

## Out-breeding behaviour and xenophobia in the Damaraland mole-rat, *Cryptomys damarensis*

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Out-breeding behaviour and xenophobia were investigated in laboratory colonies of the Damaraland mole-rat, *Cryptomys damarensis*. Foreign males and/or females were introduced into reproductively quiescent colonies and colonies which were actively breeding. Although males attempted to mate with familiar or related females, females only mated with foreign males. This suggests that female avoidance of incest is responsible for out-breeding in this species. Resident males in reproductively quiescent colonies did not attack foreign males or females. However, resident males in actively breeding colonies attacked and killed foreign males. Resident females in reproductively quiescent colonies attacked foreign females but attempted to mate with foreign males. However, in colonies in which the breeding female was approaching parturition, resident non-breeding females also attacked foreign males. Once foreign females attained reproductive status in the colony into which they were introduced they killed all the resident females. These results suggest that xenophobia in the Damaraland mole-rat is influenced by whether or not the colony is actively breeding, and by the reproductive state of the breeding female.

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An organism can increase its reproductive success by remaining in its natal area and mating with related organisms when the cost of dispersal is high and inbreeding depression low. However, inbreeding cannot proceed indefinitely as the degree of inbreeding depression increases with the length of time that inbreeding occurs within a deme. The rate of this increase is dependent on how closely mates are related to each other. Conversely, when dispersal costs (e.g. increased risk of predation and difficulties in entering and successfully breeding in a new social hierarchy — Bengtsson 1978) are low, an organism can increase its reproductive success by dispersing and out-breeding. This is so especially if it means that the dispersing individual's inclusive fitness will increase as the result of the successful breeding of relatives in the natal area (Greenwood 1980; Chesser & Ryman 1986).

The Damaraland mole-rat, *Cryptomys damarensis*, and the naked mole-rat, *Heterocephalus glaber*, are two eusocial rodent species which have very similar social structures and ecology. Both species live in subterranean colonies in which only one female reproduces with 1–3 males. Adult offspring of the breeding animals are philopatric and help raise their younger siblings and maintain the burrow system (Brett 1991; Jarvis & Bennett 1993; Jarvis, O'Riain, Bennett & Sherman 1994). Both occur in arid environments where dispersal from the natal colony is restricted by sparse and erratic rainfall. Dispersal in the Damaraland mole-rat is confined to those times when sufficient rain falls to dampen the soil enough to work it (Jarvis *et al.* 1994). Dispersal in the naked mole-rat, on the other hand, is very rare (Brett 1991; O'Riain, Jarvis & Faulkes 1996) with new colonies forming by fission (Brett 1991). The relative rarity of dispersal in *H. glaber* suggests that dispersal is more costly for this species than for *C. damarensis*. This is supported by the fact that, of animals first captured as non-reproductives, less than 0.1% of *H. glaber* compared to 8% of *C. damarensis*, were subsequently found

as reproductives (Jarvis *et al.* 1994). Outbreeding may not be the reason why organisms disperse from their natal area (Moore & Ali 1984; Bulger & Hamilton 1988; but see Packer 1979, 1985; Pusey 1980; Harvey & Ralls 1986). However, if inbreeding avoidance and dispersal are related in mole-rats, as has been shown for other rodents (Caley 1987; Wolff, Lundy & Baccus 1988), then *C. damarensis* should display a lesser tendency to inbreed than *H. glaber*, given the lower cost of dispersal for *C. damarensis*. As predicted, *H. glaber* is highly inbred (Reeve, Westneat, Noon, Sherman & Aquadro 1990; Honeycutt, Nelson, Schlitter & Sherman 1991) whereas *C. damarensis* apparently is an obligate out-breeder.

Out-breeding in *C. damarensis* has been inferred from mark/recapture studies which suggest that new colonies are founded by males and females which come from different colonies (Jarvis & Bennett 1993; Jarvis *et al.* 1994). There is also experimental evidence that suggests that *C. damarensis* out-breeds. Breeding can be initiated in reproductively quiescent (breeding female has died or been removed) laboratory colonies by the introduction of foreign males (Jarvis & Bennett 1993; Rickard & Bennett 1997). However, it is possible that the introduction of foreign males, may have stimulated reproduction between colony mates as well as between colony females and the introduced male. The paternity of the resultant offspring was not assessed and there could be no certainty that the foreign male had sired the offspring. This problem could be circumvented through the introduction of foreign females rather than males. Should the foreign female be the only female to become pregnant, out-breeding will have been demonstrated.

