Notes on the social dynamics and behaviour of reintroduced lions in the Welgevonden Private Game Reserve

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We report on the social dynamics and behaviour of five lions reintroduced to the Welgevonden Private Game Reserve. Despite initially being together in a boma for three months, the lions did not stay together. Aggression was also noted after the release of a female, which had been placed in the boma earlier after sustaining an injury. The results showed different lions associating and breaking away from the group on various occasions, which illustrated the flexibility of lion social structure when prides are disturbed. The findings are similar to those observed in the Kruger National Park after a lion-cropping programme. The lions that were reintroduced on Welgevonden were variously related, and the way in which they finally associated in prides was based on their relatedness. This raised the question of whether association took place by chance, or whether there was some kind of kin-recognition in lions, resulting in them associating mostly with kin. It was not possible to prove kin-recognition in this study, but the association with kin could lead to genetic problems in the future due to inbreeding.

Key words: kin-recognition, lions, Panthera leo, reintroduction, social behaviour.

INTRODUCTION

Several species of Panthera once ranged over four continents, but conflict between lions (Panthera leo) and humans caused lions to become restricted almost entirely to national parks and wildlife reserves (Schaller 1972; Anderson 1981). The development of the ecotourism industry in southern Africa, and the creation of new, privately owned wildlife reserves led to a demand for introductions of lions. Although translocation and reintroduction are now well-practised techniques that are used to establish lion populations in new wildlife reserves, little information is available on the way that lions behave after reintroduction. There are few documented studies on the post-release behaviour of large African carnivores, despite the fact that post-release monitoring is essential in determining whether or not a reintroduction was successful (Van Dyk 1997).

The behaviour and social systems of natural lion populations are well studied, and published information of all aspects of lion social behaviour is available. Lions live in social groups called prides that occupy stable ranges. The prides usually consist of a group of females that were born in that pride, their offspring and a coalition of adult males that took over the pride from elsewhere (Packer 1986). Lion prides usually occupy a limited area, but a proportion of females live as solitary animals in stable ranges (Packer 1986), whereas a proportion of males live outside prides and are nomadic (Schaller 1972). Membership in prides is stable but pride members are not in continuous association (Schaller 1972; Packer 1986). Adults of the same pride are often scattered in small sub-groups throughout the pride range, and each adult can also spend a considerable time alone.

Although females can be nomadic, it is especially the males who become nomadic after puberty (Bothma & Walker 1999). Such males will then wander widely until they are able to evict a resident male or males from a pride. However, some lions will stay nomads for their whole lives. Nomadic lions travel widely and the size of the area used by nomads can be as much as 10 times that of prides (Schaller 1972). Nomadic male lions are markedly tolerant of each other and usually accept strangers easily, probably because nomads occupy undefended ranges. Solitary males often join unrelated companions. Pride membership and being nomadic are not mutually exclusive and a nomad may become a pride resident, and vice versa (Bothma & Walker 1999).
In a lion pride, female companions are usually closely related, male companions can be either closely related or unrelated, and mating partners are usually unrelated (Packer et al. 1991). Female cubs born to pride lionesses show a strong tendency to remain and breed close to the site of their birth. The majority of females remain in their natal group, but some females emigrate and disperse into other areas, usually close or adjacent to their natal range (Pusey & Packer 1987). The reproductive success of females may depend on the familiarity of the area or neighbours. However, the advantage of finding an unrelated partner may be outweighed by the cost of dispersing to a new range. Sisterhood has its advantages, and pride mates will jointly defend their cubs against invading males. Although most lion prides show a fair degree of social order among females, some females live in groups with no social hierarchy between the pride lionesses (Stander 1992).

