Animal Behaviour 77 (2009) 87–94

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe

Communal nesting is unrelated to burrow availability in the common warthog

Angela M. White[a,*], Elissa Z. Cameron[b,1]

[a] *Program in Ecology, Evolution and Conservation Biology, University of Nevada-Reno*
[b] *Mammal Research Institute, University of Pretoria, South Africa*

ARTICLE INFO

Article history:
Received 11 June 2008
Initial acceptance 30 June 2008
Final acceptance 11 August 2008
Published online 29 October 2008
MS. number: A08-00392R

Keywords:
common warthog
communal nesting
cooperative breeding
ecological constraints
habitat choice
Phacochoerus africanus
reproductive strategies
site selection
sociality

Warthogs, *Phacochoerus africanus*, are an unusual ungulate. They are facultative cooperative breeders where females within the same population display both solitary and cooperative reproductive strategies. Warthogs require burrows for sleeping and rearing their young, yet they are unable to dig their own burrows and rely on aardvark excavations. Studies of warthogs have failed to show any reproductive benefits to females participating in communal care and suggest a reproductive cost to cooperation. The ecological constraints hypothesis proposes that environmental factors limit an individual's ability to successfully disperse and reproduce. In this study we investigated whether limitations in burrow sites can explain cooperative breeding in this species. We checked over 500 burrows for signs of use systematically for 1 year to determine whether burrows were a limiting resource and to investigate burrow use preferences. Our methodology allowed us to determine whether burrows were used by adults with young or by adults without young. We found that burrow availability did not appear to pose an ecological constraint on independent living, as the percentage of burrows used remained relatively low throughout the year. Additionally, the number of burrows in a warthog clan area did not influence the percentage of females breeding cooperatively. Predator avoidance appeared to be the main factor influencing individual burrow selection by warthogs and communal nesting may best be explained as a form of antipredator behaviour.

Cooperative breeding occurs when members of a social group assist with the rearing of offspring that are not genetically their own (Emlen 1991). Such assistance includes systems in which nonreproductive individuals assist in the rearing of others' young, or when reproductive individuals share in offspring care with other reproductive members of their social group (Solomon & French 1997). Studies on cooperative breeding have highlighted some of the selective pressures leading individuals to delay dispersal from their natal range and assist in the rearing of others' offspring, while often delaying their own reproduction (reviewed by Cockburn 1998). For example, cooperative breeding is often seen when dispersal opportunities are ecologically constrained, such as when habitat is saturated, when there are few mating opportunities, or when there is a low probability of successful dispersal (Emlen 1994, 1982).

While ecological constraints has been a useful framework for understanding delayed dispersal in birds, its applicability to mammals has been questioned (Russell 2004). However, many cooperatively breeding mammals use specialized burrows for living or rearing their young (e.g. rodents: Hayes 2000; mongooses: Rood 1986; canids: Moehlman & Hofer 1997). In these species, dispersal may be constrained by the energetic costs of excavating or maintaining burrows (Lovegrove 1989; Jarvis et al. 1994) or by the predation risks associated with attempting to locate, construct or modify burrows (Ebensperger & Bozinovic 2000). Thus, individuals may share burrow or denning sites because a species' reliance on these structures makes dispersal costs prohibitive. Alternatively, individuals may share burrow sites because they gain direct or indirect benefits by forming groups with conspecifics. These benefits can include decreased thermoregulatory costs, acquisition of resources and skills and group predator defence (reviewed in Hayes 2000).

Although group living is common in many ungulate species, cooperative offspring care is rare (Russell 2004). Warthogs are unique among the ungulates. They are facultative cooperative breeders, displaying both solitary and cooperative-breeding strategies within a population in roughly equal proportions (Cumming 1975; Somers et al. 1995). They are also unusual for an ungulate in that they sleep in burrows each night, and use burrows for protection against predators, for thermoregulation and for giving birth (Estes 1991). Additionally, whereas in most species one sex will disperse, philopatry is common in male and female warthogs, although females are predominately the helping sex (Cumming 1975; Somers et al. 1994; Muwanika et al. 2006). Cooperative breeding in this species includes single breeding females with

---

[*] Correspondence: A. M. White, Program in Ecology, Evolution and Conservation Biology, University of Nevada-Reno, 1000 Valley Road, Reno, NV 89512, U.S.A.
E-mail address: amwhite@unr.edu (A.M. White).

[1] E. Z. Cameron is at the Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa.

0003-3472/$38.00 © 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2008.08.030

nonreproductively aged helper(s) and two or more females rearing their young communally (Cumming 1975; Somers 1992). These cooperative associations can occur over successive years and include the sharing of burrow sites to rear their young (Cumming 1975; Mason 1982). Finally, compared to most ungulates, warthogs are fecund, with up to eight piglets produced per litter (Estes 1991). Previous work on cooperative breeding in warthogs suggests that neither group size nor the number of females rearing offspring communally affects juvenile survival (Plesner Jensen et al. 1999), and therefore, the warthog's unique life history characteristics may account for their propensity to breed cooperatively because of dispersal constraints.