Foreign conspecifics should affect the reproductive success of individuals that outbreed differently from that of individuals that inbreed. There is evidence that xenophobia is influenced by the threat that intruders represent to the reproductive opportunities of the residents (Grinnell, Packer & Pusey

1995). In *H. glaber*, reproductive opportunities arise from within the colony and are influenced by the individual's position in the colony hierarchy (Jarvis 1991; Reeve & Sherman 1991). Any intruder, male or female, would diminish an individual's chances of attaining reproductive status (O'Riain & Jarvis 1997) and should be rejected by colony members. This is in fact what happens (O'Riain & Jarvis 1997). If *C. damarensis* does out-breed, reproductive opportunities arise only from outside the colony. Foreign conspecifics of the opposite sex represent breeding opportunities while foreign conspecifics of the same sex represent competition for access to the opposite sex that is reproductively active. Thus, as in *H. glaber*, foreign conspecifics of either sex should be rejected by residents of the same sex, albeit for slightly different reasons. Reproductively quiescent *C. damarensis* colonies, on the other hand, should be relatively tolerant (less agonistic behaviour directed towards foreign animals) of foreigners (*cf.* Jarvis & Bennett 1993 and Rickard & Bennett 1997). Foreign animals of either sex entering a reproductively quiescent colony would represent a reproductive opportunity, either directly through mating with the foreign individual, or indirectly should a close relative mate with the foreigner. In terms of dispersal costs, such a foreigner would represent a relatively inexpensive breeding opportunity. Nevertheless, there should be some differences in the way foreign animals are treated by resident animals on the basis of whether they are of the same or of the opposite sex. An animal of the opposite sex represents a reproductive opportunity while an animal of the same sex may represent a threat to the reproductive status of the residents.

Here we report on a series of experiments, (a) to confirm that the Damaraland mole-rat is an obligate out-breeder, and (b) to test our predictions on xenophobia.

## Methods

Mole-rats were housed in transparent plastic burrow systems in rooms in which the temperature was maintained at 27°C. Food was provided *ad lib*. The toilet tunnels of the burrow systems were cleaned daily and the wood shavings in nest boxes changed as required, about once a week. The following four experimental colonies were used in three separate experiments.

### Colony 1

This was a captive-born colony. The colony was comprised of the breeding pair and their adult offspring which included four males and five females. Three months prior to the commencement of experiment 1 (see below) the breeding female was removed resulting in the cessation of breeding in this colony. The other females were imperforate and remained so up to the commencement of this study. The parents of the breeding pair of this colony were caught in Dordabis, Namibia in 1988.

### Colony 2

This colony was captured without the breeding female in Dordabis in 1994 and remained reproductively quiescent for the two years prior to the commencement of this study. The colony consisted of eight males and two females, all adults. Both females were imperforate.

### Colony 3

This colony was captured at Dordabis in 1994. It consisted of six animals, three males and three females. At the time of capture, one male and female (mole-rats number 5 and 6, respectively) were juveniles and the other male and female (mole-rats number 3 and 4, respectively) were recently weaned young. We therefore assumed that they were siblings from different litters. The remaining male and female (mole-rats number 1 and 2, respectively) were both adults and the female had visibly swollen teats with evidence of having suckled. It was assumed that the colony consisted of parents and four offspring. However, there was no reproduction in this colony during the two years prior to this experiment, even though female 2 remained perforate throughout. At the time of the experiment the other two females were adult but imperforate.

### Colony 4

This colony was a captive born colony started with a male and female from Colony 2 after they had been separated from each other for 18 days. This separation was done after experiment 1 (see below) and was part of a series of kin recognition experiments (Jacobs & Kuiper, unpubl.). At the time of this study the colony consisted of three adult males and four adult females.

