

Sex differences in timing and context of dispersal in Damaraland mole-rats (*Fukomys damarensis*)

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Abstract

Dispersal behaviour in cooperatively breeding mammals often differs between the sexes, which can affect how individuals of both sexes compete for breeding opportunities. However, it is largely unknown how the males and females in social mole-rats differ in frequency, timing and social context of dispersal. Here we show, in Damaraland mole-rats (*Fukomys damarensis*), that rainfall increases dispersal probabilities in both sexes. Dispersal is male biased with males dispersing earlier and more frequently in dispersal coalitions than females. Most non-reproductive individuals disperse from the natal groups before reproducing. Territory inheritance is rare, but when it occurs, female non-breeders inherit the breeding position from the previous breeding female. After dispersing from the natal group, males are more likely than females to join other established groups and to replace the resident breeder. Our study suggests that differences in dispersal strategy may generate contrasts in intra-sexual competition, where male breeders are more often challenged by competitors from outside the group and female breeders may face higher competition from individuals within the group.

Keywords: Dispersal, cooperative breeding, intra-sexual competition, males, eusociality.

Introduction

Dispersal behaviour often differs between the sexes. Individuals of one sex are frequently more philopatric than individuals of the other sex. In cooperatively breeding mammals, females are usually more philopatric than males and the competitors of female breeders are typically born and develop within her own group whereas male challengers immigrate from other groups. This generates power asymmetry between the female breeder and her developing competitors (often her daughters) that may facilitate the maintenance of her reproductive monopoly (Hauber & Lacey, 2005; Clutton-Brock et al., 2006; Young & Bennett, 2013). In contrast, dominant males may frequently face adult challengers from other groups, as dispersing males may transfer between groups more readily (Clutton-Brock, 2016a). As such, sex differences in dispersal may affect the nature and intensity of intra-sexual conflict in cooperative breeders (Hauber & Lacey, 2005; Clutton-Brock et al., 2006; Young & Bennett, 2013).

The context triggering dispersal may sometimes differ between the sexes and may be dependent on social and ecological conditions (Jarvis & Bennett, 1993; Faulkes & Bennett, 2007; Clutton-Brock, 2016b). For example, in meerkats, males are more likely to disperse voluntarily and sometimes prepare for dispersal by visiting neighbouring groups, whereas females face higher risks of eviction from the group, disperse by fissioning from the natal group, or because social conditions are unfavourable in the natal group (Clutton-Brock et al., 2002; Young et al., 2005; Clutton-Brock & Manser, 2016). Ecological constraints on dispersal over an extended period of time have been suggested to play a crucial role in the evolution of some cooperatively breeding societies, but field data showing how ecological constraints and social factors affect dispersal are scarce (Bennett & Faulkes, 2000; Faulkes & Bennett, 2016).

In Damaraland mole-rats (*Fukomys damarensis*), it has been suggested that dispersal is male biased, may occur above and below ground, and the success of dispersal may depend on individual quality and growth rate before dispersal (Hazell et al., 2000; Bennett & Faulkes, 2000; Torrents-Ticó et al.,

2018). Groups consist of a single breeding female, her non-breeding offspring of both sexes, and occasionally unrelated individuals, of which some may be breeders (Burland et al., 2002; 2004). However, it remains unclear whether males and females are affected equally by ecological constraints of dispersal and whether the context of dispersal differs between sexes.

The aim of this study is to investigate, the frequency, the timing, and the social and ecological context of dispersal in wild Damaraland mole-rats. We address these questions by examining data from a 14-years field study including longitudinal records of body mass of individually recognisable Damaraland mole-rats where detailed life-history records were available.

Material and methods

Study animals

The Damaraland mole-rat, *Fukomys damarensis*, is a singular cooperative breeder distributed throughout the Kalahari region of Southern African. It exhibits a temporal reproductive division of labour with reproduction typically restricted to one reproductive female and one or two males within a group (Bennett & Jarvis, 1988; Bennett, 1990; Burland et al., 2004; Zöttl et al., 2016a). It is an obligate out-breeder and after the loss of a breeder the group may fragment when ecological conditions become favourable (Jarvis & Bennett, 1993). Mole-rats are herbivorous, feeding principally upon underground storage organs (tubers, corms and bulbs, Bennett & Faulkes, 2000). Mole-rats live in a complex burrow system, and their presence can be detected by surface soil mounds (Jarvis & Bennett, 1990; 1991).

