

MAMMALIA

PAIR-LIVING IN THE MARA (*DOLICHOTIS PATAGONUM* Z.) *

by

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Chez le Mara le couple représente une cellule très étroitement unie. Les relations entre les deux partenaires sont d'une richesse et d'une intensité peu communes chez la plupart des Mammifères. Mâle et femelle restent constamment à proximité l'un de l'autre, aidés en cela par des signaux acoustiques et visuels.

Le mâle semble être le principal bénéficiaire de cette vie de couple qui lui assure un statut social plus élevé dans la colonie. La femelle ne joue qu'un rôle passif dans la cohésion du couple. Tout se passe comme si elle représentait le « territoire mobile » du mâle. Les parades effectuées par le mâle devant sa femelle sont autant de signaux destinés à éloigner les autres mâles de la colonie.

Le couple reste stable d'une année sur l'autre. La monogamie et une stricte fidélité persistent même quand la polygamie est possible.

Le mâle n'assure pas seulement la tranquillité de sa femelle tout au long de l'année et notamment pendant l'élevage des jeunes, il peut aussi la secourir lorsqu'elle est physiquement handicapée.

The Mara (*Dolichotis patagonum* Z.) is a large-bodied rodent (weighing approx. 8 kg.) belonging to the family *Caviidae*. It occurs exclusively over extensive dry areas with sparse vegetation in Argentina, living in fairly large colonies centered around communal burrows and feeding on a restricted plant diet (Brehm, 1876). It exhibits many anatomical and behavioural features reminiscent of open-country ungulates found on other continents.

A large colony of these rodents, acclimatised in the Branféré Park, Brittany, has been studied over a period of two years (1971-1972) by regular observation with binoculars at a distance. The animals move freely throughout the year over an area of 10 hectares, largely consisting of open meadows. They are never handled, and they are able to organise their activities spontaneously. Under such conditions of semi-captivity, one can assume that a certain number of fundamental behaviour patterns have probably remained

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unmodified. In particular, a pair-living habit would appear to be a striking characteristic of the species, in view of the large number of important biological traits which are associated with the pair. For this reason, a synthetic report on this specific aspect has been extracted from a more extensive account of the social behaviour of the mara (Dubost and Genest, in press).

The majority of the animals could be individually recognised through natural markings, and this permitted observation of the formation, maintenance and development of the various pairs.

The partners are united by strong bonds.

The male and the female always remain close to one another. The distance between them is usually no more than a few metres, though it varies according to the level of activity. The tendency to follow the partner is, of course, more marked during rapid locomotion.

The female initiates most activities (resting, walking, grazing, movement towards the burrow, etc...), and she is at once accompanied by the male. Thus, the female occupies the role of leader, though this is passive leadership, since she does not seek out her male partner when he is some distance away. Further, it has been observed in the course of searching behaviour that the maras can only effectively identify one another at short range (of the order of a few metres), so the male must necessarily remain close to the female.

Two characteristics assist the male in staying close to his partner. In this species, *D. patagonum*, the rump is marked by white « breeches ». This light patch is separated from the dorsal fur by a dark horizontal stripe which accentuates the contrast (Fig. 1). When the animal is sitting or lying down, this white patch is hidden, but it is displayed as soon as the animal stands up ; that is, its appearance marks any initiation of activity. The patch is found in both sexes as soon as they have attained sexual maturity ; but it is the male that usually follows the female and he is accordingly constrained to follow the white patch which represents

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Fig. 1. — The black-white contrast of the rump pelage in adult maras acts as short-distance visual signal.

Fig. 2. — The male urinates on the female by rearing up on his metatarsi into an almost vertical position. In response, the female directs a jet of urine towards the male's face by pointing her rump towards him. In this way, she indicates that she is in a non-receptive state.



Fig. 1.



Fig. 2.

his female (other animals of the colony usually being much farther away).

Secondly, during grazing or slow locomotion, the two partners conduct a continuing dialogue consisting of alternating calls which may be initiated either by the male or by the female. These calls do not appear to carry farther than a few metres, and they are therefore apparently adapted for very close contact situations.

It is surprising that, with a pair which is bonded to this extent, there are virtually no physical contacts other than during copulation, during the pressing together of the partners during cold weather, and during occasional olfactory investigation of the mammary or genital regions. In contacts of the latter kind, the female usually responds by abruptly presenting her rump towards the male's face and discharging a jet of urine. Allogrooming never occurs, and all of the male's displays directed towards the female take place at a distance.

