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ORIGINAL ARTICLE

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# The role of companionship in the dispersal of white rhinoceroses (*Ceratotherium simum*)

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**Abstract** Dispersal is a risky process, both through social pressures and the uncertainty in finding resources. The white rhinoceros is unusual among rhinoceros species in its incipient sociality, manifested through the formation of temporary or more persistent groups involving subadults of both sexes plus adult females without small calves. We describe the probing excursions made by subadult white rhinos out of their established home ranges which were invariably made with a companion. We suggest additional benefits of companionship in such dispersal movements, besides diluting predation risk, via (1) reducing the likelihood of being attacked by territorial males and (2) familiarization with a wider region of the environment, guided by the companion. This "buddy system" may be important in reducing the high costs potentially associated with dispersal.

**Keywords** Associations · Buddy system · Dispersal · Exploratory excursions · White rhinoceros

## Introduction

Dispersal is an important life history trait for most species of mammals and birds (Greenwood 1980; Dobson 1982). For many species, dispersal is conducted through the one-way movement of lone individuals away from natal areas (Holekamp 1986; Woollard and Harris 1990; Beaudette and Keppie 1992). In a few species, however, individuals disperse with conspecifics in groups rather than singularly. Dispersal by groups of individuals has been recorded for some primate species (Enomoto 1974; Cheney and Seyfarth 1977, 1983), lions (*Panthera leo*; Schaller 1972; Hanby and Bygott 1987; Pusey and Packer 1987), bighorn sheep (*Ovis canadensis*; Geist 1967) and suggested for voles (*Microtus*; Hilborn 1975).

Dispersal is potentially a risky process. Animals move from familiar places where forage and water have been available, even if under exploitative pressure, to novel areas where resource locations must be learnt, or where habitat conditions may even be unsuitable for settlement. Many dispersal movements lead only into population sinks, where reproductive performance would be inadequate to sustain a population in the absence of immigration (Pulliam 1988; Pulliam and Danielson 1991; Dias 1996). Conspecifics can play a role in the dispersal of individuals by acting as cues for where dispersers should ultimately settle (Stamps 1987, 1988, 1991, 2001; Smith and Peacock 1990; Reed and Dobson 1993; Dobson and Poole 1998). Through the presence of conspecifics, dispersing individuals can gain evidence that the local habitat is suitable (Stamps 1987).

The white rhinoceros (*Ceratotherium simum*) differs from other species of rhinoceros in its degree of sociality (Owen-Smith 1975, 1988). This is expressed through the occurrence of cohesive pairs or larger groups involving subadults, in addition to adult female-calf pairs. Subadult white rhinos form persistent associations with one or more subadults, of the same or opposite sex, or with an adult female without a small calf (Owen-Smith 1975). While groupings of 2–3 individuals are most common, long-lasting associations among up to six animals have been recorded. Groups including an adult female adopt the home range of this adult female (9–15 km$^2$), but dissolve when this female gives birth and no longer tolerates additional companions. Subadult groups seem to establish temporary home ranges (2–7 km$^2$), being observed in a particular region for a period then disappearing elsewhere. Overall, the subadult period extends from when a calf is chased away by its mother at the time of birth of a new offspring, at an age of 2–3 years, until socio-sexual maturity is attained. For females this occurs at first parturition around 7 years of age, while males be-

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come solitary and settle within a territory (1–2.5 km$^2$), either as a dominant or subordinate, between 10 and 12 years of age.

Rates of dispersal by subadult white rhinos, outwards from the population core towards peripheral regions where conditions were less crowded, were estimated to be 7–10% per subadult per year, during a period when the population was at high density and rainfall generally below-average (Owen-Smith 1981, 1983, 1988). Because subadults of both sexes were involved, such movements seemed to be primarily a response to resource inadequacy, rather than to social pressures (Owen-Smith 1973, 1974). During his study, Owen-Smith (1973) documented only two instances of dispersal. The first involved a 6-year-old female, which made a short movement of 5.5 km before eventually dispersing a further 20 km. The second case involved another 6-year-old female which dispersed approximately 15 km.

Subadult males are potentially subject to territorial aggression from dominant adult males, and even subadult females may sometimes be attacked (Owen-Smith 1975). Adult females occupy extensively overlapping home ranges, with little animosity. Subadult males benefit from being associated in pairs, through diluting or deflecting challenges by the dominant adult males whose territories they occupy or traverse. Solitary subadult males seem more likely to be attacked, and sometimes even killed, than subadults in groups (Owen-Smith 1973).

