Genetic and behavioural evidence of monogamy in a mammal, Kirk's dik-dik (*Madoqua kirkii*)

PETER N. M. BROTHERTON[1*], JOSEPHINE M. PEMBERTON[2],
PETR E. KOMERS[1†] AND GAVIN MALARKY[2]

[1] *Large Animal Research Group, Department of Zoology, Downing Street, Cambridge, CB2 3EJ, UK*
[2] *Institute of Cell, Animal and Population Biology, University of Edinburgh, West Mains Road, Edinburgh, EH9 3JT, UK*

SUMMARY

Little is known about the mating behaviour of monogamous mammals. Here, we present behavioural and genetic evidence of fidelity in a socially monogamous dwarf antelope, Kirk's dik-dik. DNA microsatellite analysis revealed no evidence of extra-pair paternity (EPP) in dik-diks: mothers' partners matched the paternal genotype in all 12 juveniles tested. One likely reason for the absence of EPP is that males guard their mates closely during oestrus and over-mark all female scent, thereby reducing the likelihood of other males attempting to mate. In addition, males may be limited in their ability to search for extra-pair copulations (EPCs) by activities associated with pair-bond maintenance. Year-round, males maintained proximity within pairs, followed their females' activity patterns, and spent approximately 64% of their time with their partners. However, males did attempt to obtain EPCs when the opportunity arose, and genetic monogamy in dik-diks is probably best explained by the behaviour of females: in contrast to many monogamous female birds, female dik-diks do not appear to seek EPC partners. We propose that females avoid extra-pair males because they are unable to mate with them without instigating a potentially dangerous conflict.

1. INTRODUCTION

There is increasing evidence that individuals in many socially monogamous species mate outside the pair-bond. Extra-pair copulations (EPCs) have been reported in over 115 species of monogamous birds (Ford 1983), and genetic evidence of cuckoldry is accumulating to such an extent that strict fidelity may prove to be the exception rather than the rule among socially monogamous birds (Birkhead & Møller 1992). There is a comparative paucity of data regarding the occurrence of EPCs and extra-pair paternity (EPP) in monogamous mammals. EPCs have been observed in up to six monogamous species: the titi monkey, *Callicebus moloch* (Mason 1966), the aardwolf, *Proteles cristatus* (Richardson 1987), the Mongolian gerbil, *Meriones unguiculatus* (Ågren *et al.* 1989), the siamang, *Hylobates syndactylus* (Palombit 1994), the white-handed gibbon, *Hylobates lar* (Reichard 1995), and possibly the hoary marmot, *Marmota caligata* (Barash 1981). Genetic studies have so far only been conducted on two monogamous mammals, the old field mouse, *Peromyscus polionotus* (Foltz 1981) and the California mouse *P. californicus* (Ribble 1991), and no EPP was established in either case.

In this paper we describe the results of the first genetic study of monogamy in an antelope, Kirk's dik-dik, *Madoqua kirkii*. Dik-diks are dwarf antelopes which apparently pair for life (Hendrichs 1975), and male dik-diks show no paternal care (Brotherton & Rhodes 1996). Lost paternal care may be one of the main costs of infidelity to monogamous females (Trivers 1972; Birkhead & Møller 1992), and so, since there is no male care for female dik-diks to lose, rates of cuckoldry might be expected to be high. Other predictors of the level of EPP include investment (by either sex) in mate guarding or in attempts to gain EPCs (Westneat & Sherman 1993). We therefore also describe behaviour associated with mate guarding and maintenance of the pair-bond in order to assess the opportunity for EPCs in dik-diks.

2. STUDY AREAS AND METHODS

We studied a population of Kirk's dik-dik in Etosha National Park, Namibia, (18°50′ S, 16°57′ E) between February 1991 and April 1993 and a second population in Tsavo East National Park, Kenya (2°36′ S, 35°42′ E) between September 1993 and July 1994. Each dik-dik pair occupies a territory, which both sexes scent mark and defend by chasing off intruders (Hendrichs & Hendrichs 1971; Brotherton & Rhodes 1996). Dik-diks mark the borders of their territories with large dung piles (Hendrichs & Hendrichs 1971). Territories were mapped by plotting the positions of these piles, and boundaries were subsequently

---

[*] Author for correspondence: (`pb132@cam.ac.uk`).

[†] Present address: Department of Zoology, Uppsala University, Villavägen 9, S-752 36, Uppsala, Sweden.