Long-term study

This capture, mark and recapture study used modified Hickman live traps baited with indigenous bulbs and sweet potato between 1988 and 2002 to capture 2043 individuals, of which 1127 were recaptured

over the years (584 males and 543 females). The fieldwork was undertaken on the farm Garib near Dordabis, situated 120 km south-east of Windhoek, Namibia (22°58'S 17°41'E). The size of the study site varied between 124.800 and 235.000 m². The mean number of groups in the study area was 21. The climate of this region is modified tropical continental type with two seasons each year, a brief rainy and long dry period. During the study period, rainfall data were collected by a weather station close to the study site. We then calculated the precipitation in mm/day by dividing the sum of the rainfall (in mm) between two trapping periods by the period of time (in days) between both trapping periods and used this measure for further analysis.

Twice a year, all Damaraland mole-rats in the study area were trapped. The animals were captured, individually toe-clipped for identification and sexed by inspection of the genital area. Reproductive females were recognized by their perforated vagina and protuberant nipples, and readily distinguished from the rest of the non-reproductive females. Reproductive males are more difficult to identify as they lack clear morphological differences. In this study, we identified breeder males from long-term life-history and group composition records, including body mass, capture series and by the existence large bulging abdominal or inguinal testes (Jarvis & Bennett, 1993). Body mass was measured using a precision scale, which was accurate to the 0.1 g and rounded to the nearest gram. During each trapping event, we excavated small areas of the burrow system, and the captured animals were kept out of their burrow system until the entire group was captured. A group was considered to be completely captured if it was functionally complete, i.e. it included a reproductive pair and if no animals were trapped for three consecutive days after the last individual was captured. Animals were regarded as belonging to the same group only if they were collected at the same trap site. Where suspected group members were captured at separate trap sites they were only considered to belong to the same group if an individual released at one site was then recaptured at the other site during the same trapping period. We considered a group as an intact group if it included both breeders and if it was successfully recaptured, whereas we consider groups as incomplete when one breeder had disappeared without replacement. Some groups disappeared between capture seasons and may have

moved on, died out, or fragmented. Each trapping season the study area was searched thoroughly to ensure that no groups were missed.

We considered individuals as dispersers when they had been trapped in their natal group and were later recaptured in other existing groups or founded a new group. In contrast, we considered individuals as philopatric when they were captured only in the same group throughout the study period. Because some dispersing individuals may have left the study evading recapture our data represents a subset of dispersing individuals from the total pool of dispersers within the population. The duration of philopatry is the time spent in the natal group. In a philopatric individual, the duration of philopatry represents the time between the first capture and the last capture. Whereas the duration of philopatry of dispersing individuals is the time between the first capture and the date of the last capture in the natal group (before dispersal). Therefore, our estimates use the minimum period of time the individual was in the natal group before this individual was captured in a different group and our estimates of philopatry represent a conservative underestimate.

Data analyses

We used a Fisher exact test to address the questions of whether dispersal is sex biased, and whether males and females disperse in different social contexts. To model the non-reproductive s' probability of dispersal, we fitted a logistic regression (in the framework of Generalised Linear Mixed Models) assuming binomial error structure with dispersal (yes/no) as a response, and absolute body mass at capture and rainfall as covariates. All covariates were z-transformed. Furthermore, we included the identity of the individual and the group identity as random factors. Time spent in the natal group was log transformed and analysed by fitting a linear model with sex as an explanatory variable and the group identity as a random factor. The residuals of the linear model were checked for normal distribution and homogeneity of variance. All models presented were estimated using the software R version 3.2.4 (Team R., 2013) and the package lme4 (Bates et al., 2014).

Ethical note

The project was approved by the ethics committee at the University of Cape Town and the animals were captured under permit from the Namibian Department of Nature Conservation.