Current management of the white rhino population in the Hluhluwe-Umfolozi Park in South Africa is based on the source-sink concept, with animals being captured and removed from designated sink areas around the periphery of the fenced protected area (see Owen-Smith 1983, 1988).

In this paper, we present evidence suggesting the benefits of companionship in facilitating dispersal, through familiarizing animals with novel areas beyond the bounds of their established home ranges, prior to eventual emigration. The operation of such a “buddy system” in white rhinos may underlie the widespread success of conservation actions to re-establish this species in areas of its former occurrence through southern and eastern Africa (Owen-Smith 1988), in contrast to the problems experienced with the more solitary black rhinoceros (*Diceros bicornis*; Brett 1998).

## Methods

The study was conducted over 2 years (1999–2000) in the southern Umfolozi section of the 896 km$^2$ Hluhluwe-Umfolozi Park in KwaZulu-Natal, South Africa (28°20′S, 31°51′E). Rainfall was below average during the first year of the study (614 mm), and above average (893 mm) during the second year, relative to the long-term mean of 690 mm. The total white rhino population was approximately 1,600, mostly concentrated in the Umfolozi section.

To enable individuals to be contacted regularly, MOD-125 radio transmitters from Telonics were inserted into the anterior horns of five males and two females (see Shrader and Beauchamp 2001 for procedure). Subadults over 5 years of age, with horns sufficient to accommodate the telemetry equipment, were selected. One individual without a radio observed regularly was also included in the analysis. Observations were restricted to the dry season months (March–October). During 1999, each of the seven radio-equipped individuals were located approximately every 5 days. During 2000, three pre-selected individuals were monitored each month. Two of them were observed over 10 consecutive days, one in the morning and one in the afternoon, while the third was followed throughout the day for 5 consecutive days during the subsequent week. Information routinely recorded on accompanying individuals included sex, age (following Hillman-Smith et al. 1986) and identifying marks, as well as location using a Global Positioning System (GPS) device.

The two radio-equipped females (D and E) both gave birth in early 2000, and so were socially subadult only during 1999. One of the subadult males (B) became mostly solitary and appeared to settle within a home range during 2000.

### Data analysis

Associations were recorded as cohesive if individuals moved together for several hours or longer. Those enduring more than a month were regarded as stable (following Owen-Smith 1975). The minimum duration of each association was estimated from the period between the first and last sightings of the same individuals seen together.

Home ranges were plotted by entering GPS positions from both years into the home range analysis program Calhome (Kie et al. 1996). Data from both years were used as areas utilized by the rhinos remained consistent between years. A maximum of two points per day were plotted, provided these locations were recorded more than 6 h apart. Home range limits were identified from the 85% utilization contour, using the adaptive kernel method with the least squares cross-validation for the smoothing parameter (Worton 1995; Seaman and Powell 1996). This procedure seemed most reliable for establishing the area regularly used, allowing for fairly frequent excursions by subadults. Home ranges delineated using the Adaptive Kernel, Minimum Convex Polygon and Harmonic Mean procedures gave similar estimates of home range extent for the 85% contour, but not when a higher proportion of sightings was included. This was because excursions that lasted longer than a day generated autocorrelated position records, hence exaggerating the home range delineated by the estimation procedure (Swihart and Slade 1985). Where necessary, the home range boundaries indicated by Calhome were adjusted to coincide with a physical barrier (e.g., a major river). GPS locations were plotted using ArcView (Anon 1996). Rhinos located less than 1 km beyond the 85% contour were considered to be using the periphery of their home ranges, while locations greater or equal to 1 km from this contour were interpreted as exploratory excursions.

To test whether subadults were more often accompanied by companions when making excursions, than when within their home range, we used a one tailed Fisher exact test (Zar 1996) to compare the relative frequency of associations (as defined above) with records where animals were seen alone, between these situations.

## Results

Subadult white rhinos were observed in many different associations, most of which were temporary, i.e. lasting less than a month (93%, *n*=180 associations). Grouping patterns closely matched those previously recorded by Owen-Smith (1975). However, each of the two female subadults was mainly associated with an adult female rather than another subadult.