Proc. R. Soc. Lond. B (1997) **264**, 675–681
Printed in Great Britain

confirmed by observations of territorial conflicts between neighbours. Boundaries identified using the positions of dung piles and conflicts coincided in all cases. The Namibian study site contained 23 dik-dik territories, and mean territory size (±s.e.) was 3.5 ± 0.3 ha (Brotherton 1994). The Kenyan study site contained 21 territories, averaging 2.4 ± 0.8 ha (Komers 1996*a*).

In Namibia, we darted 38 dik-diks (18 males and 20 females), and we captured two infants by hand. In Kenya, we captured 57 individuals (20 males, 21 females and 16 juveniles) on moonless nights by temporarily blinding them with a strong torch and grasping their hind legs. We ear-tagged all captured animals and radio-collared 22 adults in Namibia and 32 adults in Kenya. At both sites we were able to identify all individuals, either by artificial or natural marks. All behavioural data presented here were collected from the Namibian population either on foot or from a vehicle at distances of 2–50 m. In Namibia, female dik-diks give birth to a single offspring once a year, with a peak in births occurring between January and March (Brotherton 1994). All statistical tests presented are two-tailed.

(*a*) *Paternity study*

We took two ear clips (combined area 0.25 cm^2) from all dik-diks captured, making efforts to sample whole family groups. We also took muscle tissue from the foetuses of two pregnant females that died during capture. Tissue samples were stored at ambient temperature in a saturated salt (NaCl) solution containing 20% dimethyl sulphoxide (DMSO). We isolated DNA from each sample by standard proteinase K digestion, followed by phenol/chloroform extraction and ethanol precipitation (Sambrook *et al.* 1989). We screened five samples at 31 DNA microsatellite loci that were known to be polymorphic in cattle, sheep, or deer (the protocol for the polymerase chain reaction used to amplify the microsatellites is given in Bancroft *et al.* (1995)). Twenty-two of the primers amplified successfully; the first time that microsatellites had been amplified in an antelope. Seven of these loci proved to be polymorphic and these were used to genotype the Namibian population (see table 1). The Kenyan population had higher levels of polymorphism and so was only genotyped at three loci (table 1).

We compared genotypes between mothers and offspring, and identified paternal alleles. These were compared with the genotypes of the putative fathers, to see if any could be excluded. In most cases, the putative fathers were known to be paired with the mothers at conception. In addition, families containing offspring conceived before the start of the studies were included, provided that each parent was over three years' old, as determined by horn size (of males), tooth wear and fur condition (Hendrichs 1975; Brotherton 1994, P. E. Komers, unpublished data). In such cases, it is reasonable to assume that the pair members have not changed since conception because the dik-dik pair-bond is normally life-long (Hendrichs 1975) and replacement females are less than one year old, while replacement males are less than two years' old (Brotherton 1994).

The reliability of any genotype match was tested by (1) checking how many of the other study site males could be excluded as possible fathers; and (2) using population allele frequencies to calculate the probability of a random male matching the paternal genotype by chance. The latter analysis relies on the populations being at Hardy–Weinberg equilibrium (HWE). We tested for possible disequilibria by calculating the HWE expected frequencies and comparing these with the observed frequencies using the *G*-statistic (Sokal & Rohlf 1981, pp. 705–708). No significant departures from the HWE were found.

(*b*) *Mate guarding during oestrus*

We observed oestrous females for as long as possible whenever they were detected. We assumed that females were in oestrus if they were mating or if males attempted to copulate with them. The occurrence of oestrus was later confirmed by back-dating, assuming a gestation period of 166–172 days (Dittrich & Böer 1980). We recorded any attempted EPCs and attempts by oestrous females to leave their territories.

Using instantaneous scans at two-minute intervals (Altmann 1974), we calculated the average intra-pair distance during oestrus, and compared this with the average male–female distance (when pair members were together) at other times. We considered pair members to be 'together' if they were no more than 25 m apart.

(*c*) *Maintenance of the pair-bond*

Males may be constrained from searching for EPCs by activities concerned with the maintenance of their own pair-bonds. A male may also reduce his mate's opportunities for assessing potential EPC partners, or forming alliances with them, by retaining her within the pair's own territory. We therefore looked at the following characteristics of the dik-dik pair-bond:

(i) *Association behaviour*

We estimated the proportion of time males and females spent together using a half-weight association index:

$$\frac{n}{n+\frac{1}{2}(x+y)} \times 100\%$$

where n = the number of sightings of a male and a female together, x = the number of sightings of a male unaccompanied by a female, and y = the number of sightings of a female unaccompanied by a male. We calculated this separately for active and resting periods (the latter were those when at least one member of the pair was lying down), and compared it across three-month intervals from April 1991 to March 1993, inclusive. Dik-diks have two daily activity periods, one in the morning and one in the afternoon (Hendrichs & Hendrichs 1971; Manser & Brotherton 1995); we only used the first sighting per activity period for each pair.