## Experiment 1

The aim of this experiment was to determine if reproduction could be initiated in reproductively quiescent colonies through the introduction of foreign female conspecifics. Foreign females rather than males were used to ensure that any mating that might be initiated through such introductions only occurred with the foreign females. An imperforate female from colony 1 was isolated from the colony with a reproductively active male colony mate. A second imperforate female from a colony captured in Hotazel, South Africa, was similarly isolated with a male colony mate. These males had either mated with the breeding female prior to her removal from the colony, or had mated when paired with a foreign animal. This isolation was necessary to ensure that inbreeding avoidance was at least partly responsible for non-breeding females not breeding with their male colony mates. The alternative possibility is that non-breeding females do not breed in their natal colonies because they are reproductively suppressed by aggression from their colony mates (Bennett 1994; Bennett, Jarvis, Millar, Sasano, & Ntshinga 1994). All reproductive behaviours (solicitation, courtship, mounting and copulation) between each female and her male colony mate were recorded for a minimum of 36 h of observation over three weeks. After this period of isolation the female from colony 1 was introduced into colony 2 and the female from Hotazel was introduced into colony 1. Both females were still imperforate at the time of their introduction as foreign females into these two colonies. To ensure that there was no mating between colony mates in the test colonies prior to the introduction of the foreign females, colony 2 was observed for 36 h and colony 1 for 50 h. All interactions, including reproductive behaviour, were recorded. Reproductive behaviours were also sampled *ad lib*. After the introduction of the foreign females into their respective test colonies, each

colony was observed for the same length of time as before the introduction. Scan sampling at 3-min intervals for observation periods ranging from 2 to 4 h, with a 10-min break between each hour, was used throughout this experiment.

### Experiment 2

In this experiment we introduced four foreign males and four foreign females into colony 3 to ascertain whether foreign males and females were treated differently by resident animals. Four of the foreign animals (two males and two females) came from colony 1. The remaining four were all captured in Hotazel. The foreign animals were introduced one at a time in random order, for 1 h each, during which interactions with the resident animals were recorded using continuous focal sampling. There was a 48-h period between each introduction. The colony was observed for a total of 50 h before and after experimental manipulation to ensure that there was no mating between colony mates. The same protocol as in experiment 1 was used during this part of the experiment.

### Experiment 3

This experiment involved the introduction of a foreign male into each of colonies 1, 2, and 4 to ascertain if these males were accepted or rejected by actively breeding colonies. This experiment was conducted approximately a year after experiment 1. All three colonies were actively breeding at the time (regular litters every 3 to 6 months — D. Jacobs unpublished data). At the time of this experiment colony 1 consisted of six males and five females and colony 2 consisted of nine males and three females. All interactions between the foreign males and colony members were recorded using the same manipulation protocol as in experiment 2. Because of the outcome of these introductions and experiments 1 & 2 (see results below) it was decided not to attempt to introduce foreign females into these colonies. As in the first two experiments care was taken to ensure that animals introduced into each of the test colonies were only distantly related if at all.

## Results

### Experiment 1

In both colonies 1 and 2, the number of scans during which reproductive behaviours were observed increased after the introduction of the foreign females (from 4–28 scans and from 23–127 scans, respectively — Fisher's exact test = 80.49;  $df = 1$ ;  $p < 0.0001$ ). Reproductive behaviours before introduction consisted of unsolicited mountings by males (three males in colony 1 and four males in colony 2) of one particular female in each colony. The female mounted in colony 1 was the daughter of one of the three males and the sister of the other two males that attempted to mount her. Although the relatedness of the animals in colony 2 was not known it is likely that the female was closely related to the males that attempted to mount her (Jarvis & Bennett 1993). All resident females in both colonies remained imperforate throughout the study despite these mounting attempts. Without exception reproductive behaviours after the introduction of foreign females were either initiated by the foreign females or directed towards them.

Both foreign females remained imperforate prior to being introduced into the test colonies and did not display any reproductive behaviour either in their natal colonies, or when isolated with a familiar male colony mate. However, when placed in their respective test colonies, both females were observed soliciting males by the third day after introduction and were mounted by the fourth day. Although each foreign female solicited more than one male both females seemed to solicit one particular male more than the others (Kolmogorov-Smirnov,  $D = 8$ ;  $k = 3$ ;  $n = 18$ ;  $p < 0.002$  for colony 1;  $D = 15.6$ ;  $k = 5$ ;  $n = 83$ ;  $p < 0.002$  for colony 2). Within 6 days both females were perforate and their genitals were visibly swollen. The female introduced into colony 1 gave birth 126 days after being introduced, and the female introduced into colony 2, 112 days after being introduced. This means that they must have conceived after exposure to the foreign males in the test colonies because the gestation period of *C. damarensis* is 78–92 days (Bennett & Jarvis 1988). Both these females, which were left in the test colonies after the experiment, have given birth to subsequent litters. The resident females of both colonies remained imperforate.