The social structure of lions is well developed. It is often believed that lions are prime examples of sociality in predators. Although this might not be altogether true (Packer & Pusey 1997), there are still distinct social patterns and behaviour, as the above summary of lion social behaviour indicates. However, in the case of reintroduced lions, a major disruption in the social structure of the lions has occurred before their release in a new area. Mostly young lions are captured and removed from their natal prides. These lions, often from different prides and reserves, are then put together into a boma or a reserve and are forced to bond. It has been observed in natural lion populations that unrelated females formed new prides (Smuts 1978; Owens & Owens 1984), although the dispersal of pairs or single females is common, these small cohorts do not easily join up with other solitary lions (Packer 1986). This fact can severely reduce the chances of success of a lion reintroduction attempt. This study provided an opportunity to observe the social behaviour of reintroduced lions and to compare it with normal lion behaviour. The behaviour that was observed after the lions were released serves as the focus of this paper.

**STUDY AREA AND METHODS**

Welgevonden (24°10'S; 27°45'E to 24°25'S; 27°56'E) is a 33 000 ha, privately owned wildlife reserve situated in the Waterberg region of Limpopo Province, South Africa. Welgevonden forms part of an undulating plateau that rises to 1000 m above the surrounding lowlands. The terrain is mainly mountainous, with several plateaus and open plains on the higher-lying areas. The leached, acidic, sandy soils give rise to nutrient-poor, low-quality sourveld that cannot support large numbers of herbivores. The ability of the veld to support large numbers of grazers is further decreased by up to 60% rock cover in certain areas. The reserve falls in the Sour Bushveld (Veld Type 20 of Acocks 1988) and the Waterberg Moist Mountain Bushveld (Veld Type 12 of Low & Rebelo 1996). Welgevonden was developed in 1993 as a Big Five reserve with only leopard (Panthera pardus) still occurring there naturally at that time. The other members of the Big Five were all reintroduced. Before this, the land comprised private farms with cattle ranching the dominant form of land-use.

Competition with resident animals of the same or different species in the release area can have an influence on the behaviour of lions after their release into a reserve. On Welgevonden there were no other lions or large carnivore competitors, like spotted hyaenas (Crocuta crocuta), on the reserve during the study period that might have influenced their behaviour after release.

One male and two female lions were introduced from Pilanesberg National Park and one male and a female lion from Madikwe Game Reserve (Table 1). WLG1 and WLG3 were siblings. WLG2 and WLG4 were half-siblings (same father) within the same cohort, and their mothers were possibly

<table>
<thead>
<tr>
<th>Lion</th>
<th>Sex</th>
<th>Origin</th>
<th>Relationship with other lions</th>
<th>Age in months at reintroduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>WLG1</td>
<td>Male</td>
<td>Pilanesberg</td>
<td>Sibling of WLG3</td>
<td>36</td>
</tr>
<tr>
<td>WLG2</td>
<td>Male</td>
<td>Madikwe</td>
<td>Half-sibling of WLG4</td>
<td>35</td>
</tr>
<tr>
<td>WLG3</td>
<td>Female</td>
<td>Pilanesberg</td>
<td>Sibling of WLG1</td>
<td>36</td>
</tr>
<tr>
<td>WLG4</td>
<td>Female</td>
<td>Madikwe</td>
<td>Half-sibling of WLG2</td>
<td>34</td>
</tr>
<tr>
<td>WLG5</td>
<td>Female</td>
<td>Pilanesberg</td>
<td>Aunt of WLG1 and WLG3</td>
<td>43</td>
</tr>
</tbody>
</table>

Table 1. Sex, origin and age at reintroduction of the lions reintroduced into the Welgevonden Private Game Reserve in the Waterberg region of South Africa.
also related (from the same pride but their relationship is unknown). The mother of WLG5 was also the grandmother of WLG2 and WLG4, but her father was from a different pride than the male forefathers of WLG2 and WLG4. For clarity, the genealogy is illustrated in Fig. 1.