(ii) *Maintenance of proximity and co-ordination of behaviour*

Following Hinde & Atkinson (1970), we investigated the relative importance of each pair member in maintaining proximity to their mates using the index:

$$\frac{A_{\mathrm{m}} \times 100}{A_{\mathrm{m}}+A_{\mathrm{f}}}-\frac{L_{\mathrm{m}} \times 100}{L_{\mathrm{m}}+L_{\mathrm{f}}}$$

where A_{m} and A_{f} represent the number of approaches made by the male and female, respectively, and L_{m} and L_{f} represent the number of times the male left the female and vice versa. We considered an individual to have approached or left its mate if it crossed a hypothetical circle of radius 5 m around its partner.

When both members of a pair either returned to, or left, their territory we noted the identity of the first individual to cross the boundary. We excluded occasions when an intruding pair was chased off by the residents of the territory. In addition, we identified the sex mainly responsible for initiating transitions in the activity of the pair by analysing observation periods during which both pair members either

Table 1. *Polymorphic microsatellite loci amplified in this study*

Heterozygosity estimates are based on 34 individuals for the Namibian population, and 53 individuals for the Kenyan population.

microsatellite locus (population)	number of alleles	heterozygosity (%)	reference for locus
RBP3 (Namibia)	4	50	Fries *et al.* 1993
RBP3 (Kenya)	13	68	
OarFCB193 (Namibia)	3	50	Buchanan & Crawford 1993
OarFCB193 (Kenya)	12	80	
OPACAP (Namibia)	2	18	Bancroft 1995
OPACAP (Kenya)	5	43	
OarHH64 (Namibia)	3	53	Henry *et al.* 1993
OarVH34 (Namibia)	2	26	Pierson *et al.* 1993
MAF23 (Namibia)	4	74	Swarbrick *et al.* 1990
MAF35 (Namibia)	2	6	Swarbrick *et al.* 1991

began resting or became active. In each case, we noted the identity of the pair member which stood up or lay down first.

(iii) *Intra-pair aggression*

We recorded all acts of aggression (butts, charges, chases and displacements from feeding or resting sites) within pairs. We calculated an hourly rate of aggressive interactions for each pair when inside and outside its territory. Periods during which both pair members were resting were excluded.

3. RESULTS

(*a*) *Paternity study*

We collected tissue samples from 11 nuclear families (father–mother–offspring), including one group from which two offspring were sampled (from consecutive breeding events), giving a total of 12 juveniles for whom paternity could be tested. We obtained samples from 17 males in Namibia and 20 males in Kenya, representing 70% and 90% of resident males at each site, respectively. In all cases the paternal genotypes matched those of the putative fathers (table 2). Furthermore, the number of other males from the same study site matching the paternal genotype was low in most cases, as was the probability that a random male matched the paternal genotype by chance (table 2). The paternity that can be assigned with the least certainty is that of juvenile N3, because it is homozygous for the most common allele at all seven loci. However, since the putative father also matches the paternal genotype, this is not evidence of EPP.

(*b*) *Mate guarding during oestrus*

We obtained sightings of seven oestrous females. With the exception of one sighting in Kenya (Bowker 1978), these are the only records of dik-dik mating behaviour in the wild. In five of the seven sightings, the pairs mated without any extra-pair males in attendance. On each of the two remaining occasions, two males entered the mating pair's territory and competed

Table 2. *Results of the DNA microsatellite paternity study*

In all cases the mother's partner matched the paternal genotype. (*a*) Juvenile names begin with a letter denoting the study population (N = Namibia, K = Kenya). The juveniles marked '*' were offspring of the same parents. (*b*) Number of additional males from the study site that were not excluded as potential fathers, total $n = 16$ (Namibia) and $n = 19$ (Kenya). (*c*) The probability of a random male matching the paternal genotype at a single locus is: $p_a = 1-(1-f_a)^2$, where p_a is the probability of the individual possessing at least one '*a*' allele, and f_a is the population frequency of allele '*a*'. If the juvenile is of the same heterozygote class as its mother, either allele could be paternal, in which case the probability of an individual matching the paternal contribution at either allele '*a*' or '*b*' is: $p_{ab} = 1-(1-f_a-f_b)^2$. The probability of an individual matching the paternal genotype at all loci is the product of the probabilities p_x for each locus.

juvenile name (*a*)	number of extra-pair males not excluded as possible fathers (*b*)	probability of paternal genotype being matched by chance (*c*)
N1	1	0.042
N2*	0	0.016
N3*	9	0.462
N4	0	0.022
N5	0	0.067
N6	0	0.039
N7	1	0.095
N8	0	0.027
K1	3	0.022
K2	0	0.015
K3	2	0.185
K4	1	0.025

