

ALARM DUETTING AND PURSUIT DETERRENCE
IN AN AFRICAN ANTELOPE

Many social animals give special signals when they encounter a predator. Alarm calls in particular often have special properties suited to specific functions, and this clearly illustrates the adaptive nature of signal structure (Green and Marler 1979). Among artiodactyls the use of alarm signals is widespread, but most attention has been focused on the function of rump-patch displays and the specialized bounding gaits associated with them (Smythe 1970, 1977; Guthrie 1971; Hirth and McCullough 1977; Pitcher 1979; Coblenz 1980). In contrast, alarm calls have received little attention, even though a number of species give them, especially African antelope. One of these, the klipspringer (*Oreotragus oreotragus*), is particularly interesting because its alarm call is often delivered as a duet between a pair of monogamously mated adults (Tilson 1977). By duetting we mean an almost simultaneous rendering of the alarm call by both adults for one or more repetitions. Here we describe the circumstances eliciting loud and repeated alarm calls of this antelope and the specialized alarm behavior associated with the calls. We present evidence that the loud, repetitive, and highly directional qualities of calls could be properties to facilitate communicating the caller's alertness to potential predators rather than warning conspecifics, and that together with other components of the klipspringer's escape response, act as "pursuit deterrent" signals (Woodland et al. 1980).

STUDY AREA AND METHODS

Klipspringers are small Neotragine antelope that weigh about 12 kg and occur on isolated, rocky outcrops and steep, rocky slopes of mountains and canyons throughout southern and eastern Africa. Between June, 1976 and March, 1979 we spent over 1,900 h observing klipspringers in three widely separate areas of southern Africa (1,500 h at Kuiseb River Canyon, Namibia; 400 h at Gamka Mountain and at Springbok, South Africa). General features of alarm signalling described there were found to be essentially the same in other study areas (Naukluft, Namibia; Franschhoek and Augrabies Falls, South Africa). These sites represent a spectrum of typical klipspringer habitats in southern Africa, ranging from rocky slopes of arid desert canyons and granite outcrops to high rainfall mountains.

RESULTS

Our observations of klipspringer social organization (Tilson 1980; Norton 1980) confirm those described by Dunbar and Dunbar (1974, 1979). A typical klipspringer social group is a monogamously mated adult pair with one to two

Tilson, Norton 1981

offspring (mean group size = 2.6 ± 0.7 individuals, $N = 265$). Depending on the area, infants are born every 12 to 18 mo. At this time older offspring leave the group. Adults defend territories of less than 15 ha to more than 100 ha. In both study areas daily activities of the family group are synchronized for 77% of the daylight hours (Tilson 1980). Individuals maintain spatial proximity in all activities, spending 97% of diurnal time within 15 m of each other. Adult females initiate and lead most group progressions, including flight from potential danger. Adult males spend significantly more time in vigilance behavior than other group members, both in feeding and resting periods. Common predators upon adult klipspringers are leopards (*Panthera pardus*), caracals (*Felis caracal*), and jackals (*Canis mesomelas*). Large male baboons (*Papio ursinus*) occasionally prey upon sequestered neonates.

As with the social organization, the alarm behavior of klipspringer groups is strikingly similar in all study areas. We distinguish three typical alarm reactions: (1) When klipspringers detect a potential predator beyond their flight distance of about 100 m they give an attention response, an erect stance with head and ears oriented towards the predator (Dunbar and Dunbar 1974). One of the group usually ascends a nearby vantage point and stares intently at the predator. When the predator leaves the area the alerted individuals relax and resume their normal activity.

2. When a predator approaches closer than 100 m, one of the group usually gives a single, loud alarm call. The group then dashes up the rocky slope to a vantage point and stops to look back. Either one klipspringer continues to call with loud, single notes or, more often, both adults will duet. Alarm duetting occurs when the female's call becomes precisely timed to follow that of the male (fig. 1; Tilson 1977). If further threatened the group runs still higher to another vantage point.

3. When a predator manages to approach close enough to attack (< 25 m), klipspringers will flee immediately upon sighting it. They often give a single alarm call. The panicked adults may use different routes and become separated, but once a higher refuge is gained, the family group coalesces; and the pattern is identical to 2 above.

