

Mate desertion in response to female promiscuity in the socially monogamous aardwolf *Proteles cristatus*

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Received 4 January 1988; accepted 27 May 1988

In most monogamous breeding systems males demonstrate a high degree of paternal care. With the significant costs of this parental investment, it is clearly in the interests of males to raise only their own offspring. It has therefore been predicted, but never observed in the field, that if the female of a monogamous male is promiscuous, he will desert her and attempt to breed with an alternative female. Here we report a case of such a mate desertion in the aardwolf *Proteles cristatus*. We suggest, however, that mate desertion should occur only rarely in response to female promiscuity. This is because a cuckolded male may still be raising some of his own offspring, and should desert only on the rare occasions when an alternative receptive female is exclusively available to himself.

In meeste monogamiese paarsisteme vertoon mannetjies 'n hoë mate van ouersorg. Die hoë kostes verbonde aan hierdie ouersorg impliseer dat dit in die mannetjie se belang sou wees om slegs sy eie nasate te versorg. Gevolglik is daar voorspel, maar nog nooit werklik in die veld waargeneem nie, dat indien die wyfie van 'n monogamiese mannetjie met ander mannetjies sou paar, 'n gekulde mannetjie so 'n wyfie sou verlaat en met 'n alternatiewe wyfie probeer teel. Hierin word dan oor so 'n geval van drosting deur 'n mannetjie aardwolf *Proteles cristatus* gerapporteer. Daar word beweer dat drosting slegs in sekere gevalle van ontrouheid sal gebeur aangesien die gekulde mannetjie soms nog in elke geval van sy eie nasate sou versorg. Drosting sal dus slegs in die gevalle voorkom waar 'n alternatiewe ontvanklike wyfie beskikbaar sou wees.

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Cuckoldry is peculiar to organisms exhibiting extensive male parental care and can be defined as a male's involuntary rearing of another male's offspring as a result of one male (the 'cuckolder') having fertilized the mate of the other (the 'cuckold') (Power, Litowitch & Lombardo 1981). It is clearly a considerable waste of breeding time and effort for a cuckold to raise another individual's offspring instead of his own. It has therefore been assumed that if a male knows that his mate has been promiscuous he will desert her and attempt to breed with another female (Beecher & Beecher 1979; Gladstone 1979; Fitch & Shugart 1984). Given this potential for the mates of promiscuous females to desert, it has been suggested that a female should actively avoid extra-pair copulations (EPCs) in order to assure paternity to her mate and, hence, his care of her offspring (Gladstone 1979; Fitch & Shugart 1984).

This argument rests on two major assumptions:

- (i) a male will desert his mate if he knows that she has been promiscuous;
- (ii) in order to avoid this, females attempt to guarantee their mate's paternity by not accepting EPCs.

If these assumptions are true, then the logical conclusion to this argument is that incidences of true cuckoldry should be extremely rare, if not totally absent. For a number of years after Gladstone (1979) formulated this argument no incidences of cuckoldry in monogamous species were published. However, during detailed studies of individually recognizable birds and mammals it has recently become increasingly evident that cuckoldry is an established feature of a number of

apparently monogamous species. This suggests that one, or both, of the above assumptions is incorrect.

With regard to the first assumption Frederick (1987) has pointed out that there is no evidence for mate desertion as it has never been observed in any field study. This is not surprising, however, because if assumption (ii) is correct, then one should not witness instances of desertion in the first place.

Maynard Smith (1977) has argued that unless a male can be guaranteed 100% paternity with another female, he should remain with his present mate and guard whatever investment he has with her. It will presumably be a very rare circumstance in which a cuckolded male can be given such a guarantee, so the likelihood of witnessing a desertion will be very low indeed.

We now report a case of such an exceptional circumstance, observed in the aardwolf.

The aardwolf is a termite-eating carnivore that occurs widely throughout southern Africa (Cooper & Skinner 1979; Richardson 1987a). The social and mating behaviour of aardwolves has been studied since 1981 on Benfontein, an 11 000 ha game farm in the northern Cape Province of South Africa. Aardwolves were followed in a four-wheel-drive vehicle at a distance of 15–30 m, with observations being recorded on a pocket dictaphone. At night aardwolves were observed with the aid of the vehicle headlights and a mounted spotlight. Aardwolves appeared undisturbed by observation. From 1981 until 1985 the residents of five adjacent territories were studied. In 1986 two more territories were included in the study.