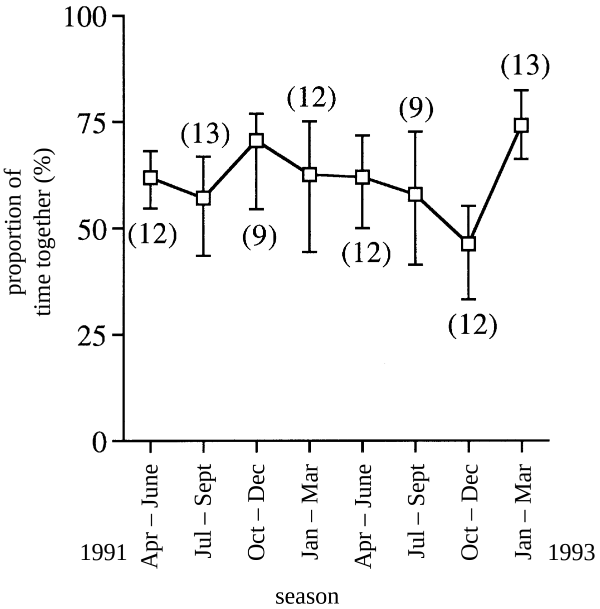

Figure 1. Proportion of time pairs spent together across different seasons. There is a single wet and dry season. The rains usually begin in September or October, and most rain falls between December and March. The rains were late in 1992. Median values and interquartile ranges for each period are shown and the number of pairs is indicated in parentheses.

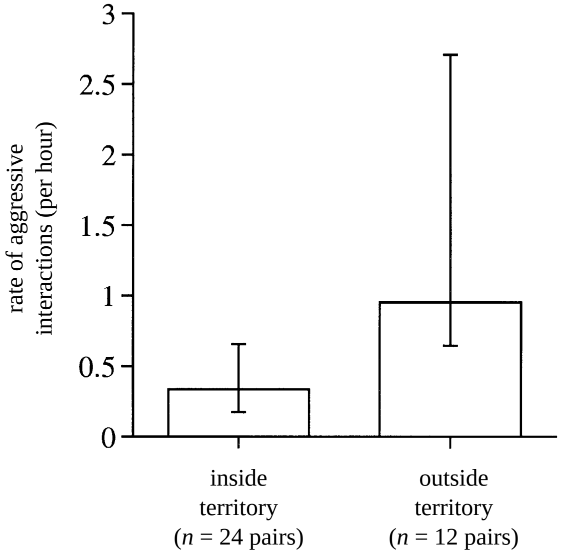

Figure 2. The rate at which males interact aggressively with their partners when inside and outside their territories. Median values and interquartile ranges are shown.

with the resident male. In one case, the intruders were a neighbour and a male from a territory about 100 m away. In the other, the two intruding males could not be identified. In both cases the scene was chaotic: the males fought aggressively with each other, while relentlessly pursuing the females, who appeared intent on escaping their attentions. Although no mating was observed in these two cases, the dates on which the females later gave birth (after 166–171 days) were consistent with the females being in oestrus (Dittrich & Böer 1980).

Oestrous females were attended continuously by their mates. As expected, average male–female distance declined during oestrus (mean distances ($\pm$s.e.): oestrous females 3.0 (± 0.31) m, anoestrous females 7.0 (± 0.53) m; paired t-test: $t = -7.08$, $n = 4$ pairs, $p < 0.01$).

(*c*) ***Maintenance of the pair-bond***

(i) *Association behaviour*

Pair members spent approximately 63.8% of their time together when females were anoestrus. This was similar during active and resting periods (median values: active periods ($n =$ 17 pairs) 63.7%, resting periods ($n = 9$ pairs) 66.7%; Wilcoxon signed ranks test: $z = -1.244$, $n = 9$, $p = 0.21$). Since there was no difference between active and resting periods, we combined both in a subsequent comparison of association behaviour across seasons (figure 1). This revealed a tendency for pairs to spend more time apart during the driest period of the year, perhaps to reduce feeding competition (Freidman analysis: $\chi^2 = 13.905$, d.f. $= 7$, $n = 7$ pairs, $p = 0.053$).

