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Association between taxonomic relatedness and interspecific mortality in captive ungulates

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ABSTRACT

Interspecific aggressive interactions are known among a variety of animals including ungulates. Nevertheless, most studies on interspecific interactions in ungulates involve case reports without testing any specific hypotheses. We tested two mutually exclusive hypotheses; that mortality rate in interspecific interactions of captive African ungulates would be higher if combatants are taxonomically (i) more closely related species or (ii) more distantly related species. In addition, we examined if mortality in these interactions was affected by the age, sex and weight difference of combatants. In total, we analyzed 101 interspecific aggressive interactions among 25 species of African ungulates kept in mixed species exhibits in Dvůr Králové Zoo over a period of 20 years. In 18 cases, one of the combatants died. We found that probability of death was higher when the target of aggression was a young animal. Since the majority of fatal attacks towards young were performed by equids, the only known explanation is that the strong defence instinct of equids may cause them to mistake young antelope for small predators. When analysing only fights between adults we found that more aggressive interactions were recorded between taxonomically more distantly related species, however the interactions between taxonomically more closely related species led to the death of combatants more frequently. A possible reason for these highly escalated conflicts among closely related species may be higher competition over resources as the resource needs of closely related species are likely to be similar. In conclusion, we recommend that closely related species should not be put together in mixed species exhibits to prevent serious injuries or fatal attacks.

1. Introduction

Interspecific aggressive interactions are known among a variety of animal groups including fish (Sloman et al., 2011), birds (Jankowski et al., 2010; Parsons et al., 2006), rodents (Eccard et al., 2011), carnivores (Dorman and Bourne, 2010; Palomares and Caro, 1999; Watts and Holekamp, 2008) and primates (Leonardi et al., 2010); however reports of these interactions between ungulates are relatively uncommon in the wild (Bartoš et al., 2002; Berger, 1985; Berger and Cuninngham, 1998) as well as in zoos (Andersen, 1992; Cave-Brown, 1983; Crotty, 1982; Gordon, 1989). Most of studies examining interspecific aggression in ungulates involve only two species (Berger and Cuninngham, 1998; Keast, 1965; Sekulic, 1978; Wickler and Seibt, 1997) or case reports (Cave-Brown, 1983; Crotty, 1982;

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Gordon, 1989; Klimov, 1988). Moreover, studies explaining this phenomenon are based on results which do not use conventional statistics (Backhaus and Frädrich, 1965; Leuthold, 1977; Walther, 1965) as datasets required to test hypotheses for interspecific aggressive interactions are necessarily large but rarely available. Therefore most hypotheses have not yet been tested.

The most common hypotheses explaining interspecific aggression among ungulates in the wild are as follows: resource competition (Berger and Cuninngham, 1998; Vaňková et al., 1999), defence against predators (Leuthold, 1977; Walther, 1965), protection of young (Gordon, 1989; Popp, 1984; Walther, 1965; Winkler et al., 2003), and taxonomic relatedness, where two mutually exclusive hypotheses were formulated (Popp, 1984; Walther, 1965). The first one says that interspecific aggressive interactions would occur less often between taxonomically more related species than between more distant species as more related species will have similar and therefore recognisable threat behaviours, and so will employ behavioural techniques in order to avoid further aggression. The second hypothesis suggests that these interactions would occur more often between taxonomically more distant species because more distant species have quite different threat displays and would fail to recognize and react to one another's threats (Popp, 1984; Walther, 1965). Only one previous study has tested these hypotheses, finding lower rates of aggression between taxonomically more closely related species (Popp, 1984).

When examined effect of other factors on interspecific aggression in ungulates, the researchers published various results. Some authors found higher rates of interspecific aggression in males than in females (Berger and Cuninngham, 1998; Gordon, 1989; Popp, 1984), while others failed to find any difference between sexes (Andersen, 1992). Aggressive interspecific interactions occurred at higher rates between species of similar size than between species of different size (Popp and Bunkfeldt-Popp, 1986). Whereas some researchers found that larger species dominate smaller ones (Berger, 1985; Lamprey, 1963; Sekulic, 1978) other studies failed to confirm this (Andersen, 1992; Bartoš et al., 1996; Popp and Bunkfeldt-Popp, 1986).