Upon introduction to the test colonies the resident females violently attacked the foreign females whenever they were encountered in the burrow system. The foreign females were, however, able to avoid these females by retreating to the far corners of the burrow system. The resident females also found it difficult to get to the foreign females as a result of the resident males monopolising the foreign females. However, subsequent to the study and prior to the birth of their first litters, both foreign females systematically attacked and killed the resident females in their respective colonies. This was unexpected because foreign conspecifics had previously been paired with no apparent aggression (Jarvis *et al.* 1994), and from time to time aggression between female colony mates within unmanipulated colonies occurs but never with fatal consequences.

### Experiment 2

Foreign males and females introduced into the test colony were treated differently. Resident females attacked (see Jacobs, Bennett, Jarvis & Crowe 1991 for a description of this behaviour) foreign females (33 attacks versus 4 mountings) but mated with foreign males (32 mountings versus 2 attacks)(Fisher's exact test = 39.13;  $df = 1$ ;  $p < 0.0001$ ). Although resident males did not attack foreign animals of either sex they tended to spar with foreign males more than with foreign females (95 versus 32 sparring interactions), and mounted foreign females more than foreign males (12 versus 9 mountings)(Fisher's exact test = 6.36;  $df = 1$ ;  $p < 0.02$ ).

There were also differences in the responses of resident females towards foreign males in terms of the frequency of reproductive behaviours. Female 4 interacted significantly more often with the males than did the other resident females (83% versus 17% and 0% — Fisher's exact test = 15.98,  $df = 2$ ;  $p < 0.001$ ). Her reproductive behaviour included courtship and solicitation, mounting and being mounted. Female 2 (the original breeding female) briefly mounted two of the males once and one of the males four times. Apart from this she did not show any interest in the males. Female 6 displayed no interest in the males whatsoever. Similar to the results of

experiment 1, although female 4 solicited all the foreign males, she tended to solicit some males more than others (Kolmogorov-Smirnov,  $D = 6.5$ ;  $k = 4$ ;  $n = 22$ ;  $p < 0.05$ ). More importantly, in terms of out-breeding, female 4 became perforate by the time the seventh animal (fourth male) was introduced. The attacks by female 4 on the eighth animal (a female) introduced increased in intensity, and even though she was carefully watched, she was still able to severely wound the foreign female towards the end of the hour long observation period. The period and the experiment were immediately terminated. Fortunately the foreign female recovered fully from her injuries. In light of the results of experiment 1, the increase in intensity of attacks by female 4 on the foreign female is probably an indication that female 4 was becoming reproductively active.

At no time during this experiment was any agonistic or reproductive behaviour observed between colony mates. Female 6 who displayed very little interest in the males and who was older than female 4 remained imperforate. During the 50 h of pre- and post-manipulation observation no reproductive behaviours were observed between colony members.

### Experiment 3

There was a marked increase in agonistic behaviours in all three colonies after the introduction of the foreign males (Table 1). All agonistic behaviours were directed towards the foreign males and were so intense that the foreign males had to be removed from two (colonies 2 and 4) of the three colonies before the end of the hour (after 32 and 56 min, respectively) to avoid serious injury to them. Despite this, the male introduced to colony 2 nevertheless died after being removed from this colony even though it had no visible signs of injury. During the hour of observation on the foreign male introduced into colony 1, there was a minimal amount of agonistic behaviour directed towards it (Table 1). It was also observed at rest in the nest box alongside some of the resident animals. It thus appeared to have been accepted by colony 1, and it was decided to leave this mole-rat in the colony overnight. However, the next morning the foreign male was found dead.

In all three colonies male residents were responsible for most of the attacks on the foreign males and, with the exception of colony 2, largely prevented interaction between the foreign males and non-breeding females (Table 2). At no time did the breeding females of each colony interact with the foreign males. It thus appears that reproductively active colonies are less tolerant of foreign conspecifics than reproductively quiescent colonies.