Elsewhere it has been shown that klipspringer calls, which are usually given in response to potential predators, begin and end abruptly, are high-pitched and have a rich harmonic structure (fig. 1; Tilson 1977). The calls are audible to a human observer up to about 700 m. Unlike the supposed ventriloquial alarm calls of small birds and mammals (Perrins 1968), these characteristics of the klipspringer's alarm call give it a strongly directional quality and should allow the caller to be accurately and quickly located over considerable distances by recipients making binaural comparisons of phase, time, and intensity (Marler 1955; Konishi 1977; Green and Marler 1979). In addition, the rapid repetition of the calls gives recipients ample opportunity to locate the caller. During 46 time-recorded calls from five different groups, alarm calls occurred about every 3–5 s for a mean duration of 2.4 min ($SD \pm 4.7$ min, range = 1–32 min). This would include between 30 to 50 consecutive alarm calls. Thus, the loudness, repetition, and spectral complexity of the calls are all properties which would aid a potential predator to locate the caller.

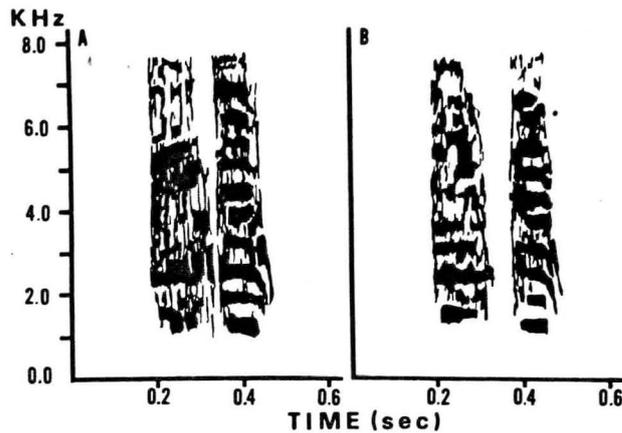


FIG. 1.—Ink tracing of sound spectrograms illustrating two typical duetted alarm calls by a mated pair of klipspringers. In each duet the first note is given by the male, the second by the female. Vocalizations were recorded in the Kuiseb River Canyon, SWA/Namibia, with a Uher 4400 tape recorder at 9.5 cm/s using an AKG D-160 microphone fitted to a 50-cm parabola. Recordings were converted into sound spectrograms using the Kay Elemetric sound spectrograph set on wide band settings (from Tilson 1977).

Klipspringers occasionally give alarm calls in situations where predators are not actually present. For example, sudden gusts of wind, rock slides, or noises from gemsbok (*Oryx gazella*) and mountain zebra (*Equus zebra*) sometimes elicit alarm calls. However, of 154 situations in which alarm calls were given and the probable cause of alarm was identified, a significant number of the calls were in response to jackals, baboons, humans, or spotted hyenas (*Crocuta crocuta*; table 1). The remaining 34 calls were given in response to other animals or unfamiliar noises from the environment ($P < .001$ from parity, $G = 49.22$; Sokal and Rohlf 1969).

These data can be further subdivided. Of the 154 alarm call bouts, 106 (69%) were calls that included duetting (table 1). A significant number of these duetted alarm calls were in response to the presence of a potential predator ($P < .001$, $G = 94.44$) and were repeated significantly more often than when given in response to causes other than predators ($P < .001$; $G = 13.68$, table 1). In contrast, there was no difference between the number of single calls an individual gave when predators were present and the number it gave when they were not (NS, $G = 0.42$). Thus, duetted alarm calls were given more often than single calls and were of longer duration when potential predators were present.

