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The use of tail-flagging and white rump-patch in alarm behavior of goitered gazelles

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ABSTRACT

Tail signals and rump patch exposure in ungulates are well-documented phenomena, but there is no consensus about their functional significance, which has remained disputed. In addition, these patterns have been analyzed for only a limited number of ungulate species; and until now did not include goitered gazelles. This paper, then, will discuss these aspects of goitered gazelle antipredator behavior. I chose human harassments as predator threats and found that tail-flagging, stotting and presentation of the white rump-patch were displayed mostly by adult females, less often by adult males, and least in sub-adults. Adult females used tail-flagging and rump-patch exposure primarily for communication with their fawns especially frequently in July when fawns finished their hiding period. In August, adult females further strengthened their alarm signals by frequent stotting. Unlike females, of encountered threats. However, females and males both displayed tail-flagging significantly more frequently than stotting (with a few exceptions) suggesting that tail-flagging and white rump-patch exposure likely as an alarm and cohesive signal for conspecifics, and adult females communicated by these signals mostly with their fawns.

1. Introduction

1.1. General provisions

Predation is one of the most obvious forces shaping animal traits, resulting in prey animals acquiring a number of antipredator defenses, including behavioral and morphological, which serve to either reduce the likelihood of detection by a predator or enhance the chances of surviving after detection (Caro, 2005; Langerhans, 2007). Therefore, alarm signals exchanged among members of a herd minimizes the predation risk of gregarious animals compared to animals that prefer a solitary lifestyle (Smith, 1991a; Yahner, 2012). Also, larger groups are more likely to spot a predator than smaller groups (LaGory, 1987). The use of conspicuous alarm signals by prey species in encounters with potential danger is a widespread phenomenon among artiodactyls (Hirth and McCullough, 1977). Apart from exaggerated gaits and specific vocalizations, prey animals also use a number of morphological adaptations involved in escaping behaviors to minimize their risk (Caro, 2005; Langerhans, 2007). Among these are the presentation of contrasting colored patches and body parts, such as the white rumppatch and tail, which are frequently used by artiodactyls as alarm signals (Hirth and McCullough, 1977; Caro et al., 1995). Despite the fact that tail-flagging is one of the most widely discussed antipredator behaviors of ungulates (Kiley-Worthington, 1976; Hirth and McCullough, 1977; Bildstein, 1983; LaGory, 1981, 1987; Smith, 1991a; Caro et al., 1995; Stankowich, 2008), there is no consensus in its functional meaning: whether this is a pursuit-deterrent signal for a predator or alarm signal for conspecifics (Stankowich, 2008).

Recently, there have been three classic hypotheses presented for the function of coloration in mammals: physiological demands, concealment, and communication (Caro, 2005). Rather than overall coloration, animals often use patches of color for interspecific communication, which is the second evolutionary force responsible for the coloration of particular body parts (Caro, 2005). Usually, markings are located on the outward body parts, such as ears, face, tails, legs, and rumps, and typically contrast in color with the rest of the body (e.g., a black tail on a white colored rump) (Ortolani, 1999; Caro, 2005). These markings are associated with socio-ecological conditions in which they are most visible: the contrasting tail coloration in ungulates is strongly related to their diurnal and social habits; and ungulates with white rumps are

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Table 1

Description of the recorded behavioral patterns (ethogram) during escaping in goitered gazelles within the study period based on research by Walther (1969), Kiley-Worthington (1976), Alados (1986), Stankowich (2008), Blank et al. (2015).

Behavioral patterns	Description
Alarm for assessment Tail flicking (wagging, swaying)	Standing or lying immobile. Gazelle erects its neck, puts its ears forward, lowers its croup, and tenses its muscles. Repeated lateral tail movements: the brief swaying of the tail from one side to the other or sometimes in a complete circular rotation, when the tail begins in a relaxed downwards position and quickly rotates clockwise or counterclockwise to 90-180° before returning to a downward position. This pattern occurs mainly during relaxed conditions just at the beginning of a bout of locomotion. Rump-patch is uncovered repeatedly (flashing).
Tail hanging down	The black tail is relaxed down (neutral position), vertically, in calm situations with minimum excitement and divides the white rump-patch in the middle into two equal parts.
Raised tail Horizontal tail Tail-flagging	Tail is erected up to a horizontal position (not above the spine) in cases of intermediate arousal (excitement) Keeping the tail strongly in a horizontal position (level with the spine). The tail is held vertically or erected higher than horizontal up to a strong vertical position, or even putting it on the back in some situations of
	great agitation, exposing the white ramp patch to its maximum degree. In this position, the tail can make stereotypically repetitive motor lateral movements from left to right across the hindquarters and back again one or more times in succession. The white rump-patch is completely uncovered, with a black spot only around the anus. At the same time, the white hairs of the rump-patch of the outline are projected outwards, making rump patch more prominent
Tail moving	Making pendulous movements of the tail in side to side and/or up-down directions. During movements, the tail can be erected to various degrees: vertically, horizontally, higher and lower than horizontal.

gregarious and inhabit open environments (Caro, 2005). Tail movements are common in mammals and have taken a role in communication and escaping predators (Kiley-Worthington, 1976; Hickman, 1979). There are at least four not entirely mutually exclusive hypotheses offering possible explanations of the adaptive value of tailflagging (Smith, 1991a): flash behavior (Edmunds, 1974), alarm signal (Estes and Goddard, 1967), cohesive signal (Hirth and McCullough, 1977), and pursuit-deterrent signal (Caro et al., 1995; Stankowich, 2008).

