Possible predator avoidance behaviour of hominins in South Africa

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KEYWORDS:
Paranthropus robustus; Aepyceros melampus; Papio ursinus; australopithecine; human ancestors

HOW TO CITE:
Badenhorst S. Possible predator avoidance behaviour of hominins in South Africa. S Afr J Sci. 2018;114(7/8), Art. #a0274, 2 pages. http://dx.doi.org/10.17159/sajs.2018/a0274

PUBLISHED:
30 July 2018

There are many factors that contribute to the evolutionary success of species[1], for example, species often develop elaborate predator avoidance behaviour[2]. Such behaviours can be studied by ethologists in extant animals[3], but supporting empirical evidence is often lacking for such behaviours in extinct organisms[4]. Using living animals as proxies for extinct species usually allows for behavioural analogies, such as the use of baboon behaviour to infer the behaviour of our human ancestors and relatives.[5] South Africa is inhabited by a large primate, the chacma baboon (*Papio ursinus*). Baboons are comparable in size and weight to australopithecines like *Paranthropus robustus* and *Australopithecus africanus* and their human-like behaviour has long been recognised.[5,7-11]

Our understanding of the evolution of hominins is largely based on direct evidence from skeletal remains (gait, brain size, mobility, diet, etc.) and material culture (bone and stone tools), and very little is known about their behaviour. *Paranthropus robustus* was a robust australopithecine that lived between 2 and 1.2 million years ago in South Africa and remains of this species have been found at sites like Kromdraai, Swartkrans, Drimolen, Gondolin and Cooper's Cave in the Cradle of Humankind.[12] In the main, *Paranthropus robustus* was small statured but bipedal[13] and followed a patrilocal form of residence[14]. They were dietary generalists.[15] Apart from these main lines of evidence, very little is known about the behaviour of *Paranthropus robustus* during the Early Pleistocene.

From an evolutionary ecological perspective, prey species develop mechanisms to avoid being caught by predators. These anti-predatory devices are varied in animals and behavioural and anatomical adaptations may include a combination of sound, smell, colour, pattern, form, posture and/or movement devices.[2] Natural selection promotes the evolution in prey animals of features that reduce the probability of success for their predators. Animals with such anti-predatory devices tend to have a higher probability of escaping predation than animals without them.[16] Today, lions (*Panthera leo*) and leopards (*Panthera pardus*) are the main predators of baboons. Lions stalk baboons during daytime when they feed on the ground, and leopards attack them during the night.[17] Baboons have evolved numerous predatory avoidance behaviours to counter these attacks to ensure survival. The main behaviours include living in large troops, moving in a patterned way on the landscape[5], using sentries (elderly male individuals to sound alarms and defend the troop), sleeping in inaccessible places at night[18] and stone throwing[19].

Baboons also display another form of predatory avoidance behaviour: they are often found, during daytime, with other animals including buffalo (*Syncerus caffer*), elephant (*Loxondonta africana*)[20], bushbuck (*Tragelaphus scriptus*), rock hyraxes (*Procavia johnstoni*), tree hyraxes (*Heterohyrax brucei*)[21], guinea fowls (*Numida meleagris*), blue duiker (*Philantomba monticola*)[9], and, most often, with impala (*Aepyceros melampus*). The visual powers of baboons complement the acute sense of smell of impala, allowing for their mutual protection from predators.[14,17,22-27] Washburn and De Vore[11] found that olive baboons (*Papio anubis*) are closely associated with impala in open country, while in forested areas, they associate with bushbuck. The bark of these two antelope species will set a troop of baboons to flight, and a mixed herd of baboons and impalas are almost impossible to take by surprise.[11] Impala have the ability to distinguish between the alarm and contest calls of chacma baboons.[28] Both species are found in similar environments, and both are predated by lions and leopards.[29]

It is likely that hominins employed similar behaviour by associating themselves with medium and large ungulates during daytime, especially before the controlled use of fire, which would have enabled them to successfully survive for several hundreds of thousands of years. However, testing this proposed association is challenging. For example, using a simple presence–absence approach with respect to medium to large Bovidae and Equidae faunas associated with *Paranthropus robustus*[30-33] from the Cradle of Humankind does not reveal any significant absence of species (Figure 1). An absence or lower occurrence of species may indicate successful anti-predator behaviour, although sample size and taphonomic history[34,35] are also important considerations.

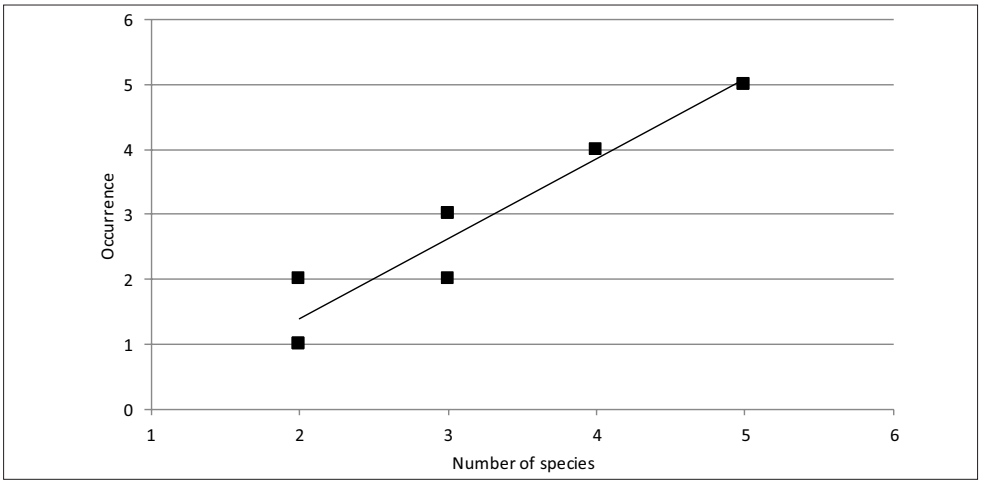

Figure 1: The number of medium and large Bovidae and Equidae species and occurrences at Kromdraai B, Sterkfontein Member 5, Swartkrans Members 1, 2 and 3, Drimolen and Cooper's D Cave. Trend line indicated.

Impalas are the perfect ungulates for primates such as the chacma baboon to associate themselves with during daytime. In addition to their acute ability to sense predators, impalas prefer woodland savanna, rarely wonder more than 2 km from permanent water, and are sedentary, in that they move less than 3 km per day within their home range.[6] During Plio-Pleistocene times, it is possible that hominins such as *Paranthropus robustus* and *Australopithecus africanus* as well as other primates associated themselves with ungulates with similar characteristics. The extinct *Gazella helmoedi* is thought to be an ancestral local form of the extant impala *Aepyceros melampus*.[36,37]

Novel approaches are required to investigate these likely associations between hominins and ungulates to reveal more about the evolution and behaviour of our human ancestors and their relatives. For example, a consideration of the predators, feeding and water requirements, habitat preference, distribution, herd size, home ranges, and anti-predator behaviour of ungulates can potentially reveal behavioural aspects of hominins like *Paranthropus robustus* and *Australopithecus africanus* to complement research on skeletal elements.

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