Some interspecific interactions between ungulates involve attacking young of other species (Backhaus and Frädrich, 1965; Leuthold, 1977; Walther, 1965; Winkler et al., 2003). This behaviour could be based on other motivation than that which involves attacks towards adults. It is explained by "defence instinct (against predators) that cannot be satisfied at all in captivity" and thus equids confound young of antelopes with small predators (Walther, 1965). Therefore, we differentiated between attacks towards adults and those towards young in our study.

Aggressive interactions between different ungulate species sometimes lead to the death of one combatant in the wild as recorded in fights between African elephant (*Loxodonta africana*) and plains zebra (*Equus quagga*; Smuts, 1974) or white rhinoceros (*Ceratotherium simum*; Berger and Cuninngham, 1998), or between addax (*Addax nasomaculatus*) and scimitar-horned oryx (*Oryx dammah*; Gordon, 1989). Since mixed exhibits are a common trend in the captive environments (e.g. zoos), the knowledge about the causes of mortality due to interspecific aggression is of high importance and could contribute towards improved welfare of captive animals.

In this study we focus on mortality during interspecific interactions in African ungulates kept in large enclosures in the captive environment. Based on previous studies we tested the following predictions: The mortality in interspecific interaction is higher (1) in young than in adults, (2) in males than in females (3) when the weight difference of combatants will be higher, (4) when combatants are taxonomically (a) more distantly related species and (b) more closely related species.

2. Material and methods

2.1. Animals

The data were collected at Dvůr Králové Zoo, Czech Republic. We used data about interspecific aggressive interactions recorded in six large enclosures. The animals were introduced to these enclosures in May and were moved out in October each year. Two of these enclosures were part of a Safari area where buses with visitors went through the enclosures. The size of enclosures ranged from 6,000 m^2 to 150,000 m^2. All were grass enclosures with trees and shelters and there were several feeders in each enclosure. Food was supplied every morning.

Keepers performed every day records of all important events (births, deaths, mating, injuries, conflicts, etc.) that occurred. Using this evidence we collected data on interspecific aggression (this means any prolonged conflict or conflict involving injury or even the death of one of combatants) between species had occurred. We checked all daily records from 1987 to 2008. In total 25 species from 8 different subfamilies of three ungulate families (Equidae, Camelidae, Bovidae) were included: addax, roan antelope *Hippotragus equinus*, eland *Tragelaphus oryx*, sable antelope *Hippotragus niger*, Arabian oryx *Oryx leucoryx*, scimitar-horned oryx, gemsbok *Oryx gazella*, blesbok *Damaliscus pygargus*, hartebeest *Alcelaphus buselaphus*, impala *Aepyceros melampus*, bongo *Tragelaphus eurycerus*, greater kudu *Tragelaphus strepsiceros*, lowland nyala *Tragelaphus angasii*, lesser kudu *Tragelaphus imberbis*, black wildebeest *Connochaetes gnou*, wildebeest *Connochaetes taurinus*, Arabian camel *Camelus ferus f. dromedarius*, Nile lechwe *Kobus megaceros*, southern lechwe *Kobus leche*, waterbuck *Kobus ellipsiprymnus*, Watussi cattle *Bos taurus*, African wild ass *Equus africanus*, Grevy's zebra *Equus grevyi*, mountain zebra *Equus zebra*, and plains zebra (for detailed species composition in each enclosure see Table 1). All other data concerning the animals (i.e. date of birth and death, sex, identity of parents, etc.) were obtained from curators of the Dvůr Králové Zoo. In most cases the weight of the individual was unknown so we substituted the average weight published for the species in literature (Estes, 1991; Kingdon, 1997). Young animals were defined as individuals of the age less than one year. Any individuals severely injured in interspecific fights that were in need of veterinary treatment and separated from the herd were regarded as dead in the analysis because these individuals doubtless would