All five lions arrived together on Welgevonden and were first put into a holding boma of 50 x 50 m, where they were kept for three months. The boma was screened on the side from which the lions were fed to prevent them from seeing humans and associating them with the food. At the time of release it appeared that the lions had formed a cohesive single group as no excessive aggression was observed between any of the lions while they were in the boma. Upon their release, the lions were monitored daily by visual observation and radio-tracking equipment. Four lions (WLG1, WLG2, WLG4 and WLG5) were fitted with radio-collars. These radio-collars each consisted of a MMK4 transmitter from Telonics™ (Mesa, Arizona, U.S.A.) in the 148–151 MHz wavelength range. A Yaesu FT 290RII receiver and a four-element Yagi antenna were used to locate the radio signals from the collars. The distance from which the signal could be received ranged from 300 m in mountainous areas, to 3–4 km in higher-lying or flat areas. The radio-collars were replaced on two occasions when their battery life expired, or when they became too tight, especially on the male lions. Each lion could be recognized individually during the study period that lasted from January 1998 to February 2002. It was only possible to do long-term, continual monitoring of the lions up to October 1999. Time restraints prevented continual observation during the latter part of the study.

RESULTS
The results are given as a detailed case history of the events and behaviour of the lions after they were reintroduced into Welgevonden. The lions were released on 16 January 1998. During the night female WLG5 broke away from the group and was located the following morning about 6 km from the boma and the other lions. On the 21 January 1998, she was located at a bushpig kill with a fresh puncture wound on her back, probably sustained while killing the bushpig. The other lions could not have inflicted the wound, as they were about 5 km away at that time. She was seen again on 28 January 1998. The wound on her back was now infested with maggots, infected and she was weak. She was darted the following morning, the wound was treated and she was returned to the boma to recover. As follow-up treatment of the wound was necessary, the lioness was kept in the boma for another month.

In this period, the other lions had settled on the plains close to the boma, staying within a 3–4 km radius of the boma. On the morning of 6 March 1998, they were observed to approach the boma for the first time after their release and appeared to be interested in the female inside. As the wound on the back of WLG5 had recovered well it was decided to release her while the other lions were in the immediate area, expecting that they would join. The other lions immediately approached her after she moved out of the boma. She was aggressive towards the two males, not allowing them to approach her. Every time they approached her, she would snarl and growl at them, warning them to keep their distance.

All five lions rested close to the boma for the rest of the day, with WLG5 lying about 40 m away from the others. Whenever the males moved closer to her during the day, she became aggressive and growled at them. This situation continued for the following two days. However, she allowed female WLG4 to come close to her, and they even socialized. Female WLG3 appeared unconcerned with the events around her and did not attempt to make any contact with WLG5. However, the continued
aggression of WLG5 towards the males resulted in them returning the aggression, culminating in an attack by the males in the late afternoon of the second day after her release from the boma. When the males attacked WLG5, WLG3 joined them in the attack. WLG4 also joined the skirmish, but attacked the males and WLG3 instead, and chased them off. This happened twice more during the evening. During the night, WLG4 and WLG5 broke away from WLG1, WLG2 and WLG3 and moved away together. They rejoined them three days later, but the aggression between the males and WLG5 continued, although no more fighting was observed. WLG4 intervened every time that the males showed any aggression or moved towards WLG5, snarling at them and chasing them off. WLG4 and WLG5 broke away again the following day. During the following 10 weeks the groups were observed to rejoin on five different occasions, but the situation described above repeated itself every time. They would only stay together for a short time, three times for one day and twice for two days, before going their separate ways again.