In the Kuiseb River Canyon 18 predation attempts by black-backed jackals upon a family group of klipspringers were observed. In each case a solitary jackal attempted to approach klipspringers feeding in acacia woodland on the floor of the canyon. In such areas klipspringers are particularly vulnerable to predation because they must venture 20–50 m away from the refuge of steep, rocky slopes while the dense vegetation provides cover to approaching predators (Tilson 1980). In 13 of the predation attempts, which were distinguished by characteristic stalking postures, the jackals were detected before they could approach close enough

TABLE 1
 NUMBER OF SINGLE OR DUETTED ALARM CALLS PER KLIPSPRINGER CALLING BOUT ELICITED BY
 DIFFERENT TYPES OF DISTURBANCE

SOURCE OF ALARM	MEAN NUMBER OF ALARM CALLS PER ENCOUNTER			
	Single Calls	(N)	Duetted Calls	(N)
Potential predators				
Jackal (<i>Canis mesomelas</i>)	6.2	(5)	28.5	(35)
Human	5.0	(9)	19.8	(42)
Baboon (<i>Papio ursinus</i>)	5.5	(5)	13.5	(12)
Hyena (<i>Crocuta crocuta</i>)	3.0	(2)	10.8	(10)
	4.9	(21)	22.7	(99)
Nonpredators				
Other animals	4.8	(15)	4.4	(5)
Environmental noise	2.3	(12)	4.0	(2)
	3.5	(27)	4.2	(7)

to initiate a chase. In 10 of the 13 attempts the jackal was spotted at a distance of more than 50 m. The group typically responded by running up on to the rocky slope, where they began to alarm call. After a few single notes the adult pair began duetting. In the other three attempts the jackal was spotted by a vigilant individual standing on higher ground. As soon as this individual gave a single call it was joined immediately by the other two group members. In each of these attempts the jackal stopped stalking the group and turned away once the adults began duetting.

In five approaches a jackal closed to within 10 m, rushed out, and just missed catching one of the group. A single call was given four out of five times. After the group had reached safety, the adults immediately gave loud alarm duets. In all 18 situations, the jackal showed no interest in pursuing the group once they reached the rocks. Also, as soon as alarm duetting started, the jackal turned away and left the area.

DISCUSSION

Klipspringers are small antelopes that are specialized for open habitats and rely on rocky escarpments rather than dense vegetation for protection. Their ability to outrun predators on a rocky substrate is more important for them than the ability to hide. Therefore, they keep sources of danger in view while remaining conspicuous. An unusual characteristic of klipspringers is that their loud alarm calls are given as a duet by the adult pair. We believe duetted alarm calls are not just warnings to conspecifics for the following reasons. Klipspringer alarm duets are louder than necessary to warn immediate group members, and cues for their localization are maximal. Signal detection theory suggests that the signal should be far louder than the average threshold to minimize the probability of nondetection, but because klipspringers stand together when they duet it seems unnecessary for their calls to carry to 700 m. Call repetition provides the receiver ample

opportunity to locate the caller. Callers further enhance localization by remaining in full view. Duetted calls cannot serve to warn other group members, as the group is already aware of the predator's presence and has ascended the escarpment to a safe calling site. This evidence suggests that duetted alarm calls are directed toward the predator, that the callers are communicating their alertness and that this serves to encourage the predator to seek alternative prey elsewhere.

Our hypothesis is the same as that of Woodland et al. (1980), who propose that tail flicks of the swamphen (*Porphyrio porphyrio*) act as "pursuit deterrent" signals by communicating the signaler's alertness to a potential predator and serve to encourage it to hunt elsewhere. In our case, klipspringers have a loud, repetitive duet rather than a conspicuous visual display. The reasons why klipspringers duet when alarm calling is unclear. The male's greater role in vigilance for predators (Dunbar and Dunbar 1979; Tilson 1980) may explain why he always calls first, but why the female times her call to follow precisely that of the male is unexplained. One possible explanation is that duetting enhances localization of the callers by doubling the signal's duration. Another explanation is that there is no selective advantage and that duetting evolved as an adjunct of alarm signalling to promote the monogamous mating system of adult klipspringers (Tilson 1977).

Earlier Smythe (1970, 1977) proposed a related hypothesis, suggesting that white rump-patch displays of certain herbivorous mammals act as "pursuit invitation" signals by inducing predators into chases that have a predictably low probability of success. We agree that such signals are directed towards the predator, but our interpretation of how the predator is likely to respond to the signal is different. Rather than to goad the predator into an attack, we believe that klipspringer alarm signals are to inhibit the predator from making an attack. Both species may benefit if alarm signals inform the predator that a successful attack is unlikely. For the predator there is selective advantage in knowing that its chances of capturing the prey are negligible, and it should go elsewhere to hunt (Woodland et al. 1980). For the prey the cost of deterring the predator from attacking, including the probability of being caught, should be less than the advantage it accrues by regaining maintenance behavior. The distinction is that pursuit invitation generally refers to savanna dwelling prey and cursorial predators while pursuit deterrence is more likely to apply to predators that hunt by stealth.