During such displays, the male exhibits long bouts of marking of the ground with his anal glands and with his faeces, by dragging his rump across those areas which his female has previously occupied whilst stationary. He may also move in circular sweeps or in figure 8 patterns in front of the female. Frequently, the male will stand up on his hind legs and project a powerful jet of urine forwards onto the rump of the female (Fig. 2), and she immediately responds by producing a jet of urine backwards onto the male's face. This projection of urine by the male onto the female may be considered as a simple display (Kirchshoffer, 1960), but it can also be interpreted as marking of the female from a distance, since close physical contact is not normally tolerated. On the other hand, emission of urine by the female — who plays only a passive role in maintenance of the pair bond — appears simply to represent a form of rejection behaviour, since such urination is directed towards any approaching individual when she is non-receptive to approach.

The different forms of marking and display directed at the female also function as signals to the other males of the colony. In fact, these behaviour patterns are particularly frequent whenever a rival approaches or has just been repulsed. The male of any pair will not tolerate the approach of another adult male to within 10 metres of his female. If such a close approach occurs, he begins by performing displays and marking behaviour directed towards his female. If the intruding male does not withdraw, the male of the pair advances with his head lowered. Usually, the rival will take flight during these initial stages; but if he does not do so, he is violently attacked and chased. Subsequently, the male of the

pair returns to the proximity of his female and exhibits further display and marking. If two males accompanied by their females approach one another too closely, one can observe mutual displays, threats and chases which only cease when the distance between the two females is sufficiently large to prevent the males from reacting to each other. This obligatory distance between any two pairs is uniquely dependent upon the links between paired males and females, since females on their own will tolerate a greater degree of proximity.

All of the male's behaviour with respect to his female indicates that he is acting as the « owner » of his partner and of the ground which she occupies. He marks the female with his urine, he marks the ground near to her with his anal glands and with his faeces, and he defends the zone surrounding her from the approach of other males. Whilst the pair is moving, the defended zone moves with them, thus representing a « mobile territory ». Since all pairs in the colony use the same overall terrain (the same grazing areas, the same resting places, the same burrows, etc...), there is at any one time a mosaic of micro-territories which are continuously shifting over the entire area occupied by the colony, as a function of the activities of the individual pairs.

The pair ensures increased social status for the male.

The results of encounters between different males of the colony have clearly shown that a male alongside his female almost always emerges victorious from an interaction with a solitary male. Apparently, the principal factor underlying this superiority is the greater motivation of the paired male. If a male which is involved alone in an encounter is otherwise normally accompanied by a female he has some chance of dominating the male of the pair, but a bachelor male never dominates. Similarly, whenever two lone males encounter one another, if one is a bachelor he will typically emerge as the loser.

In the mara colony, where so much is common ground, the only notable form of ownership is that of the female by the male. Only a male accompanied by a female has something to defend, and during any physical encounter with a rival he is more highly motivated and therefore more aggressive. Bachelor males, like sub-adults and females of all ages, lack aggressiveness. They never exhibit agonistic encounters with one another. The minimal distance which always separates two paired males is not present in these other categories, and one can observe close proximity between such animals, particularly during resting periods.

Bachelor males are always chased by paired males, since they represent a constant source of danger in that they are continuously seeking a female. Such males occupy the lowest rank in the male hierarchy.

The partners in a pair show mutual fidelity.

On the basis of natural individual markings on the animals, it was possible to observe that the pairs remain stable from one year to the next. The only changes were due to the death of one of the partners of a pair, followed — usually with a certain time-lag — by replacement of the missing partner. For example, one male whose female had died in parturition six weeks previously was found to be still alone and exhibiting typical searching behaviour, although there were numerous single females available.

In fact, if a male becomes separated from his female he at once sets out to find her, producing brief, high-pitched whistles, which are far more powerful than the contact call and are audible over a distance of thirty metres or more. The whistling call is repeated at regular intervals and calling only stops when the male has found his female. The female never replies to the male's call and she does not exhibit any overt behaviour which might facilitate the reunion with the male, though it is possible that the male's call restricts her movements. The whistling call is comparable to the distress-call of an animal handled by a human being, and this may indicate that there is an element of alarm in the male's behaviour.

On several occasions, the male of a pair has been seen to be attracted by another female. However, this situation is always short-lived and the male consistently exhibits great fidelity towards his partner. For example, in the course of agonistic encounters between the males of two pairs, it may sometimes happen that one male is clearly dominant and chases the other away. The victor remains close to the strange female and subjects her to olfactory control, his presence preventing the subordinate (but still displaying) male from approaching. But the victor never takes over the strange female, returning instead quite soon to his own female, with the result that the two pairs are eventually reunited.

Similarly, when a pair returns to the colony after mating, the vulval marking odour of the female in post-oestrus strongly attracts the various surrounding males, which leave their own partners and hurriedly attempt to follow the female and to mount her. Violent battles occur at such times, with each male opposing his rivals and being attacked by the female's usual male partner.