Results

Dispersal events increased with rainfall in both sexes (Table 1, Figure 1). Males were significantly more likely to disperse (Fisher test; p-value = 0.029, Table 2) and remained in the natal group for shorter periods than females (Figure 2; Mean duration of philopatry females: 411 days \pm 279 SD (Standard deviation), Males: 371 days \pm 257 SD; LMM: Duration of philopatry: Estimate female = 5.82, SE=0.029; Estimate male: -0.12, SE= 0.04, p-value =0.004; N= 1017).

Table 1. Body mass and rain day affect the probability of dispersal in males and females. Reported are coefficients (estimate), SEs, and P values from LMMs. Bold terms (body mass and rainfall) are significant factors. (N=563 non-reproductive males, N=509 non-reproductive females).

Predictors	Estimate	SE	P- value
a) Male			
Intercept	-3.15	0.27	
Body mass	1.07	0.14	<0.001
Rain day	0.75	0.15	<0.001
b) Female			
Intercept	-3.50	0.35	
Body mass	0.73	0.17	<0.001
Rain day	0.55	0.17	0.001

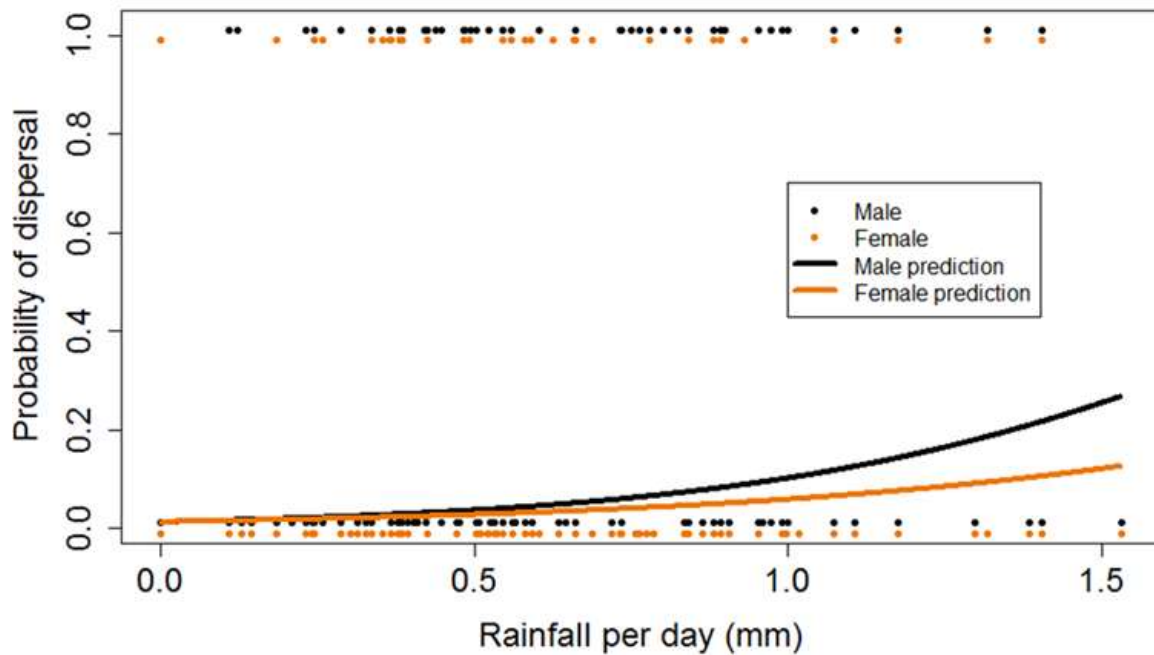


Figure 1. Male and female probability of dispersal depending on rainfall per day (N=563 subordinate males, N=509 subordinate females). Lines indicate the prediction from the glmer.