Aardwolves are socially monogamous, a mated pair and their most recent offspring occupying a well-defined perennial territory (Richardson 1987b). The mating system is described as social monogamy, because although the pair occupy the territory throughout the year, mating is not exclusively within the territorial pair. During June, the first month of the two-month-mating season, males do a great deal of 'scouting' around and latterly scent marking of each other's territories. We have interpreted this behaviour as advertising by the males to the neighbouring female and assessing her male's ability to defend access to her (Richardson 1987b).

Most females come into pro-oestrus during the first week of July. Pro-oestrus lasts for about a week, and often a great deal of chasing and fighting occurs around the mates of the males who are least able to defend their territories. It is these females that take part in extra-pair copulations (EPCs). As females may remain receptive for one to three days, a promiscuous female has the opportunity to mate with her resident male (which she always does) and also to take part in EPCs. These EPCs presumably result in some males cuckolding their neighbours (Richardson 1987b). Most females become receptive within two weeks of each other. However, if a female is not fertilized during this period she may cycle again about two weeks later.

The cubs are born in October, at the end of a three-month-gestation period. For the next two to three months all males (including the cuckolds) become diligent babysitters, guarding the cubs at the den for up to 6 h a night while the female is away foraging. As the cubs are born during early summer, after a period of low food availability during winter (Richardson 1987a), this forgoing of foraging in order to guard cubs must represent a considerable sacrifice for the males (Richardson 1987b). Guarding the cubs appears necessary to prevent jackal *Canis mesomelas* predation, and we have circumstantial evidence that this does occasionally occur (Richardson 1987b).

From July 1981 until February 1986 each territory was occupied by one adult male and female, except one territory which had two males. [In this territory — which is regarded as exceptional — both the males mated with the female and both guarded the cubs (Richardson 1987b)]. Between February and April 1986 seven adult aardwolves, mostly males, died during a locust poisoning campaign. Some of these adults were replaced by their subadult offspring, but five females were left without resident males during the mating season in June/July. Only two territories had a resident male and female. One of these males, Apollo, mated with all the unpaired females, except one, Zebra, who lived in the territory farthest from his. Although the copulation was not seen, it is assumed that Apollo mated with his own female as well, because after the mating season he returned to his own territory and was extremely diligent in guarding the cubs.

The other male, Don Quixote, was copulating with his own female, Jezebel, when he was attacked by Apollo. The two males fought briefly, then Don Quixote chased

Apollo from the territory. However, Apollo followed him back towards Jezebel, and Don Quixote spent the rest of the evening chasing Apollo and being followed back into his territory. At about midnight the two males returned to their respective dens. By the time I (P.R.K.R.) arrived early the next afternoon Apollo was busy mating with Jezebel and there was no sign of Don Quixote. After this copulation, which lasted for another 4 h, Jezebel was unreceptive towards Don Quixote.

Judging from the behaviour of Apollo, the female Zebra was in pro-oestrus at the same time as Jezebel and most of the other females. However, she was not seen to mate during this period. For the next two to three weeks after Jezebel had been involved in the EPC with Apollo, Don Quixote remained in his territory with her, but then abandoned it and moved into the adjacent territory with the unpaired female, Zebra. This occurred shortly after Zebra had shown signs of being in pro-oestrus again — travelling extensively outside her territory (Richardson 1987b). Although Don Quixote was not seen to mate with Zebra, it is reasonable to assume that he did, because when Zebra's cubs were born in November, he showed a great deal of paternal care towards them.

This example appears to be a clear case of desertion in response to female promiscuity. The prolonged absence of a territorial male in Zebra's territory was a most unusual circumstance, and arose owing to the extraordinary die-off of aardwolves. Don Quixote was probably the only male to mate with Zebra, owing the scarcity of males and the distance between Apollo's and Zebra's territories. Apollo was not seen to visit Zebra during her second pro-oestrus period. In 1987 Apollo again copulated with Don Quixote's mate (Maid Marion, who moved into his territory when Zebra died in March), but also with all the unpaired females. Thus Don Quixote did not have any alternative unmated females with which to breed and remained in his territory and guarded the cubs. Thus he was potentially cuckolded by Apollo, depending on who actually sired the cubs.