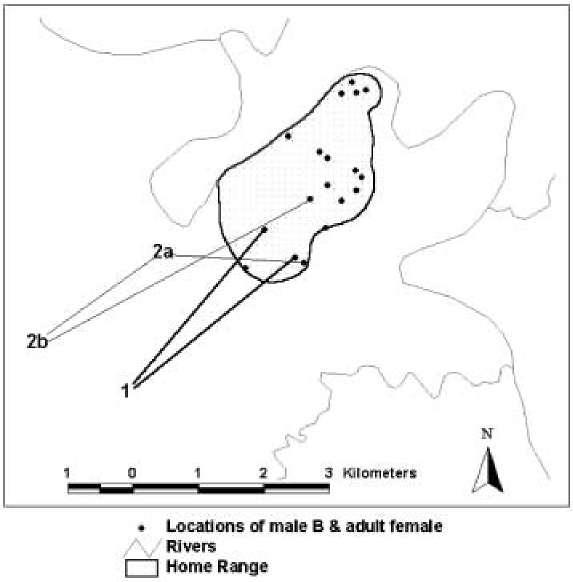

**Fig. 1** Locations of subadult male B, when he had formed a stable association with an adult female. During the association subadult B's movements were restricted to the adult female's home range, except when he followed her as she made two excursions (*1* and *2a–2b*), possibly in search of water. Excursions lasted less than a day and covered approximately 5 km (*1*) and 6 km (*2*) outside of the female's home range

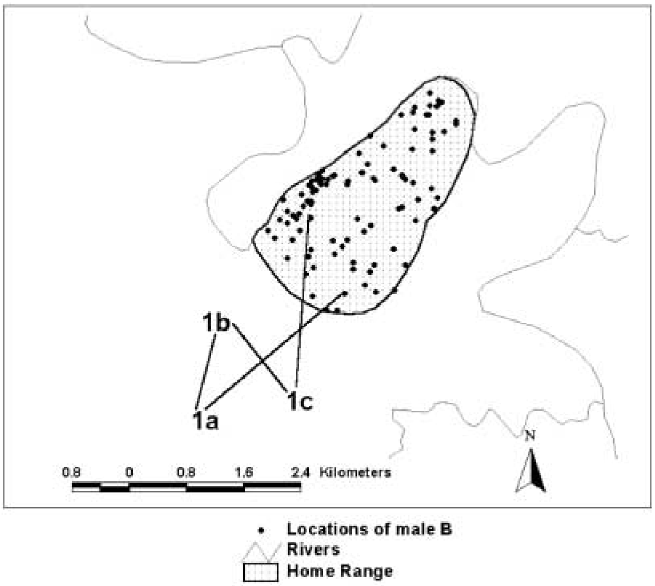

**Fig. 3** Exploratory excursion of subadult male B outside of his home range. Excursion was made with an adult female and her calf with which the subadult had formed a temporary association. The excursion lasted 2 days, covered approximately 7.5 km outside of the subadult B's home range and was into an area familiar to the adult female

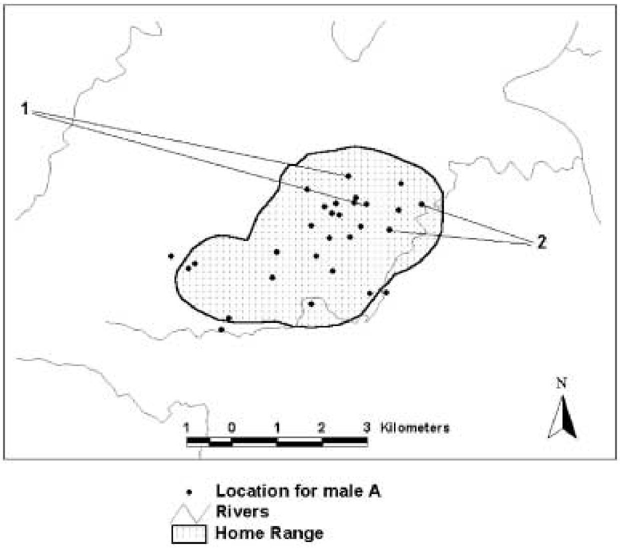

**Fig. 2** Two exploratory excursions of subadult male G out of his home range. Both excursions were made with the same stable subadult companion. Each excursion lasted 1 day and covered approximately 10 km (*1*) and 4 km (*2*) outside of subadult G's home range

Twenty excursions beyond home range limits were recorded (Tables 1, 2 and 3). All eight of the monitored subadults made such excursions. About one-quarter of the excursions were made together with a subadult that had been a stable companion (Table 1), and another quarter with a long-term adult female companion (Table 2). The remaining half of the excursions were made with animals that had been companions for less than a month, in a few cases just briefly for the duration of the excursion (Table 3). Specific examples of some excursions are described below, illustrated by maps.