Males and females differed in the context of dispersal. Males dispersed more often from intact groups, whereas females dispersed more frequently from incomplete groups or groups that disappeared during the previous trapping interval (Fisher test; p -value < 0.001, Table 2). Although dispersal coalitions were rare, males were more likely to disperse with other individuals of the same sex than females (Fisher test; p -value = 0.02, Table 2). Males were more likely to join established groups than females (Fisher test; p -value = 0.015, Table 2) and when male dispersers joined an established group, it was more likely that the previously dominant male disappeared than when females joined an established group (Fisher test; p -value = 0.006, N=32). Although territory inheritance was uncommon, it happened more frequently in female non-breeder than in male non-breeders (Fisher test; p -value = 0.005, Table 2). 6 % of all re-captured non-reproductive individuals became reproductive after dispersal (Table 2), whereas less than 1 % of the philopatric non-reproductive individuals became reproductive (Table 2).

Table 2. Summary of dispersal frequencies of non-reproductive Damaraland mole-rats

	Number		
	Female	Male	Total
Recaptured	509	563	1072
Dispersed	60	93	153
Dispersed from fragmented groups	31	22	53
Dispersed from intact groups	29	71	100
Dispersed alone	53	72	125
Dispersed in coalition	7	21	28
Dispersers creating a new group	52	69	121
Dispersers joined an established group	8	24	32
Dispersers reproductive after dispersal	26	40	66
Philopatric individuals that became reproductive (inheritance)	7	0	7

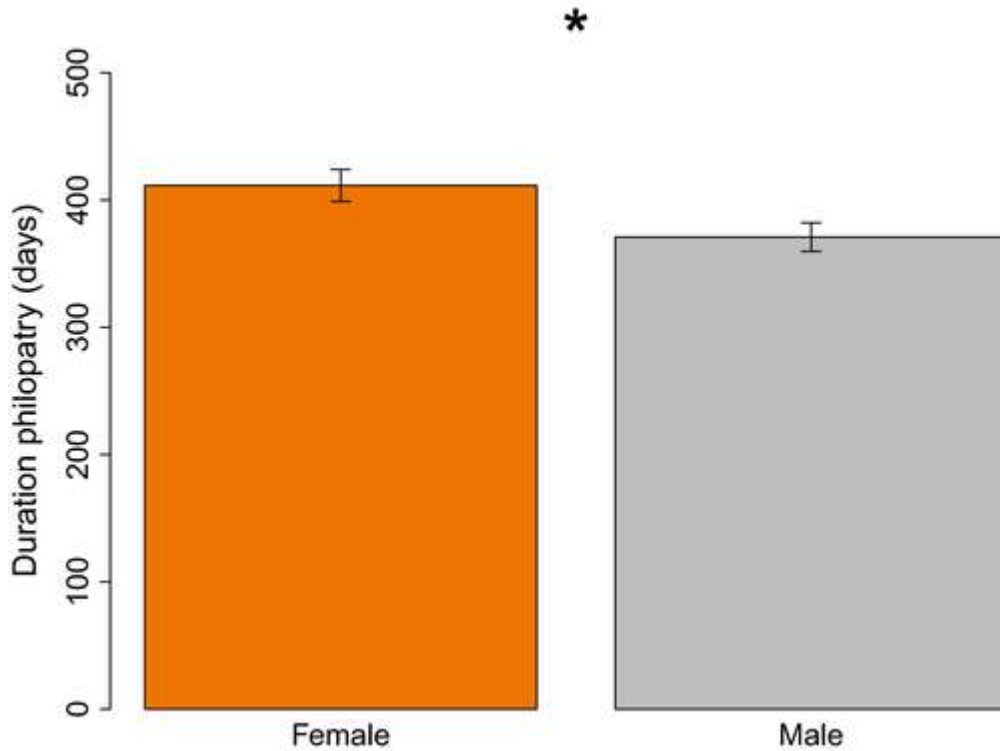


Figure 2. Time spend in the natal group by non-reproductive Damaraland mole-rats. Sample sizes is N=1017 non-reproductive individuals (527 males and 490 females). See main text for statistical results. Asterisk denotes significance.