The behaviour of WLG4 in attacking the males after they had attacked WLG5 appeared unusual because WLG4 and WLG5 came from different prides in Pilanesberg. Female WLG4 attacked the males with whom she had been familiar since release and to whom she did not previously show any aggression. However, it did not result in permanent disharmony between them and she remained friendly with the males whenever they came together for short periods, but still did not allow them too close to WLG5. When WLG4 and WLG5 joined the group for the sixth time on 25 May 1998, WLG5 appeared to be in oestrus. The previous aggression was no longer apparent and there was no sign of aggression from either WLG4 or WLG5 towards the males, or from either of the males towards WLG5. WLG1 then mated with WLG5 over a period of three days. During this time WLG3 broke away from the group and moved away to the Elandshoek region in the southern part of the reserve, about 15 km from the release boma. She remained on her own for seven months before she moved back to the central part of the reserve, apparently searching for the other lions. She joined WLG1 for two days while they mated, after which she returned alone to Elandshoek. She had her first litter of four cubs 14 weeks later and managed to raise them on her own. When her cubs were 21 months old she mated a second time, but this time WLG1 went looking for her on Elandshoek, 14 km away from the core area of his range. He returned to the central part of the reserve after they had mated, and she had her second litter of four cubs on Elandshoek 14 weeks later. She has stayed with her offspring in the southern part of the reserve ever since, which is now over two years, and did not once move into the range of the western pride. However, WLG1 joined her permanently in August 2001 and established his territory in the southern parts of the reserve, while WLG2, WLG4 and WLG5 remained in the central and western parts of the reserve. The original group in the boma has therefore eventually split into two prides, the western pride consisting of WLG2, WLG4, WLG5 and several cubs, and the southern pride consisting of WLG1 and WLG3 with their offspring.

**DISCUSSION**

The events described above reveal interesting aspects of lion social behaviour. It has previously been observed that reintroduced lions tend to stay close to their release site after their release (Hunter 1998), before slowly dispersing into the neighbouring areas. In natural populations a lack of social stability results in increased mortality and movement (Stander 1990). When lions are reintroduced, especially from different prides, there is an obvious lack of social stability, and although it appeared as if a cohesive social bond had developed between all the lions while they were in the boma on Welgevonden, it was not permanent enough to prevent later disintegration.

The described events have similarities with what was observed in the Kruger National Park after a lion-cropping programme (Smuts 1978). Most lions that recolonized cropping areas came as individuals or small groups and some banded together. It was also noted that unrelated groups showed tolerance towards one another, and although they squabbled considerably, they eventually calmed down. This indicated that different groups utilizing the same area and showing a degree of tolerance towards one another could join and form a pride. However, in one area in the Kruger National Park, the lions that banded together still remained unstable 17 months after the cropping operation. Smuts (1978) speculated that the recovery period of 17 months was too short to have attained a high level of social stability.

The effects of a cropping programme share similarities with reintroduction in the sense that individuals from a pride are left alone after a distur-
bance. This leads to unfamiliar and often unrelated animals being forced to bond to eventually form prides. Although it can appear as if different lions bonded while in the boma, this might only be tolerance towards the others and does not reflect true bonding. The three months that the lions were together in the boma on Welgevonden were probably not long enough for them to attain social stability and to form a stable group. Furthermore, the fact that females broke away on two occasions from the group might be in line with what Packer (1986) observed in that single females or small cohorts of females do not easily join other solitary females.

Although this gives clues as to why the reintroduced lions did not stay together, it does not provide insight into the reasons for certain individuals reacting the way they did, or the reasons for the aggression between some individuals. There are obviously other factors involved that are not clear at first glance. The effects of kinship and relatedness on the way that lions associate into groups cannot be excluded (Packer et al. 1991). There is a tendency for females to associate only with kin. This may result from the strong advantages of natal philopatry (Pusey & Packer 1987). Close investigation of the genealogy of the Welgevonden lions (Fig. 1) reveal some interesting results when compared with the current group associations. The genealogy in Fig. 1 indicates two distinct groupings of related individuals. These groupings are also the way in which the lions currently associate in the two prides. The association of WLG2, WLG4 and WLG5 in one pride and WLG1 and WLG3 in the other pride could be chance, but the fact that the individuals are associating according to their relationship on their mother’s side cannot be ignored. There is a distinct possibility that the lions are associating in the way that they do because of their kinship. However, if it is true that the lions associate because of their kinship, questions on how individuals recognize their relatives are raised. WLG1 and WLG3 are siblings and it is understandable that they will know and recognize each other. Likewise WLG2 and WLG4 are half-siblings from the same cohort and pride. Furthermore, although WLG5 is related on her mother’s side to WLG2 and WLG4, they originate from different reserves (Table 1) and would never have had contact before they came to Welgevonden. As described in the results, WLG4 and WLG5 did associate, and WLG4 even defended WLG5 after she was released from the boma. Therefore, it appears as if there could possibly be some kind of kin-recognition in lions for individuals that are related, but have not met each other previously. However, no references on kin-recognition in lions could be found in the literature. Although the current study does not provide sufficient evidence for kin-recognition, it does create an interesting avenue for future research.