1. Subadult male B attached himself to an adult female and restricted his movements to her home range. During the 3 months they were associated subadult B accompanied this female on two excursions (1 and 2), each lasting a day and extending about 3 km beyond their shared home range limits (Fig. 1). The first (1) was 2.5 km beyond her home range and occurred 12 days after he had joined this female, and the second (2a–2b) was 50 days later and extended 3 km beyond her home range. During this second excursion, a territorial male accompanied the pair for 2 h, but was not aggressive towards either individual.
2. Subadult male G accompanied another subadult male, which he had been associated with for 12 days, on a single day excursion 5 km beyond his home range (Fig. 2, point 1). These same two subadults then made another 1-day excursion 2 km beyond G's home range, in a different direction, 69 days later (Fig. 2, point 2). No other rhinos were encountered.
3. Subadult male B, previously solitary, joined an adult female with a calf that occupied an overlapping home range. The first day they were associated, he followed this adult female on a 2-day excursion that took him 2.5 km beyond his home range limits (Fig. 3, points 1a–1c). On the second day, a territorial male joined them. On the third day, this trio moved back within

the home range boundary of the subadult, who remained associated with this adult female until the afternoon of the following day.

4. Male subadult C accompanied an older subadult male A, who had been his companion for 33 days, on an excursion taking him 4.5 km beyond his own home range limits (Fig. 4, points 1a–1b). The next day, male C had separated from subadult A and had joined a resident adult female plus calf (Fig. 4, point 1c). That afternoon he was found alone, (Fig. 4, point 1d), and was followed while he moved alone back into his home range.

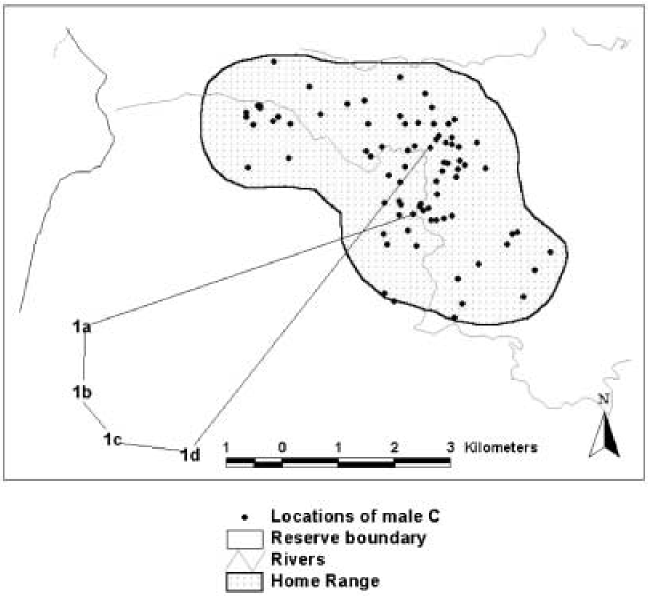

**Fig. 4** Exploratory excursion of subadult male C outside of his home range. Excursion was made with a stable subadult companion. However, subadult C split from the male during the excursion and temporarily joined with an adult cow before returning to his home range. The excursion lasted 2 days and covered 12 km outside of subadult C's home range

Subadults were significantly more likely to be associated with a companion while making an excursion than was found when they were seen within their home range (20 out of 20 cases, compared with 92% of 143 records, $P$=0.013, $n$=163 associations).

Generally, subadults seemed to form associations with individuals inhabiting an overlapping home range. In two instances, two different subadults transferred their attachment from the companion during the initial excursion to another individual while they were out of their home range. When subadults were associated with adult females, they restricted their movements to the adult female's home range. On six occasions, subadults accompanied these adult females while they made long distance excursions, possibly in search of water. On two of these excursions, the adult females moved into areas where they had been observed prior to the excursions. On four occasions, excursions made by subadults out of their home ranges were restricted to the companion's home range or within an area familiar to the companion. However, little information was known about many of the different companions, so we are unsure to what extent the remaining 14 excursions were into areas previously known by the companion.