(ii) *Maintenance of proximity and co-ordination of activity*

The median Hinde–Atkinson index was $+38.3$, indicating that males are most important in maintaining proximity within pairs (interquartile range: $+33.3$ to $+49.1$; Wilcoxon one-sample test: $T^+ = 168$, $n =$ 18 pairs, $p < 0.001$). When pairs crossed their territory boundaries there was a trend towards females leading intrusions (G-test: $G = 2.795$, d.f. $= 1$, $p < 0.10$) and females initiated returns to the territory significantly more often than males (G-test: $G = 4.496$, d.f. $= 1$, $p <$ 0.05). In total, 33 movements across boundaries were observed in ten different pairs. These data were pooled because contingency analysis was impossible if pairs were treated separately due to small expected frequencies. Females also initiated significantly more resting periods than males (G-test: $G = 6.413$, d.f. $= 1$, $p < 0.02$) and females initiated more periods of activity (G-test: $G = 3.859$, d.f. $= 1$, $p < 0.05$). The latter analysis was based on 73 transitions of activity observed in 18 pairs (range: 1–11 transitions per pair), and again used pooled data because of low expected frequencies.

(iii) *Intra-pair aggression*

Despite being approximately 10% lighter than females, males are dominant in intersexual interactions because only they have horns (Bowker 1978). Males were more aggressive to their mates when pairs were outside their territories (figure 2; Wilcoxon signed ranks test: $z = -2.312$, $n = 11$ pairs, $p < 0.05$). In addition, males were seen chasing their partners back to their territories on ten separate occasions, including once when the female was approaching oestrus. While some aggressive interactions were apparently related to competition for feeding sites, many occurred outside of any obvious context.

4. DISCUSSION

The microsatellite analysis did not indicate any deviations from strict monogamy: the males' genotypes matched the paternal contribution in all putative father–mother–offspring trios. In addition, with two exceptions, the probability of the paternal genotype being matched by chance was low (see table 2). The sample size of 12 breeding events in 11 social groups is comparable to the number of broods sampled in many avian paternity studies (see table 12.2 in Birkhead & Møller (1992)). Few such studies have attached confidence intervals to their estimates of EPP (but see Hunter *et al.* 1992). In the case of dik-diks, the data indicate a maximum level of EPP (with 95% confidence) of 22.1%, calculated as: $y = 1-(1-x)^n$, where y = the probability of producing at least one illegitimate young (0.95); x = the frequency of EPP; and n = sample size (12). This apparently high value of 22.1% is a product of the sample size; it does not imply that there is any EPP in dik-diks. Achieving an upper 95% confidence limit of 10% EPP would require samples from 29 complete families, while 58 families would be needed to obtain an upper limit of 5% (assuming no evidence of EPP was obtained).

The relatively small number of complete dik-dik families sampled in this study is a reflection of the difficulties of working on a mammal in which the young are not confined to a nest. In particular, juvenile dik-diks proved difficult to sample because infant mortality was over 50% (Brotherton 1994), and because juveniles either had to be captured within the first few days of life, when they were too young to run away, or after they were old enough to dart, but before they dispersed from their natal territories. The genetic data presented here (for 12 cases) were obtained from the study of 44 known dik-dik families. We know of no behavioural field study of a large monogamous mammal in which this number of social groups has been exceeded.

Mating was contested on two out of seven occasions, and no EPCs were observed, indeed the females seemed intent on escaping the attentions of the intruding males. Moreover, due to the commotion that accompanied mating attempts by extra-pair males, contested matings are easy for observers to detect, and so are likely to be over-represented in the sample. This lack of EPCs is consistent with the results of the paternity study, and it therefore seems reasonable to conclude that extra-pair paternity occurs at a very low level in dik-diks, or not at all.

The two previous genetic studies of monogamous mammals, conducted on Peromyscus polionotus (Foltz 1981) and *P. californicus* (Ribble 1991), also revealed no EPP. In monogamous *Peromyscus* species, males generally show a substantial amount of parental care (Elwood 1983), and males have been shown to be important for offspring survival in *P. californicus* (Gubernick *et al.* 1993). The absence of EPP in these species is consistent with studies of monogamous birds, where high levels of male care are often associated with a high degree of paternity certainty (Møller & Birkhead 1993). Evolutionary theory also predicts this relationship provided parental care has a cost either in terms of lost mating opportunities or reducing parents' residual reproductive value (Westneat & Sherman 1993). This contrasts with the situation in dik-diks where we found no evidence of EPP, despite there being no paternal care (Brotherton & Rhodes 1996). Since male dik-diks are not constrained by parental duties, and both sexes potentially benefit from EPCs (Westneat *et al.* 1990; Birkhead & Møller 1992), the lack (or at least low level) of EPP found in dik-diks warrants explanation.

