Introduction

Predation is an important factor in primate evolution. Predation risk includes the possibility of being attacked by predators in the future, as well as incidents in which animals have escaped from predation after encountering predators (Hart and Sussman, 2005). Predation risk has been a factor in the morphological evolution of prey primates because escape from predators is favoured by the ability to run faster and/or the possession of larger bodies (Hurov, 1987; Cheney and Wrangham, 1987). Predation risk has also affected the behavioral evolution of prey primates (Wright, 1989; Zuberbühler, 2007; McGraw and Zuberbühler, 2008).

In human evolution too, predation must have been a major selective force. Although the hypothesis that early hominids primarily hunted, termed ‘man the hunter,’ was part of mainstream anthropology around the 1960s (Dart and Craig, 1959; Ardrey, 1961), it is now recognized that early hominids could more accurately be described as prey, ‘man the hunted’ (Brain, 1981; Hart and Sussman, 2005). There are several reports suggesting that early hominids were killed and eaten by predators in almost the same ratio as living primates under natural conditions (Brain, 1970); the frequencies of living primates being preyed upon are almost the same as those of gazelles and antelopes (Hart, 2000).

To date, there is insufficient evidence regarding primates’ counter-strategies to predation. Many animals use counter-strategies to evade risks at locations frequented by predators; however, there is some debate as to whether predation on primates is frequent (i.e. van Schaik, 1983; Dunbar, 1988; Hart and Sussman, 2005) or rare (i.e. Wrangham, 1980; Cheney and Wrangham, 1987). There are effective strategies to reduce the risk of predation, such as formation of large groups, larger numbers of males in groups, the very fact of group living, philopatry, the use of alarm calls, increased vigilance, and greater cognitive ability (Pulliam, 1973; Alexander, 1974; Seyfarth et al., 1980; Cheney and Seyfarth, 1981; van Schaik, 1983; van Schaik and van Hooff, 1983; Anderson, 1986; Cheney and Wrangham, 1987; Lima and Dill, 1990; Isbell, 1994; Cowlishaw, 1997; Sterck et al., 1997; Hill and Dunbar, 1998; Lima, 1998; Zuberbühler and Jenny, 2002; Shultz et al., 2004; Willems and Hill, 2009). An animal that acquires such strategies is less likely to be killed and eaten by predators and more likely to escape from them.

However, most research on primate predation has focused on individuals that were killed and eaten, whereas few studies have described the behaviors of individuals that survived. Despite theoretical emphasis on predation as a major selective pressure (e.g. van Schaik, 1983, 1989; Dunbar, 1988; Sterck et al., 1997; Janson, 2003), many of the presumed adaptations to predation currently have little empirical support, at least in the case of primates (Cheney and Wrangham, 1987; Isbell, 1994; Miller and Treves, 2007).

Evidence from prehistoric sites is not sufficient to infer how hominids developed counter-strategies to defeat predators. The best way to infer these strategies is by investigating the behaviors of non-human primates. Among the primates, the most suitable species for inferences regarding hominid behavior is the baboon. Early hominids and baboons were preyed upon on a large scale by leopards 1–2 million years ago in South Africa (Brain, 1970). Baboons have the largest bodies among living primates inhabiting the transitional zone between forests and savannas, and their body size is...
similar to that of early hominids. Baboons and early hominids were frequently hunted and eaten by Felidae species (Brain, 1978; Busse, 1980).

This study reports the behaviors of wild baboons that were not killed when an adult male was preyed upon by a leopard in the early morning. Predation by leopards is the main cause of death in adult baboons (Busse, 1980; Cowlishaw, 1994). Leopards hunt both at night and in the daytime. However, the success rate of predation is highest at baboon sleeping sites (Cowlishaw, 1994), suggesting that baboons are often preyed upon at night. It can be difficult to know how individuals other than the victim behave because researchers have reduced visibility at night (Busse, 1980). Busse (1980) observed baboon predation events by leopards at night and reported only that the baboons produced alarm calls in five of six cases. Our report provides new information on baboons’ counter-strategies in response to leopard predation.

Methods

Study site
This study was conducted at the Mpala Research Centre on the Laikipia Plateau, Kenya (0°20’N, 36°50’E). The Mpala covers an area of 200 km² and is located at an elevation of 1700 m. The climate is semi-arid, having an average annual rainfall of about 550 mm, and the vegetation is dominated by Acacia spp. (Franz et al., 2010).

Study subjects
An anubis baboon (Papio anubis) group, AI, has been habituated since 2011 by the author (A.M.O). In October 2014, the AI group comprised 60 individuals, including 11 adult males and 20 adult females. The group had several sleeping sites, but the main one was on a cliff that was about 300 m long and half covered by bushes. The open area of the cliff was about 22.5–38.0 m high from the top to the base, and there were two shelves on its slippery surface (Figure 1). The northern side of the cliff was connected to a big rock that faced the cliff. In addition, there was a cave large enough for two adult humans to sleep on the floor. The inside of the cave was hidden by rocks and could not be seen from either the top of the cliff or the front of the cave without approaching.