There are several alternative hypotheses that have been proposed to explain the evolution of alarm calls. These involve kin selection (Hamilton 1964; Maynard Smith 1965), group selection (Wilson 1975), or manipulation of conspecifics (Charnov and Krebs 1975). Three general hypotheses, based on the assumption that alarm calls are altruistic, have been suggested. Alarm calls may have evolved by kin selection to alert relatives of danger (Hamilton 1964; Maynard Smith 1965); they may have evolved through group selection (Wilson 1975); or they may be a form of reciprocal altruism (Trivers 1971). Kin selection operates when the recipients of alarm calls share some degree of relatedness with the caller (e.g., Dunford 1977; Hirth and McCullough 1977; Sherman 1977, 1980). With klipspringers it is important to differentiate the immediate family group that stays together from the subpopulation of neighboring groups that are spatially separate but often in audi-

ble contact. Because klipspringer calls are much louder than needed to warn the immediate family, it is likely that they are directed at the predator or at neighboring conspecifics that may be kin. The extent to which neighboring klipspringers are related is not known. The available evidence suggests that they probably are not closely related. There is no indication that offspring attempt to establish new breeding groups in audible range of their parents. Instead, mature offspring disperse over great distances after leaving their group. In many parts of their range, klipspringers live on small, isolated, rocky outcrops where conspecific neighbors are not present or within earshot. Yet klipspringers on these rocky outcrops give loud and repeated alarm calls to predators in precisely the same way that groups with near neighbors give them.

Alarm calls may evolve through reciprocal altruism, providing benefits can be withheld from nonreciprocators (Trivers 1971). Because klipspringer alarm calls alert all individuals within perceiving distance, this condition is rarely or never met.

An alternative hypothesis is that alarm calls discourage a predator from returning to an area in future hunts by reducing their overall hunting success (Trivers 1971). Because predators are more likely to return to areas where previous hunting forays were successful, callers could reduce their own future vulnerability to predators by alerting neighbors or other group members to danger. This enhances their own fitness. The fact that other individuals also benefit would be coincidental. There is some evidence that predators often do hunt near sites of previous success (Curio 1976), but whether alarm calling reduces the likelihood of a predator returning to an area is not known.

Individuals may obtain direct benefits from warning others of danger by creating confusion among group members, thereby diverting the predator's attention away from the caller (Charnov and Krebs 1975; Hoagland and Sherman 1976; Owens and Goss-Custard 1976). The scattering of many individuals may confuse the predator enough to reduce the caller's risk of being caught. This hypothesis is inappropriate because klipspringer alarm calls have the effect of attracting a predator's attention to the family group whose escape response is orderly and highly coordinated.

An alternative option is for individual prey to give high-pitched ventriloquial alarm calls that may cause the predator to look in the wrong place for the caller (Perrins 1968). The effect would be to increase the predator's search time, thereby encouraging it to give up and to direct its attention toward other group members. This hypothesis is rejected because the cues for localization in the klipspringer's call are maximal, and in alarm situations klipspringers enhance their conspicuous image by remaining in view of the predator.

Thus, several features of the klipspringer's escape response support the pursuit deterrent hypothesis as an explanation of their alarm calls. These are: (1) The exceptionally loud, repetitive, and strongly directional properties of the calls should attract attention to callers over considerable distances. (2) Callers enhance their chances of being localized by conspicuous movements and by remaining in view. (3) The audibility of the alarm signal is reinforced by duetting. (4) The

coincidence between alarm signalling and the presence of predators. (5) The observation that predators immediately turn away once alarm duetting begins.

The evidence suggests that while single alarm calls might only serve to warn the family group of immediate danger, repeated alarm duets of adult pairs are pursuit deterrent signals directed at predators.

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