One possibility is that males are prevented from searching for EPC partners by activities concerned with pair-bond maintenance. When females were not in oestrus, pair members spent approximately 63.8% of their time together. Most females enter oestrus between July and September (Brotherton 1994), but we found no significant tendency for males to spend less time with their partners during this period, as might be expected if males were searching for EPCs. Throughout the study period, it was usually the male that followed the female, and this was true in terms of movements around the territory, movements across territory boundaries, and changes in activity.

Why do males spend so much time with their partners when they are anoestrus? When males are with their partners, they over-mark the females' scent, and this appears to be important in advertising the paired status of the females, and reducing the risk of male territorial challenges (Brotherton 1994). Males may also follow their mates in order to restrict their movements: by being more aggressive to their mates outside their territories, males may cause females to leave their territories less (see also Komers (1996*b*)). However, if females are not in (or approaching) oestrus, it is not obvious why males should prevent them from leaving. Perhaps this indicates that there is a risk that females might switch territories, although this has never been reported.

The maintenance of close proximity is not in itself sufficient to explain the apparent absence of EPP. Oestrus is asynchronous (Brotherton 1994), males spend a substantial amount of time on their own, and extra-pair males were observed competing for access to oestrous females. It is more likely that the lack of EPP is the result of the behaviour of oestrous females and of the males guarding them. Throughout the oestrous period, males remain very close to their partners and over-mark all female scent (Brotherton 1994), and this appears to be effective in concealing oestrus from other males. However, this does not explain why females allow themselves to be guarded in the first place.

There is growing evidence that, far from being passive or unwilling EPC partners, monogamous female birds may actively solicit EPCs (Smith 1988; Kempenaers *et al.* 1992), and that multiply mated females can control paternity of their offspring (Birkhead & Møller 1993). EPCs may also represent an alternative reproductive strategy for monogamous female mammals. Female titi monkeys and Mongolian gerbils leave their territories and solicit extra-pair matings (Mason 1966; Ågren *et al.* 1989), while oestrous female aardwolves apparently attract neighbouring males to their territory by scent marking, and proceed to mate with them in the presence of their regular partners (Richardson 1987). We found no evidence of female dik-diks attempting either of these tactics. Only one of seven oestrus females left her territory, and, if the purpose of the intrusion was to obtain EPCs, it is perhaps surprising that she only remained outside for 40 minutes and that she did not scent mark at all during this time (Brotherton 1994). Although Kranz (1991) noted an increased rate of preorbital marking by one female dik-dik after she entered oestrus, no increase was found in this study (Brotherton 1994). Moreover, in Günther's dik-dik (*Madoqua guentheri*), L. Fitzgerald (personal communication) found no change in pre-orbital marking rates.

It therefore appears that female dik-diks do not attempt to obtain EPCs. This is perhaps surprising, because there are at least two possible benefits of EPCs to females (see also Westneat *et al.* 1990; Birkhead & Møller 1992). The first is to improve the genetic quality of their offspring. Throughout the year, female dik-diks have ample opportunity to assess neighbouring males and, in the likely event that their partner is not the 'best' in the vicinity, should be in a good position to select a high quality father for their offspring. A second possible benefit is insurance against a mate's infertility, which may account for the only case of EPCs observed in siamang (Palombit 1994).

Given these potential benefits of EPCs, why do female dik-diks remain faithful? In some species males may retaliate if their partner is unfaithful by witholding parental care (Trivers 1972; Møller 1988); however, male dik-diks do not show any paternal care (Brotherton & Rhodes 1996). It seems more likely that the main cost to females of obtaining EPCs would be harassment from their partners and extra-pair males. In several ungulates, male harassment has been shown to be costly to oestrous females (Geist 1971; Rubenstein 1986), and females may even be drowned during forced copulations in waterfowl (McKinney *et al.* 1983). On both occasions, when male dik-diks were observed competing for access to oestrous females, the females appeared intent on escaping the fray. In many socially monogamous birds, females obtain EPCs when their partners are absent (Birkhead & Møller 1992). Oestrous female dik-diks, on the other hand, are attended constantly by their mates and so are unlikely to be able to mate with extra-pair males without instigating a prolonged and potentially dangerous conflict. An additional cost might be incurred by females showing a post-partum oestrus, as occurs typically in East Africa (Hendrichs & Hendrichs 1971), and occasionally in Namibia (Brotherton 1994). Oestrus lasts 24 hours (Dittrich & Böer 1980) and females suckle their young at least four times during this period (Hendrichs & Hendrichs 1971). Oestrous females attended by several males may be prevented from suckling their infants, or their young might be injured in the process.