Use of burrows is common for diurnal species that experience high predation pressure, and the unusual use of burrows by warthogs may be best explained by their susceptibility to predation (Spinage 1972). As all available burrows may not satisfactorily meet the needs of a warthog, burrow type and distribution may be more important than actual numbers. For example, the habitat in which a burrow is located can influence its use by providing cover from predators and proximity to feeding areas (Schradin & Pillay 2006; Hayes et al. 2007). Similarly, soil can influence vegetation type, affect the ability of fossorial species and predators to excavate and modify burrows, and can influence burrow humidity (Kinlaw 1999). Predator defence and evasion are likely to influence choice of burrows by warthogs since, compared to other savannah ungulates, warthogs lack speed and endurance and retreat to the confines of a burrow when pursued (Estes 1991). Warthogs, therefore, may preferentially use burrows with shorter entrances that inhibit predators from entering or that provide refuge close to favoured feeding areas. Reproductive females may also require specific types of burrows for giving birth and rearing their young, including characteristics that decrease infanticide by larger males (Somers et al. 1995), such as burrows with smaller entrances or in more isolated areas, burrows closer to water to meet the demands of lactation, or burrows located in harder soils that limit a predator's ability to dig them out. If burrows with preferred characteristics are a limiting resource, then the costs of sharing a desirable burrow may be less than the costs associated with independent use of less suitable burrows.

In this study we investigated whether limitations in burrows may influence the incidence of cooperative breeding in warthogs through ecological constraint. Warthogs use several burrows, which are shared simultaneously with other members of their social group and sequentially with other groups with overlapping home ranges (Cumming 1975; Somers 1992). Consequently, burrows could be a limiting resource for warthogs, since (1) warthogs do not dig their own burrows, relying instead mostly on aardvark excavations (Cumming 1975), (2) warthogs not only compete intraspecifically for access to these burrows, but also with several other species including hyaenas, wild dogs and porcupine (Somers 1992) and (3) predators may destroy burrows as they attempt to dig out their prey (Cumming 1975; Funston et al. 2001). The time of year may also influence burrow availability. For example, most interspecific competition over burrows is temporally segregated because of the diurnal nature of warthogs and the nocturnal nature of their competitors. However, during the farrowing (i.e. birthing) season, adults leave their offspring in a burrow during the day and therefore compete directly with other species for burrow access during this time.

METHODS

Study Area

We conducted this study between August 2004 and November 2005 in the iMfolozi Section of Hluhluwe-iMfolozi Park (HiP), in the KwaZulu-Natal province of South Africa (28°S, 31°E). HiP is a 965 km^2 fenced game reserve, with the iMfolozi section being composed predominately of savannah/bushveld habitat. Average annual rainfall in iMfolozi is 650 mm, with most rain occurring in the summer months between October and March. With the exception of a few springs, the Black and the White iMfolozi Rivers are the only permanent water sources in this area. In addition to warthogs, iMfolozi is home to a full guild of herbivores and contains several warthog predators (Cumming 1975) including African lion, *Panthera leo*, spotted hyaena, *Crocuta crocuta*, leopard, *Panthera pardus*, cheetah, *Acinonyx jubatus*, and African wild dog, *Lycaon pictus*. In 2004, warthog densities in iMfolozi were estimated at 3.89 warthogs per km^2. In southern Africa, warthogs give birth once a year in late-October/early November (Skinner & Chimimba 2005).

Burrow Classification

We identified 510 burrows used by warthogs within a 30 km^2 study area in the southern section of iMfolozi Game Reserve. Some characteristics of burrows can be measured externally, while other measurements require internal exploration. We investigated only a small subset (10%) internally, by crawling through the burrow entrance, because of the risks associated with the accidental encounter of an animal inside the burrow. Our exploration of these burrows did, however, reveal that burrows varied greatly in their shape and complexity. We found that the most common burrow type included an entrance tunnel terminating in a circular chamber. Burrows differed in the circumference, length and curvature of their entrance tunnel, as well as the size, shape and number of chambers, the slope and slope complexity of the burrow and the number of entrances. Our observations are consistent with previous descriptions of burrows (Cumming 1975; Mason 1982). Additionally, we found that the dimensions of a burrow can change rapidly because of erosion and periodic excavation. For these reasons, characteristics included in this study were limited to features that could be measured externally and reliably. Obvious burrow changes were noted during biweekly sampling.

For each burrow we recorded its GPS location and measured the entrance height and entrance width. Based on the location, we identified the soil type and surrounding habitat type using preexisting GPS maps. Habitat was classified into six structural vegetation types based on the canopy cover (Grassland, Open woodland, Medium woodland) and understory thickness (Open thicket, Medium thicket, Dense thicket) using a vegetation map generated from Landsat ETM bands (Dora 2004). We found burrows in all available habitat types. Burrows were found primarily in five soil types (Table 1). Burrows found in other types of soil were rare and classified as 'Other' for analysis. Distance to a permanent water source and burrow densities were calculated using ArcMap (ESRI, Redlands, CA, U.S.A.).

Burrow Use

We systematically checked burrows on sampling days by walking one of six established routes such that individual burrows were checked every 14 days (range 7–21 days) for evidence of use by warthogs and other semifossorial species. We recorded whether a burrow had been used, and by what species, based on footprints leading into the burrow. For burrows used by warthogs, we determined whether the burrows had been used by a mother with young, based on the presence of two distinct footprint sizes, but no other social class could be reliably distinguished. After establishing whether a burrow had been used, we swept the entrance smooth. Unused burrows were also swept to standardize any disturbance from our methodology. Consequently, when we next visited the burrow we could determine whether the burrow had been used in