In some cases, multiple excursions were made by subadults together with a single stable companion. Subadult G made two excursions with the same subadult male (Table 1; Fig. 4), while subadult D made three excur-

**Table 1** Excursions of subadults made with stable subadult companions

| ID | Rhino age (years) | Sex | Companion Age (years) and sex | Duration of association prior to excursion (days) | Duration of excursion (days) | Max. distance from home range (km) | Total distance of excursion (km) |
|---|---|---|---|---|---|---|---|
| G | 5–6 | ♂ | 7 ♂ | 12 | 1 | 5.0 | 10.5 |
| G | 5–6 | ♂ | 7 ♂ | 81 | 1 | 2.0 | 4.0 |
| G and H | 5–6 | ♂ | 5–6 ♂ | 17 | 1 | 2.5 | 4.5 |
| C | 7–8 | ♂ | 10 ♂ | 13 | 1 | 1.5 | 2.0 |
| C | 7–8 | ♂ | 9 ♂ | 32 | 2 | 4.5 | 12.0 |

**Table 2** Excursions of subadults made with adult females with which they had formed stable associations

| ID | Rhino age (years) | Sex | Companion Age (years) and sex | Duration of association prior to excursion (days) | Duration of excursion (days) | Max. distance from home range (km) | Total distance of excursion (km) |
|---|---|---|---|---|---|---|---|
| D | 6–7 | ♀ | Adult ♀ | 51+ | 2 | 7.0 | 14.0 |
| D | 6–7 | ♀ | Adult ♀ | 114+ | 1 | 2.5 | 4.5 |
| D | 6–7 | ♀ | Adult ♀ | 160+ | 1 | 1.0 | 2.0 |
| B | 7–8 | ♂ | Adult ♀ | 12 | 1 | 2.5 | 5.0 |
| B | 7–8 | ♂ | Adult ♀ | 62 | 1 | 3.0 | 6.0 |
| E | 6–7 | ♀ | Adult ♀ | 69 | 1 | 1.5 | 3.5 |

**Table 3** Excursions of subadults made with adult females plus companions with which they had formed temporary associations

| ID | Rhino age (years) | Sex | Companion Ages (years) and sex | Duration of association prior to excursion (days) | Duration of excursion (days) | Max distance from home range (km) | Total distance of excursion (km) |
|---|---|---|---|---|---|---|---|
| F | 6–7 | ♂ | Adult ♀, 3 ♀, 6 ♂, 6 ♂, 3 ♂ | 4 | 2 | 1.5 | 3.0 |
| F | 6–7 | ♂ | Adult ♀, 6 ♂ | 2 | 3 | 1.5 | 5.0 |
| B | 7–8 | ♂ | Adult ♀, 1? | 2 | 1 | 1.5 | 3.0 |
| B | 7–8 | ♂ | Adult ♀, 1 ♀ | ? | 3 | 6.0 | 14.0 |
| B | 7–8 | ♂ | Adult ♀ / <1 ♀ | 0 | 2 | 2.5 | 7.5 |
| B | 7–8 | ♂ | 3 ♀ | ? | 1 | 2.0 | 4.0 |
| C | 7–8 | ♂ | Adult ♀, 3 ♂ | 0 | 1 | 4.0 | 7.5 |
| C | 7–8 | ♂ | 10 ♂ | 21 | 1 | 2.0 | 4.0 |
| C | 7–8 | ♂ | 4 ♀ | ? | 1 | 4.0 | 8.0 |

sions with an adult female (Table 2) and subadult 20 made two excursions with the same adult female (Table 2).

All subadults observed eventually returned to their own home ranges following excursions, either together with the companion or alone. No subadults were observed making solo excursions, and no long-term shifts in home range were documented during the study period.

## Discussion

The basic benefit of group formation by ungulates is generally recognized to be a reduction in the risk of predation (Jarman 1974; Bertram 1978). While predation on white rhinos by lions and other carnivores appeared to be negligible in the study area, this fundamental benefit of companionship cannot be excluded. Owen-Smith (1988) noted how groups of subadults commonly adopted a rump-against-rump defensive formation when disturbed, which, although maladaptive against humans, could offer some protection in the event of a predator attack. White rhinos are probably big enough to be able to ward off attacks by lions alone when they approach full adult size.