**Table 1** Frequency of agonistic behaviours per hour per mole-rat (mean  $\pm$  SD;  $n = 20$  h) before and after the introduction of a foreign male into three reproductively active colonies

	Before	After*	One sample $t$
Colony 1	0.47 $\pm$ 0.65	21	$p < 0.001$
Colony 2	0.59 $\pm$ 0.81	181	$p < 0.001$
Colony 3	1.08 $\pm$ 1.04	172	$p < 0.001$

\* Frequency of agonistic interactions experienced by the foreign male.

**Table 2** Frequency of agonistic behaviours per resident male and female of reproductively active colonies directed towards foreign males

	Males	Females
Colony 1	8	0.3
Colony 2	46.5	28.5
Colony 3	23	0

### Discussion

Small sample sizes are an important caveat in the interpretation of our data. Development of large sample sizes were precluded by the unexpected fatalities and the logistics of having to separately house (to avoid fatalities) a female (and her mate) that had become reproductively active. However, none of the data contradicts the conclusion that *C. damarensis* only breeds with unfamiliar animals.

The above caveat aside, this study confirms that *C. damarensis* out-breeds, and suggests that it is female avoidance of incest that results in out-breeding. Firstly, females that were initially imperforate non-breeders became breeders (experiment 1) or at least perforate (experiment 2), only after they had been exposed to foreign males. Secondly, all reproductive activity ceased when a colony was no longer exposed to foreign individuals (experiment 2). Lastly, males attempted to mate with familiar female colony mates (a daughter in one instance — experiment 1) suggesting that they were willing to mate incestuously, but were prevented from doing so by the unwillingness of their female colony mates.

Nevertheless, it is possible that females rejected familiar male colony members on criteria other than familiarity, e.g. on the basis of the 'attractiveness' of the male. This seems unlikely, however, because both females in experiment 1 solicited more than one of the resident males, and all of the foreign males in experiment 2 were solicited. However, in both experiments, the females showed a preference for one particular male, suggesting that females will mate with any unfamiliar male but may develop a preference when faced with a number of unfamiliar males.

Thus, although the social system of *C. damarensis* is very similar to that of *H. glaber* (Jarvis & Bennett 1993; Jarvis *et al.* 1994), *C. damarensis* out-breeds while *H. glaber* readily inbreeds (Faulkes, Abbott & Mellor 1990; Reeve *et al.* 1990; Honeycutt *et al.* 1991). The selection of inbreeding and out-breeding as mating strategies should be strongly influenced by inbreeding depression and the cost of dispersal. If inbreeding depression is low and the cost of dispersal high, inbreeding should be favoured. If the inbreeding depression is high and the cost of dispersal low, out-breeding should be favoured (Smith 1979; Chesser & Ryman 1986). This suggests that the cost of dispersal in *H. glaber* must be higher than that in *C. damarensis*, and inbreeding depression lower. Unfortunately, data on inbreeding depression in these two species are not available.

Mark/recapture studies indicate successful dispersal rates of 8% for *C. damarensis* (Jarvis *et al.* 1994) and less than 0.1% for *H. glaber* (Jarvis *et al.* 1994; Braude S.H., pers.

comm.). The value for *C. damarensis* may be higher because it is based on mark/recapture data collected over six years which covered a period of unusually low rainfall. Average rainfall fell in only one of the six years and for that year the successful dispersal rate was 14% (Jarvis & Bennett 1993). The differences in the mating strategies of these two species may thus partly be due to differences in dispersal costs.

Out-breeding may also be precluded in *H. glaber* because it forms new colonies by fissioning, breeders arising from within the splinter group (Brett 1991). In *C. damarensis* out-breeding is facilitated by the dispersal of individual animals, and new colonies are started by pairs of animals from different colonies (Jarvis & Bennett 1993). Differences in the formation of new colonies are probably due to differences in thermoregulation and the burrowing abilities of the two species. *H. glaber* is smaller (mean = 30 g) than *C. damarensis* (mean = 131 g). It is also naked and poikilothermic whereas *H. damarensis* is hairy and endothermic (Jarvis *et al.* 1994). *C. damarensis* is, therefore, able to disperse individually because it is large enough to excavate burrows on its own in the softer soil in which it lives (Jarvis *et al.* 1994). *H. glaber*, on the other hand, needs the help of conspecifics to extend its burrows in the harder soil in which it lives (Jarvis *et al.* 1994) and to maintain a constant body temperature by huddling (Buffenstein & Yahav 1991). Hence it forms new colonies by fissioning.