Females are no longer viewed as passive components of mating systems under the control of males, and this is particularly true in the case of monogamy (Gowaty 1995). At the same time, there is mounting evidence that male harassment can affect female mating behaviour (Clutton-Brock & Parker 1995). These two views need not be at odds. In dik-diks, we suggest that any potential genetic benefits of EPCs are outweighed by their phenotypic costs, and so females opt for monogamy by allowing males to guard them. There may, however, be some 'quality control' applied by females: through scent marking at their normal rate, they may at least ensure that their male is of sufficient quality to guard them.

We are grateful for the help and support of the Ministry of Wildlife and Tourism, Namibia, and the Kenyan Wildlife Service. For field assistance, we thank A. Rhodes, M. Manser, W. Hugo, J. Le Roux, P. Morkel, H. Reuter, N. Brain, E. Komers, J. Mwanzia and K. Roth. We also thank T. H. Clutton-Brock for supervising this study, and R. Woodroffe and three anonymous referees for helpful comments on the manuscript. Financial support was provided by the NERC, Downing College, Cambridge, Sigma Xi, the NSERC of Canada and the National Geographic Society.

REFERENCES

Ågren, G., Zhou, Q. & Zhong, W. 1989 Ecology and social behaviour of Mongolian gerbils, *Meriones unguiculatus*, at Xilinhot, Inner Mongolia, China. *Anim. Behav.* **37**, 11–27.

Altmann, J. 1974 Observational study of behaviour: sampling methods. *Behaviour* **49**, 227–267.

Bancroft, D. R. 1995 A microsatellite polymorphism at the ovine pituitary adenylate cyclase activating polypeptide gene in sheep which can be co-amplified with two other loci. *Anim. Genet.* **26**, 59.

Bancroft, D. R., Pemberton, J. M. & King, P. 1995 Extensive protein and microsatellite variability in an isolated, cyclic ungulate population. *Heredity* **74**, 326–336.

Barash, D. P. 1981 Mate guarding and galivanting by male hoary marmots (*Marmota caligata*). *Behav. Ecol. Sociobiol.* **9**, 187–193.

Birkhead, T. R. & Møller, A. P. 1992 *Sperm competition in birds: evolutionary causes and consequences*. London: Academic Press.

Birkhead, T. & Møller, A. 1993 Female control of paternity. *Trends Ecol. Evol.* **8**, 100–103.

Bowker, M. H. 1978 Behavior of Kirk's dik-dik (*Madoqua kirkii*) in Kenya. Ph.D. thesis, Northern Arizona University.

Brotherton, P. & Rhodes, A. 1996 Monogamy without biparental care in a dwarf antelope. *Proc. R. Soc. Lond.* B. **263**, 23–29.

Brotherton, P. N. M. 1994 The evolution of monogamy in the dik-dik. Ph.D. thesis, University of Cambridge.

Buchanan, F. C. & Crawford, A. M. 1993 Ovine microsatellites at the OarFCB111, OarFCB128, OarFCB193, OarFCB266 and OarFCB304 loci. *Anim. Genet.* **24**, 145.

Clutton-Brock, T. H. & Parker, G. A. 1995 Sexual coercion in animal societies. *Anim. Behav.* **49**, 1345–1365.

Dittrich, L. & Böer, M. 1980 *Verhalten und Fortpflanzung von Kirk's Rüssel-Dik-diks* (Madoqua (Rhynchotragus) kirkii) *im Zoologischen Garten. Hannover: Freimann & Fuchs.*

Elwood, R. W. 1983 Paternal care in rodents. In *Parental behaviour of rodents*. (ed. R. W. Elwood), pp. 235–257. Chichester: John Wiley.

Foltz, D. W. 1981 Genetic evidence for long-term monogamy in a small rodent, *Peromyscus polionotus*. *Am. Nat.* **117**, 665–675.

Ford, N. L. 1983 Variations in mate fidelity in monogamous birds. *Curr. Ornithol.* **1**, 329–356.

Fries, R., Eggen, A. & Womack, J. E. 1993 The bovine genome map. *Mammal. Genome* **4**, 405–428.

Geist, V. 1971 *Mountain sheep: a study in behavior and evolution*. Chicago University Press.

Gowaty, P. A. 1995 Battles of the sexes and origins of monogamy. In *Partnerships in birds* (ed. J. L. Black), pp. 21–52. Oxford University Press.

Gubernick, D. J., Wright, S. L. & Brown, R. E. 1993 The significance of fathers' presence for offspring survival in the monogamous California mouse, *Peromyscus californicus*. *Anim. Behav.* **46**, 539–546.

Hendrichs, H. 1975 Changes in a population of dik-dik *Madoqua* (*Rhynchotragus*) *kirkii* (Günther 1880). *Z. Tierpsychol.* **38**, 55–69.