A second potential benefit of companionship is to reduce the chance of being attacked, and hence injured, by territory holders. Territorial males have been recorded violently attacking, chasing and in even a few instances killing subadults that were intruding into their territories (Owen-Smith 1975). Owen-Smith (1974) reports an instance where a solitary subadult male (aged 11–12 years) was challenged tensely for 32 min by a territorial male. However, another territorial male had confronted this same subadult only briefly 5 months earlier, when the latter had a subadult male companion. This social security from group formation would apply primarily to males, although subadult females are occasionally attacked (Owen-Smith 1975).

During the present study, groups of subadults were challenged only briefly, or ignored completely, by territory holders, except in two cases. In the first case, two subadult males were chased from where they were sleeping by a territorial male. The male chased the two subadults for a few minutes, then left them and lay down. The following day the subadults were found outside of the adult male's territory. In the second case, a territorial male was courting an adult female when two subadult males approached. The subadults were accosted and chased by the territorial male for about 50 m. Solitary subadults were rarely encountered, and never observed interacting with territory holders.

A third potential advantage is familiarization with new areas (Owen-Smith 1973). Through joining other conspecifics, animals may be led through novel regions of the environment, and more specifically towards the locations of the food and water resources that these areas contain (Stamps 1987; Johnson 1989). This "public information" (Valone 1989) may enable less experienced animals to evade temporary resource shortfalls, and ultimately guide them towards less crowded habitat into which they may disperse. Geist (1967) suggested that a similar process operates among bighorn sheep (*Ovis canadensis*), whereby young males are led towards wintering areas, salt licks, rutting grounds, summer ranges and migratory routes by following older males. Exploratory trips prior to dispersal have been recorded for other species of mammals (Lidicker 1976; Holekamp and Sherman 1989; Johnson 1989; Woollard and Harris 1990; Lidicker and Stenseth 1992; Larsen and Boutin 1994; Künkele and von Holst 1996). However, in all of these cases individuals moved alone.

The benefit of experience, passed on from older to younger animals, has been widely recognized for elephants (Laws 1969; Geist 1971; McKay 1973). However, elephants move in enduring family groups based on mother-daughter associations (Owen-Smith 1988). Dispersal involving shifts in home ranges by such groups is evident from the history of elephant recolonization of South Africa's Kruger National Park (Owen-Smith 1983). White rhinos, although comparably long-lived, lack persistent mother-daughter bonds. Nevertheless, through forming transient bonds with various other individuals, young white rhinos may gain some benefit from the wider experience of older individuals. This was evident as in approximately a quarter of the excursions subadults moved with rhinos that were familiar with the new area. In particular, subadult white rhinos seemed to form attachments preferentially with adult females, although such opportunities are restricted by the intolerance of adult females with young calves for additional companions (Owen-Smith 1973).

In contrast to white rhinos, black rhinoceroses are typically solitary, with social groups rarely extending beyond adult female-calf pairs (Goddard 1967). Subadults do occasionally form temporary associations with adult females and other subadults (Hamilton and King 1969; Adcock et al. 1998), but such opportunities are limited by the much lower densities attained by black rhino populations, relative to white rhinos. High rates of mortality among black rhinos translocated into new reserves have posed a conservation problem (Hitchins 1984; Adcock et al. 1998; Brett 1998). Deaths have been ascribed largely to fighting, but include females as well as males. The additional role potentially played by nutritional stress among animals introduced into unfamiliar areas has perhaps not received adequate recognition.

We suggest that the “buddy system”, exemplified by shifting temporary associations among subadult white rhinos, and between subadults and some adult females, could be of great importance in ameliorating the costs of dispersal into unfamiliar habitat. Although we did not observe actual dispersal, in terms of settlement within a new home range, we were able to document some of the probing excursions beyond established home ranges, in detail. In all observed cases, these movements were conducted together with one or more companions, either a long-standing subadult or adult female associate or an adult female sharing an overlapping home range. Thereby young white rhinos are able to explore an area much larger than the home range they usually occupy, under the guidance of another individual which potentially is familiar with the locations of resources in the novel area. This experience may guide them when ultimately they embark on the large scale dispersal movements documented by Owen-Smith (1988).

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