reported by Parker (1990) but was lower than the 12 to 27 pups per birth in naked mole rat (*Heterocephalus glaber*) reported by Jarvis (1981). This high reproductive prolificacy might have been engendered by the kind of competition that ensued among the males of the polyandrous group which Dawkins (1998) aptly called intra-sexual competition, characterized under this study by incessant chasing and fighting among the males for the only available female. Respect for the dominant males in terms of monopoly of mating with the only female was not adhered to as all the males "shared" her amongst themselves and increased the frequency of mating with her to an average value of 8.7 times per minutes in the polyandrous group as opposed to 1.01 times per minute for the monogamous group during the six hours receptive period for the cycling doe.

The average number of pups weaned per female was 4.16 for their monogamous group and 3.57 for the polyandrous group, while the percentage pre-weaning survival of pups was 94.44

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and 37.95, respectively. 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 (Dawkins, 1998). The 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 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 conclusion.

4.2 Perinatal parental behavior: Table 2 shows the perinatal maternal and paternal behaviour of the two social groups of rats. Hostility by the females to their cage mates i.e. the males, graduated from mild in the first day after parturition to none as from the second day in the monogamous group while it ranged from intense to mild and to none for the first, second and third day of parturition in the polyandrous group. The moderate or mild hostility displayed towards the males during the first day of parturition in the monogamous group could be connected with the skeptical attitude by the female that the male might become infanticidal and hence the need to protect her pups from such tendency by the males. D'Amato *et.al* (2006) reported such infanticidal posturing by some male rodents, especially if they are not the sire of the pups.

The domineering attitude of the females towards their male cage mates was not manifested in the monogamous group. The female in this group were not for once observed to cordon off the feeding area for their exclusive use during the perinatal period. This domineering behaviour however progressed from intense to mild and finally to total withdrawal by the females in the polyandrous group for the first three days after parturition. The domineering attitude manifested in the polyandrous group was probably because of the higher ratio of males to female. The more the number of individuals in a social group, irrespective of their sexes, the more the aggression. Barton and Brian (1994) worked on three social groups of mice and reported that the most aggressive group was the triad that housed three mice together.

Table 2: Perinatal maternal and paternal behaviour of Wistar rats in monogamous and polyandrous experimental groupings.

	Day of parturition					
	1		**2**		**3**	
Behavioral parameters	**Mono**	**Poly**	**Mono**	**Poly**	**Mono**	**Poly**
Hostility to cage mate by the doe	mild	intense	none	mild	none	none
Domineering attitude to the cage mate by the doe	none	intense	none	mild	none	none
Biting of cage mate assessing the pups' area by the doe	none	intense	none	mild	none	none
Nursing of the pups by the doe	intense	intense	intense	intense	intense	intense
Retrieval of the pups by the doe	intense	intense	intense	intense	intense	intense
Retrieval of the pups by the buck	mild	none	mild	none	intense	none
Hostility to humans by the doe	mild	intense	mild	intense	mild	mild
Hostility to humans by the buck	mild	none	mild	none	mild	none

Mono = Monogamous group
Poly = Polyandrous group

Biting of the cage mate was not observed in the monogamous group but this behaviour varied from intense in the first day to total cessation by the third day after parturition in the polyandrous group. The need to protect the pups from prospective infanticidal males as proffered by D'Amato *et al* (2006) and increased aggression due to the higher number of individuals per cage (Bartos & Brian, 1994) might explain this behaviour by the females in the polyandrous group.

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The female rats in the two social groups engaged in intense nursing (suckling) and retrieval especially in the first two weeks of lactation but the effort of the polyandrous females was not as successful because of the incessant disturbance from the males. In this aspect, more of the parental investment lies on the females of the *Rattus norvegicus* and they have been known to actively involve in this to the extent of resorting to cooperative breeding and allo-mothering (Myers & Armitage, 2004).

Retrieval of the pups by the males was not observed in the polyandrous group but graduated from being mild to being intense in the monogamous group. The male rats of this group not only helped the females to retrieve any straying pup but also helped to keep them warm by crouching over them and sandwiching them between their own bodies and those of the does. They also exhibited mild aggressive behaviour against human interference within the first three days -a behaviour not elicited by the males of the polyandrous group. This behaviour by the males of the monogamous group did not support the observation of Parker (1990) who reported that the males of *Rattus norvegicus* do not participate in parental care.