Discussion

In this study, we investigated ecological constraints and sex-differences of dispersal behaviour of Damaraland mole-rats using data from a 14-years study of a wild population. Although dispersal was dependent on rainfall in both sexes, there were contrasts between males and females in the timing and the context of dispersal. Dispersal was male biased and males dispersed marginally earlier and more frequently in dispersal coalitions than females. Males were also more likely to join established groups and to replace the resident dominant male. Territory inheritance was rarely observed, and if it occurred, it was limited to females. Most individuals obtained a breeding position by dispersing from their natal group. Males departed more frequently from stable groups that were captured over a long period of time. In contrast, females dispersed more frequently from disturbed groups which disappeared, or where one or both breeders had died.

The sex bias in dispersal behaviour and frequency may generate differences in intra-sexual competition among male and among female Damaraland mole-rats. Males were more likely to join established groups than females, suggesting that resident male breeders may more frequently face highly competitive, unrelated intruders. When males joined an established group, it was more likely that the reproductive individual of the same sex went missing than when females joined a group. This may explain shorter tenures of reproduction in males, larger body size of males and lower reproductive skew in lifetime reproductive success among males than among females (Young & Bennett, 2013; Zöttl et al., 2016b). These results combined suggest that philopatric females may sometimes have access to unrelated males (Bennett & Faulkes, 2000; Young & Bennett, 2013) which is also consistent with the genetic structure of wild Damaraland mole-rats (Burland et al., 2004) and the closely related Ansell's mole-rat (*Fukomys anelli*, Šklíba et al., 2012; Patzenhauerova et al., 2013).

The sex differences in dispersal behaviour observed in this study are consistent with the results of previous studies in Damaraland mole-rats and related mole-rat species. Genetic studies of the group compositions of social mole-rats showed that unrelated male non-breeders may be present in the

groups suggesting that immigration into groups in the wild may occasionally occur (Bishop et al., 2004; Burland et al., 2004; Patzenhauerova et al., 2013) and the examination of Damaraland mole-rats that drowned in a channel suggested that males may more readily disperse than females (Hazell et al., 2000). Similarly, males of several other social mole-rat species may be more likely to disperse and may disperse further, whereas females may be more likely to establish a territory in close proximity to their natal group (O'Riain et al., 1996; Braude, 2000; Šumbera et al., 2012; Lövy et al., 2013; Patzenhauerova et al., 2013). Overall, male biased dispersal appears to be the norm across the African mole-rats and it is probably the ancestral state in this clade. As such, differences in intra-sexual competition are probably the consequence of conserved sex-differences in ecology of dispersal.

As previously suggested, life-time reproductive success in Damaraland mole-rats is highly skewed and few individuals ever reproduce successfully (Jarvis & Bennet, 1993; Faulkes & Bennett, 2001). We found that 6 % of all re-captured non-reproductive individuals became reproductive after dispersal, and less than 1 % of the non-reproductive individuals became reproductive without dispersing from the natal territory. Variation in life-time reproductive success and reproductive skew may be substantially more pronounced in females than in males because males show shorter tenures as dominant breeder and reproduction could be shared among several males within groups (Burland et al., 2004; Young & Bennett, 2013). This may also lead to an overestimation of reproductive skew in males in the absence of genetic parentage data.

Our data suggests that territory inheritance is rare but occasionally occurs in females, and reproductive skew is pronounced in this population of Damaraland mole-rats. Our findings suggest that the increased readiness of males to disperse and their more frequent immigration into existing groups may generate contrasts in intra-sexual competition between males and females. Like in many other cooperatively breeding vertebrates, individuals of the more dispersive sex are more often challenged by competitors from outside the group, whereas individuals of the more philopatric sex

may face higher competition from individuals inside the group (Hauber & Lacey, 2005; Clutton-Brock et al., 2006; Young & Bennett, 2013).

Data, code and materials

The datasets supporting this article will be published in publically available repository (Dryad).

Competing interests

'I/We have no competing interests'.

Authors' contributions

M.Z and M.T.T. conceived the idea; N.C.B and J.U.M.J. collected data; M.T.T. and M.Z. analysed data; M.T.T. and M. Z. wrote the paper. All authors commented provided input on the manuscript draft.

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