Hendrichs, H. & Hendrichs, U. 1971 *Dik-dik und Elefanten.* Munich: Piper Verlag.

Henry, H. M., Penty, J. M., Pierson, C. A. & Crawford, A. M. 1993 Ovine microsatellites at the OarVH34, OarHH35, OarHH41, OarHH44, OarHH47 and OarHH64 loci. *Anim. Gen.* **24**, 222.

Hinde, R. A. & Atkinson, S. 1970 Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother–infant relations in rhesus monkeys. *Anim. Behav.* **18**, 169–176.

Hunter, F. M., Burke, T. & Watts, S. E. 1992 Frequent copulations as a method of paternity assurance in the northern fulmar. *Anim. Behav.* **44**, 149–156.

Kempenaers, B., Verheyen, G. R., Van den Broeck, M., Burke, T., Van Broeckhoven, C. & Dhondt, A. A. 1992 Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature*, *Lond.* **357**, 494–496.

Komers, P. E. 1996 *a* Conflicting territory use in males and females of a monogamous ungulate, the Kirk's dik-dik. *Ethology* **102**, 568–579.

Komers, P. E. 1996 *b* Obligate monogamy without paternal care in Kirk's dik-dik. *Anim. Behav.* **51**, 131–140.

Kranz, K. R. 1991 Monogamy in the dik-dik. *Appl. Anim. Behav. Sci.* **29**, 87–105.

Manser, M. B. & Brotherton, P. N. M. 1995 Environmental constraints on the foraging behaviour of a dwarf antelope (*Madoqua kirkii*). *Oecologia* (*Berlin*) **102**, 404–412.

Mason, W. A. 1966 Social organisation of the South American monkey, *Callicebus moloch*: a preliminary report. *Tul. Stud. Zool.* **13**, 23–28.

McKinney, F., Derrickson, S. R. & Mineau, P. 1983 Forced copulation in waterfowl. *Anim. Behav.* **86**, 250–294.

Møller, A. P. 1988 Paternity and paternal care in the swallow (*Hirundo rustica*). *Anim. Behav.* **36**, 996–1005.

Møller, A. P. & Birkhead, T. R. 1993 Certainty of paternity covaries with paternal care in birds. *Behav. Ecol. Sociobiol.* **33**, 261–268.

Palombit, R. A. 1994 Extra-pair copulations in a monogamous ape. *Anim. Behav.* **47**, 721–723.

Pierson, C. A., Hanrahan, V., Ede, A. J. & Crawford, A. M. 1993 Ovine microsatellites at the OarVH34, OarVH41, OarVH58, OarVH61 and OarVH72 loci. *Anim. Gen.* **24**, 224.

Reichard, U. 1995 Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). *Ethology* **100**, 99–112.

Ribble, D. O. 1991 The monogamous mating system of *Peromyscus californicus* as revealed by DNA fingerprinting. *Behav. Ecol. Sociobiol.* **29**, 161–166.

Richardson, P. R. K. 1987 Aardwolf mating system: Overt cuckoldry in an apparently monogamous mammal. *S. Afr. J. Sci.* **83**, 405–410.

Rubenstein, D. I. 1986 Ecology and sociality in horses and zebras. In *Ecological aspects of social evolution*, vol. (ed. D. I. Rubenstein & R. W. Wrangham), pp. 282–302. New Jersey: Princeton University Press.

Sambrook, J., Fritsch, J. E. & Maniatis, T. 1989 *Molecular cloning: a laboratory manual.* New York: Cold Spring Harbor Laboratory Press.

Smith, S. M. 1988 Extra-pair copulations in black-capped chickadees: the role of the female. *Behaviour* **107**, 15–23.

Sokal, R. R. & Rohlf, F. J. 1981 *Biometry.* New York: W. H. Freeman.

Swarbrick, P. A., Buchanan, F. C. & Crawford, A. M. 1990 Ovine dinucleotide repeat polymorphism at the MAF23 locus. *Anim. Gen.* **21**, 191.

Swarbrick, P. A., Buchanan, F. C. & Crawford, A. M. 1991 Ovine dinucleotide repeat polymorphism at the MAF35 locus. *Anim. Gen.* **22**, 369–370.

Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man*, 1871–1971. (ed. B. G. Campbell), pp. 136–179. Chicago: Aldine-Atherton.

Westneat, D. F. & Sherman, P. W. 1993 Parentage and the evolution of parental behavior. *Behav. Ecol.* **4**, 66–77.

Westneat, D. F., Sherman, P. W. & Morton, M. L. 1990 The ecology and evolution of extra-pair copulations in birds. *Curr. Ornithol.* **7**, 331–369.

Received 20 November 1996; accepted 3 January 1997