4.3 Parental and Neonatal Investment: Table 3 shows the parental and neonatal investment in the survival of the pups in the two social groups of rats. The care for the young by the parents showed that a bilateral relationship was established between the monogamous pair in carrying out this duty, unlike in the polyandrous group where this was the exclusive preserve of the doe. All the males in the monogamous group showed that they were ready to invest resources in their offspring. That is why they were able to establish a sexual pair bond or monogamy. The males however had the option as we observed in the polyandrous group to copulate frequently with the only female or with as many females as possible if the mating system is polygynous. It is this scenario that was actually played out in these social groups of rats that established a bilateral care of the young in the monogamous group and a unilateral one in the polyandrous group. Kohl *et al* (2001) opined that this helps to ensure that either a large number of offspring survive without significant paternal investment or that paternal investment occurs primarily when another male does not sire offspring.

Table 3: Parental and neonatal investment in the survival of pups of Wistar rats in monogamous and polyandrous groupings.

Parameters	**Monogamous group**	**Polyandrous group**
Care of the pups by the parents	Bilateral(both parents)	Unilateral(by the female only)
Domineering tendency of the doe	Negative(non-existent	Positive(existent)
Nursing	Positive(doe only)	Positive(doe only)
Retrieval of pups by parents	Bilateral(both parents)	Unilateral(doe only)
Insulation of pups from cold	Bilateral(both parents)	Unilateral(doe only)
Skin colour (of the neonates)	Pink(healthy)	Pink(healthy)
Onset of respiration(by the neonates)	Immediate & regular	Immediate & regular
Suckling reflex(by the neonates)	Established	Established
Movement(of the neonates)	Active	Active
Viability score(of the neonates)	High	High

The domineering tendency of the female was absent in the monogamous group. This could be because of the pair bond that was established between her and the only male (the monogynous male). Shedding off the domineering garb by the female minimizes her maternal investment but maximizes overall investment through the added male assistance (Kohl *et al*, 2001). The polyandrous female on the other hand had to don the domineering garb as a precaution for self-preservation and protection for the pups (D'Amato *et al*, 2006). The overall parental investment was therefore better in the monogamous group.

The retrieval of pups by the parents was bilateral in the monogamous group but unilateral in the polyandrous group. This same behavior was observed with regard to insulation of the pups from cold by the parents. Both parents in the

monogamous group invested in the survival of their pups by retrieving them back to the nesting area and insulating them from cold especially in the early hours of the morning. These observations did not support the work of Grizmek (2003) who concluded that males of this species of rats do not contribute much to the care of the young. Our observation also differed from those of Parker (1990) indicating that males do not participate in parental care in the Norway (*Rattus norvegicus)* rats. Their observations only held true for the polyandrous group.

The pups' investment in their own survival was viewed under the premises of skin colour, onset of respiration, suckling reflex and locomotion. These parameters were adjudged excellent for the two social groups investigated. This would then mean that those indices for measuring viability or thriftiness of the newly born pups were not negatively affected by these social groups. This explains why pups in both groups received high viability appraisal. The high mortality rate and relatively lower weaning weight recorded for the pups in the polyandrous group could be explained by the theories of parental investment (Trivers, 1972) and inclusive fitness (Dawkins, 1998) that played out to reduce the survivability of the pups compared to the monogamous group
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5 CONCLUSION

This study revealed that in the absence of monogamy, which is a rare occurrence among rats in the wild, the more usual forms of mating association like polyandry, promiscuity, polygynandry, polygyny, would subsist in which the males contribute little or nothing to parental investment in the survival of the pups. However, once a pair bond is formed between the male and the female, the tendency is for the male to fulfill its conjugal commitment of the "wedlock" by assisting the female to ensure the overall inclusive fitness of both sexes by way of active paternal investment in the neonates.

Though the polyandrous group is a better reproductive optimizer (because it recorded shorter generation interval, larger litter size and better birth weight), it ranked low on the inclusive fitness scale which is an indicator of the group's overall reproductive success because most of its reproductive optimum were eroded by a significantly fewer pups that survived the lactation stage. In addition, social stress as encountered in the polyandrous group could significantly lower reproductive success of rats and probably of any mammalian species.

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