Relatively short tails do not just flick or wag repeatedly from side to side during different behaviors (foraging, walking, alarm), they are also used to make the rump-patch more visible when held vertically and conceal the rump-patch when relaxed and held down (Guthrie, 1971). Using the white rump-patch as an alarm signal originated apparently from acts of urination-defecation and piloerection, which are automatic, physiological (emotional) responses of ungulates to stressful situations (Alvarez et al., 1976). Similar to tail-flagging, there are four hypotheses to explain the rump patch function. The first suggests that ungulates flash their white rump- patches to conspecifics to warn of approaching danger. The second proposes that the rump-patch means "follow me", with two versions: a signal to the entire group to maintain cohesiveness in flight, and a signal to primarily the young to keep their mothers in sight (Guthrie, 1971). The third postulates that rump- patches have evolved and function as part of a sexually submissive intraspecific display and serve to appease dominant animals (Guthrie, 1971). And the fourth hypothesis suggests that apart from an alarming signal to conspecific, the presentation of the white rump-patch could be used as a predator pursuit- deterrent signal (Stankowich (2008).

1.2. Tail-flagging definition

Many authors have confused the definitions of "tail-flagging" with "flicking" (wagging or swaying), combining them into the same behavior. Different authors have also named specific tail movements and positions in different ways (Kiley-Worthington, 1976; Alvarez et al., 1976; LaGory, 1981; Alados, 1986; Caro et al., 2004), or applied the term "tail-flagging" to a specific trajectory of tail movements, identifying a vertical tail as a separate behavioral pattern from tail-flagging (Stankowich, 2008). Such disagreements have led to a muddled mixture of patterns and functions. Similarly to the opinion of Stankowich (2008), I think two main and diverse behavioral patterns exist in tail movements that are different in function: tail-flicking (wagging or swaying) and tail-flagging. Tail-flicking is displayed during calm situations and maintenance activities (feeding, walking) and does not carry an antipredator function (Kiley-Worthington, 1976; Stankowich, 2008); this pattern is likely an indication of social comfort, staying in a large group in a calm state (Alvarez et al., 1976; Caro et al., 2004). Also, tail flicking often may be used often as an insect-repelling action (Mooring et al., 2007). In contrast, tail-flagging is displayed mainly in alarm situations (also during excretions – Walther, 1984) and is a signal of agitation and excitement both before and during flight (Stankowich, 2008), as well as during social play (Walther, 1984). In addition, differences in tail trajectories as seen in black-tailed deer when flicking or flagging their tails (Stankowich, 2008) were also observed in this study.

In contrast to Stankowich's (2008) understanding, I considered a vertical tail as tail-flagging even if it was not accompanied by tail movements, though an immobile vertical tail was observed rarely in alarm situations. In my study, I had a strong impression that tail position was much more important for understanding tail function in antipredator behavior than tail movements, because the degree of tail erection was almost directly dependent on the degree of arousal (excitation) related to the animal's level of alarm (or fear) (Kiley-Worthington, 1976). Tail elevation as a consequence of an increase in arousal, in turn, indicates preparation for running and acts as an alert signal for conspecifics to warn of an approaching threat (Kiley-Worthington, 1976; Alvarez et al., 1976). In investigating the significance of tail position and tail movement in antipredator behavior, I considered "tail moving" as a separate behavioral pattern and identified four main positions of the tail, which was raised to different degrees depending on the gazelle's excitement: neutral position (hanging down) with absence of agitation; raised and horizontal tail with intermediate level of agitation; vertical tail with highest degree of excitement; and side-to-side and/or up-down moving tail, observed for situations when the threat level could not be clearly ascertained. Detailed descriptions of tail positions have been organized in Table 1. In addition, since there are many uncertainties in the definition of "tail-flagging" found in various papers devoted to antipredator behaviors of ungulates, I followed Caro et al. (2004) and interpreted tail-flagging as holding the tail vertically when alarmed. Many other authors had the same opinion, and under "tail-flagging", they had in mind the vertical position of a tail - or at least higher than horizontal, while a raised tail (lower than horizontal) and moving tail (according to my classification) were not referred to as "tail-flagging" (Guthrie, 1971; Alvarez et al., 1976; Hirth and McCullough, 1977; Bildstein, 1983; Alados, 1986; LaGory, 1987; Smith, 1991a; Caro et al., 1995).

1.3. Statement of problem

Tail movements and rump- patch exposure in ungulates are welldocumented phenomena, but the functional significance of each still have to be experimentally tested (Stankowich, 2008). Moreover, these specific behavioral patterns have been analyzed in detail for only for a Download English Version:

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