The initial aggression of WLG5 after she was released from the boma was possibly not due to kin-recognition or the lack thereof, but rather a defence reaction, as she might have felt vulnerable because of her injury. However, kin-association can explain the alliance of WLG4 and WLG5 that followed. Then the behaviour of WLG4 of stepping in between WLG5 and the other lions when they attacked her is not that unusual. It will also explain why WLG5 and WLG4 socialized in a friendly manner from the beginning, as well as them breaking away from the others. Lions that are establishing new prides might be subjected to less harassment from their relatives than from unrelated neighbours (Pusey & Packer 1987).

When WLG4 and WLG5 were still with the original group, WLG3 kept her distance and only once joined a skirmish between the males and WLG5, but eventually left the pride. It is interesting to note that WLG3, who at first was associated with a group, became nomadic after the other two females had joined the group. She left the group without any apparent reason. After that, she never sought the company of any of the other lions, except when she was apparently in oestrus. Kinship and the fact that single lionesses do not easily join other small cohorts (Packer 1986) could be the likely cause for her behaviour.

The way in which the lions finally associated into two groups on Welgevonden, be it because of kin-association or whatever other reason, is not ideal. It resulted in related individuals joining to form a group which allowed for breeding between close relatives. WLG3 had two litters with WLG1, her sibling. To make matters worse, WLG1 mated with his daughter (WLG11) from WLG3, and she had one litter from him. Also, WLG4 had two litters from WLG2, her half-sibling. Consequently the two males, WLG1 and WLG2, were vasectomized to prevent further breeding with close relatives. Unfortunately inbreeding can be expected on small reserves with their small founder populations. On Welgevonden there was no dispersal by either the males or females to avoid inbreeding.
(Pusey & Packer 1987), probably because there was no chance to find unrelated partners elsewhere on the reserve. This will probably be the case on most small reserves that introduce lions, and managers will have to be wary of the possible problems of a population bottleneck (Packer et al. 1991).

CONCLUSIONS
The reintroduction of lions into Welgevonden was a success, despite the fact that the lions did not stay together and that breeding between relatives occurred. For a reintroduction attempt to succeed, especially where the animals come from different reserves or prides, the reintroduced lions will have to behave outside what could be described as normal lion behaviour. The fact that various successful reintroductions in the recent past on various reserves have included abnormal lion behaviour indicates that we still lack enough knowledge on lion social behaviour, especially in small, reintroduced populations. This study revealed interesting aspects of lion social behaviour. It illustrated again the flexibility of lions when prides are disturbed. Although the behaviour observed on Welgevonden had similarities with that observed in the Kruger National Park after a cropping programme (Smuts 1978), and with what was observed in East Africa (Pusey & Packer 1987), it does raise the possibility of kin-recognition in lions. Research focussing specifically on the possibility of kin-recognition and association are necessary to get a better understanding of lion social behaviour after reintroduction. It will be difficult to test kin-recognition in natural populations, and can possibly only be done by introducing unfamiliar, but related lions into a reserve or population. However, it will have disadvantages, as it will result in inbreeding which small reserves with small founder populations cannot afford. It will be interesting to know whether the behaviour observed on Welgevonden is an isolated case, or whether similar behaviour has been observed in other reserves that have introduced lions.

REFERENCES