Nevertheless, however strong this attraction may be, each male returns one or more times to his own female — which has remained at a distance — thus ensuring that she has remained alone, before the pursuit of the post-oestrous female is continued.

This strict monogamy and fidelity of the male towards a particular female persists even when the prevailing conditions favour polygamy ; that is, when there is an excess of sexually mature females. In fact, a few of the males do briefly visit the bachelor females under such conditions and this assures that the latter are regularly mounted. This phenomenon, which is of a transitory but nonetheless compensatory kind, seems to represent an adaptation ensuring that the entire colony is reproductively active, and it disappears as soon as the sex-ratio of the breeding adults has returned to normal.

The lack of interest shown by males towards the females belonging to others pairs is understandable since such females are not receptive at such periods. In fact, oestrus represents an infrequent event in the colony ; for any given female, oestrus occurs only once every 3-4 months and lasts only half-an-hour. At the time of oestrus, the pair can move away from the colony without being disturbed, despite the fact that the entire colony has been alerted to the advent of oestrus, since it occurs only a few hours after birth, which evokes active interest from all members of the colony. When the female returns to the centre of the colony, she is no longer receptive and it is at this point only that she is pursued by other males. Thus, it is a surprising fact that even during the brief and rare period of oestrus the pair has a protected status in the entire colony.

Pair-living corresponds to necessity.

In general, one can consider an adult male not accompanied by his female as a male of diminished social status. If he loses his female temporarily, he becomes alarmed and at once sets off in search of her. If he is an adult bachelor male, his efforts are concentrated towards finding a partner. Since all of the adult females in a colony are usually already paired off and it is not possible to take over a female from another male, the bachelor will court a young female prior to weaning, sometimes when she is no more than 6 weeks old. The young female will continue to spend the night in the burrow with other young of various litters. The « courting » male arrives at the burrow early in the morning and waits for the mother to call her daughter to be suckled. He follows the young female all day across the meadows, and whenever she

is following her mother he will thus be in immediate proximity to the young female's father, since the latter is always close to his own female (the mother). At such times, one can observe a form of tolerance which is unique between two adult males accompanied by females.

This apparent need for a male to live permanently with a particular female seems to extend beyond straightforward social requirements. The consequences of this habit can in fact also be seen in young animals. 70 % of births involve twins and the two offspring are always seen together. If there is a single offspring (25 % of births), an excess animal from triplets (5 % of births), or a young which has lost its brother or sister, it will seek to join up with a partner at once. Later on, young males still exhibit a tendency to approach one another while excess females remain separate.

The bonds uniting the two partners of a couple include elements of mutual aid.

The expressions of bonds within the pair are constant in frequency and intensity throughout the year. This is far removed from temporary pair-formation for reproductive purposes. The male does not take part in the rearing of the young, but — since he is always present close to the female — he ensures the isolation from other animals necessary for successful rearing. The male may also assist a female in difficulty. We observed one case of a female with partially paralysed hindquarters, which was unable to move with ease. In order to flee more rapidly from the observer, she supported herself against the flank of her male, who approached her at such times. In another pair, in which the female had lost an eye, the male always placed himself between the blind side of the female and any source of danger on that side.

CONCLUSIONS

The characteristic of pair-formation seems to have reached an extremely advanced stage in the mara, in terms of the complexity and intensity of the relationships between the two partners. The pair is a vital unit, closely-knit and permanent, within which bonds of mutual aid develop. The male seems to be the primary effector of the pair, since the female only plays a passive role in pair-cohesion. Nevertheless, it is the female which initiates activities and rears the offspring. On such occasions, she presumably benefits from shielding against conspecifics provided by male. Thus, there is division of labour.

The pair represents the basic unit of social organisation in the mara, but the importance of bonds is determined by relationships within the colony as a whole. However, in the absence of information on the biology of this species under natural conditions, we cannot fully appreciate the role played by pair-living, nor can we judge whether it is a response to specific ecological conditions.

SUMMARY

In the Mara sexual pairs are closely united. The relationship between the two partners is more intense and rich than it is in most mammals. The male and female always stay close to each other, aided by visual and acoustic signals.

The male seems to be the chief beneficiary in the relationship, as it assures him of a raised social position in the colony. The female plays only a passive role in the relationship, so that she seems to represent the « moving territory » of the male. The parading of the male in front of his female serves to keep away the other males of the colony.

The couple remains constant from one year to the next. Monogamy is strict, persisting even when polygamy is possible.

The male protects the female throughout the year, especially while the young are being raised, and may also assist her if she is physically handicapped. (Summary translated by A. Dagg).

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