Apollo's mating with Jezebel in 1986 was one of five occasions in which EPCs involving paired females had been witnessed since 1983, giving an EPC incidence of 42% ($n = 12$; n is the number of copulations in which both the males and females had mates). Furthermore, there is strong circumstantial evidence for at least four more EPCs during this period (Richardson 1985, 1987b). In all these incidences the above is the only clear case of mate desertion, although there is one other which deserves mention.

In 1982, while he was copulating with his mate, Maid Marion, Robin Hood was attacked by Achilles. Achilles won the fight that ensued, then walked off followed by Maid Marion. I (P.R.K.R.) lost sight of them in the long grass, but assumed that copulation took place. Robin Hood remained in the territory and showed normal paternal care, although at a lower level than that displayed by Achilles in his own territory (Richardson 1987b).

The following year no copulations were seen, but judging by Achilles's behaviour during the pro-oestrous period (Richardson 1987b) he cuckolded Robin Hood

again. Robin Hood remained in the territory until the cubs were born but showed very little paternal care. However this was compensated by the fact that his putative son, Telemachus, remained in the territory and guarded the cubs. Over the next few months Robin Hood seemed to establish himself in another territory outside the study area. He presumably had another female in this territory but I was unable to establish this as it was on another farm.

During the 1984 mating season Robin Hood regularly visited his old territory. Both he and Achilles showed great interest in Maid Marion while she was in pro-oestrus, but Achilles defeated Robin Hood in a fight the day before she became receptive and was the only one to mate with her. Robin Hood left this territory and returned to the territory outside the study area. It should be noted that this year Robin Hood did not mate with Maid Marion, and therefore he had no chance of paternity and would not be expected to have remained in her territory.

These examples demonstrate that mate desertion does occur, but it seems to be restricted to situations when a male has higher chances of paternity with an alternative female — as predicted by Maynard Smith (1977). Elsewhere (Richardson, unpublished data) I have argued that, in the long term, females gauge the potential reaction of males (by the availability of alternative receptive females) and hence accept or reject EPCs. We suggest that it was the unusualness of the above circumstances which led to the desertion by the aardwolf Don Quixote.

Normally aardwolf territories are fully occupied by adults, so cuckolded males do not have the choice of desertion and females are 'safe' in accepting EPCs. Of course, through the natural death of males, territory vacancies occur all the time. However, for a potentially cuckolded male to make use of it, the territory must be vacant during the short and highly seasonal period when the female is receptive. Furthermore, the female must be exclusively available to this male — a rare probability considering the competition by males for receptive females, and the fact that it was because of his inability to defend his own female that he came to be considering desertion in the first place. The cuckolding males make the most of any opportunities to mate with additional females, but return to their own territories in order to help raise one set of cubs (Richardson 1987b).

It is now pertinent to reconsider Gladstone's (1979) two assumptions concerning: (i) male desertion in response to female promiscuity; and (ii) females not accepting EPCs simply to guarantee that the male will do his share of parental care.

It is evident from the recent literature on birds (Frederick 1987; Hatch 1987; Moller 1987; Westneat 1987) and the above data on the aardwolf that there are exceptions to both these assumptions as many females readily accept EPCs and, at least in the case of the aardwolf, the mates of these females know this has happened but very rarely desert them. We suggest therefore that these assumptions apply only in the special circumstances of the availability of an alternative

adult female with which the potentially cuckolded male can breed exclusively.

As alternative and exclusive breeding opportunities are rarely available to males, cuckoldry has become an established feature in those species where promiscuity is advantageous to the female (increased genetic diversity, 'better' genes from the cuckold; and see Frederick 1987) and the likelihood of mate desertion is low. Nevertheless the potential for mate desertion always remains, because males are likely to respond individually to local conditions, whereas female behaviour may be determined more over the long term by general conditions within the population; thus there is always room for exceptions, as demonstrated by the aardwolf.

Acknowledgements

We thank De Beer's Consolidated Mines for access to Benfontein. Financial support was received from the following sources: Endangered Wildlife Trust, Kango Wolf Power Tools and Wolf Tools. P. Apps and two anonymous referees critically read the manuscript.

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