The treatment of foreign individuals in reproductively active colonies of both species should be influenced by the potential impact of that individual on the reproductive success of the residents (*cf.* Grinnell *et al.* 1995; O'Riain & Jarvis 1997). In both *H. glaber* and *C. damarensis* foreign conspecifics could dilute the reproductive success of the breeding animal of the same sex through direct competition for the opposite sex. This should result in foreign conspecifics of either sex being rejected by the resident breeders of the same sex.

Non-breeders in both species should also reject foreign conspecifics to prevent the dilution of their reproductive success. This dilution would occur in different ways in the two species. In *H. glaber* colonies, foreign conspecifics and colony mates of the same sex represent direct competition for mates because breeding opportunities arise from within the colony. The reproductive success of non-breeding *C. damarensis* would be reduced if a foreign conspecific mated with one of their parents because then they would be helping to raise offspring that are not full siblings. This means that in both species reproductively active colonies should reject foreign conspecifics of either sex, albeit for slightly different reasons. This is in fact the case. *H. glaber* is highly xenophobic towards foreign conspecifics of either sex (O'Riain & Jarvis 1997). Similarly, in the reproductively active colonies of *C. damarensis* (experiment 3) the attacks on the foreign males were so violent and continuous that resident females had very little opportunity to interact with the foreign males (Table 2). Unfortunately, because of the fatal consequences of male introductions into reproductively active colonies (experiment 3), and the results of experiment 1 and 2, it was decided not to attempt female introductions into reproductively active colonies. There is therefore no data on how foreign female conspecifics are treated by reproductively active

*C. damarensis* colonies.

Reproductively quiescent laboratory colonies of *C. damarensis* may have an analogue in the wild in the form of colonies which have lost a reproductive, but which have not yet dispersed. There is evidence that such colonies may delay dispersal (in three cases for at least 12 months) if the summer rains fail (Jarvis & Bennett 1993). In these reproductively quiescent colonies foreign males may represent an opportunity to at least increase indirect fitness in a situation where the only alternative is no reproduction at all. This possibly explains why resident males in reproductively quiescent colonies were more tolerant of, and only sparred with, foreign males (Rickard & Bennett 1997; experiment 2 this study). It is likely that sparring was simply a means of incorporating the foreign individual into the colony's hierarchy (Rickard & Bennett 1997).

The situation for females of reproductively quiescent colonies may be different from that of males. If a foreign female became established in the colony as the breeding female it would put an end to any direct reproductive success a resident female might have (at least in that particular burrow system), and might even represent a threat to her life (experiment 1). One would thus expect resident females to reject all foreign females in all situations. This possibly explains the attacks of the resident females on foreign females in experiments 1 and 2. Although there is no data on the response of reproductively active colonies to foreign females, the fact that foreign males were attacked by the females of one of the reproductively active colonies (colony 2, Table 2), suggests that foreign females would be treated in the same way.

It is not known what eventually causes colony fragmentation in the wild. It may simply be the onset of rain which makes burrowing and dispersal easier (Jarvis *et al.* 1994). Alternatively, it is possible that some dispersal might be initiated by foreign conspecifics entering reproductively quiescent colonies and, together with a resident of the opposite sex, becoming established as a reproductive. The aggression that then ensues between the foreigner and resident non-breeders (experiments 1 and 2) might be incentive for the remaining residents to disperse. It is probable that foreigners would win such encounters because they would be fighting for a reproductive opportunity while the residents would simply be fighting to stay in the burrow system.

Attacks on the foreign male by non-breeding females in colony 2 (experiment 3) is more difficult to explain. It might be related to the fact that the breeding female in this colony was nearing parturition at the time of the experiment. She gave birth one week after the experiment. A foreign male may represent some threat to the newly born siblings of these non-breeding females. Resident females may thus be sacrificing the potential reproductive success they might have achieved in the relatively distant future had they mated with the foreign male, in order to protect their immediate reproductive output in the form of siblings. If so, it provides further support for the hypothesis that xenophobic behaviour in *C. damarensis* is influenced by the effect foreigners will have on the reproductive success of resident animals.

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