Observation
17 September 2014
06:15 We arrived at the top of the cliff. All of the baboons were sitting on the shelves. About 10 baboons were gathered under a big tree, looking in the direction of the cave.

06:20 We moved to the big rock facing the shelves by following the northern edge of the cliff while all of the baboons sat silently. It seemed odd that baboons did not engage in grooming or playing, because they usually showed such behavior in other circumstances.

06:28 Male baboons emitted alarm calls (Figure 2). Four adult males ran and climbed up the tree. Females and youngsters produced alarm calls. An assistant detected a leopard in the bushes. From the side of the cave and toward the north, the leopard surreptitiously circled past the big rock. The assistant pointed his finger in the direction of the leopard’s movement.

06:30 The sun rose. The leopard disappeared quickly into the bushes, and each of the baboons resumed its activity.

06:31 The alarm calls stopped.

07:44 The baboons moved slowly to the south along the cliff.
08:30  The baboons moved into the bushes and down from the cliff. We then stopped the observation. During the observation, we checked which of the baboons were present and found that an old male was missing. We walked down into the cave.

09:10  We found the dead body of the old male, MK, on a big rock in the cave (Figure 3). The body was missing its left leg, and some of the internal organs had spilled out. Additionally, the body had some injuries on the left side of the nose and neck and in two parts of the abdomen (Figure 4). Some small bloodstains were seen from the center to the back of the cave.

16:45  We returned to the cliff.

16:50  A leopard was observed, holding the body of MK in its mouth and running off northward from the direction of the cave into the bush. None of the baboons was at the cliff.

17:30  We left the cliff.

17:32  We found 58 baboons moving and eating on the plain 650 m from the cliff.

17:56  The baboons went back towards the cliff.

18 September 2014

06:15  We arrived at the top of the cliff.

06:18  A young male (EL) looked into the cave from the shelf.

The baboons remained almost silent until they started to move (07:57).

19 September 2014

The baboons were relatively quiet, and there was neither fighting nor screaming until they started movement (between 06:16 and 07:57).

From 20 to 24 September, the baboons shifted their nighttime sleeping site (L.R. Bidner and L.A. Isbell, unpublished data) to a place they rarely used (0.2% of 533 nights: A. Matsumoto-Oda unpublished data).

Discussion

Baboons may know of places that are safe from surprise attacks by leopards. When we came to the cliff early on the morning of 17 September, MK had already been preyped upon by a leopard. Therefore, it is not known how the leopard caught MK or whether other baboons raised alarm calls at that time. We observed, however, that the baboons did not run away while the leopard took MK into the cave and ate his left leg, which took approximately 1.5 hours. The baboons gathered at the north end of the shelf and watched the cave, suggesting that they might have recognized that something significant had happened. The baboons may have thought that leopards could not reach the shelf on the cliff side, and they may have judged that when it was dark they were safer if they stayed there rather than if they moved around blindly on the ground when a leopard was nearby. Baboons may not leave a sleeping site when it is dark even if a group member is killed there. A previous study reported that baboons did not leave a sleeping site in the darkness even when they were surprised by a threat. When Brain (1981) hid in the depths of a cave and then appeared suddenly as a group of baboons slept, the baboons became excited but did not leave the cave. A review showed that protection against predators (especially leopards) was the major determining factor in sleeping site selection (Hamilton, 1982). Baboons use alarm calls and silence, as appropriate. On the rock shelves on ordinary mornings, the baboons of the AI group engaged in typical activities, including grooming, playing, sleeping, and following females. Up until the time the leopard left the area in the morning, however, all of the
members of the baboon group sat in silence, suggesting that they felt tense. One anti-predator strategy of animals is to produce no sound when a predator is near (Zuberbühler, 2001). The baboons emitted alarm calls when the leopard started to move from the cave. Giving an alarm call incurs the risk of being caught by the predator. Therefore, the baboons may have known that this leopard now posed little danger; they gave two messages by producing alarm calls: they prompted other members of the group to pay attention because the leopard was moving; and they let the leopard know that they were aware of its presence. On the mornings of 18 and 19 September, the baboons remained quiet at the cliff, perhaps showing that they were still tense. It has been reported that leopards tend to remain near the hunting place until they devour their kill, which they cache for several days on a tree or in a cave (Bailey, 1993).

Our observations suggest that baboons shift their sleeping sites to avoid subsequent risk of predation by leopards. The AI group changed is sleeping site starting 3 nights after the predation. Leopards hunt at intervals of about 7 days after successful predation on animals of a size similar to impalas (40–50 kg), although there are differences due to individual size and seasonality (Bailey, 1993). Considering the mean weight of male baboons (about 25 kg), leopards that succeed...
in predation of a baboon are likely to hunt again 4–5 days later. Although factors such as seasonality of food resources affect shifts in sleeping sites, the shift of the AI group corresponded to the hunting cycle of leopards. If a leopard tends to stay near the ‘site of the kill’ (Bailey, 1993), staying near the cliff is very dangerous for baboons. Thus, sleeping sites may be abandoned, at least temporarily, if they have been sites of predation events (Altmann and Altmann, 1970).

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References