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Stotting in Thomson's gazelles: an honest signal of condition

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Summary. The incidence and context of stotting were studied in Thomson's gazelles. Results suggested that gazelles were far more likely to stot in response to coursing predators, such as wild dogs, than they were to stalking predators, such as cheetahs. During hunts, gazelles that wild dogs selected stotted at lower rates than those they did not select. In addition, those which were chased, but which outran the predators, were more likely to stot, and stotted for longer durations, than those which were chased and killed. In response to wild dogs, gazelles in the dry season, which were probably in poor condition, were less likely to stot, and stotted at lower rates, than those in the wet season. We suggest that stotting could be an honest signal of a gazelle's ability to outrun predators, which coursers take into account when selecting prey.

Introduction

Stotting is a display performed by Thomson's Gazelle *Gazella thomsoni* and many other species of *Bovidae*, *Antilocapridae* and *Cervidae* (Byers 1984). It is defined as leaping off the ground with all four legs held stiff and straight (Walther 1969). Stots are generally performed by adults in response to predators, but are also observed in immatures during play (Walther 1969).

The large predators that hunt adult Thomson's gazelles employ two main strategies to capture their prey. They either stalk, like cheetahs *Acinonyx jubatus* and lions *Panthera leo*, relying on surprise and short fast chases (Schaller 1968, 1972) or course, like African wild dogs *Lycaon pictus*, chasing over long distances and relying on stamina to outrun their prey (Kruuk 1972; Estes and Goddard 1967). Although the incidence of stotting has

never been quantified, it appears to be an uncommon response to stalkers but occurs frequently in response to coursers (Estes and Goddard 1967; Walther 1969).

While eleven hypotheses have been suggested for the function of stotting, only one attempt has been made to distinguish between them (Caro 1986a). Caro (1986b) concluded that, in response to cheetahs, stotting by adult gazelles serves to inform the predator that it has been detected, but that the behaviour does not invite or deter pursuit. Stotting may, however, have another function when performed under different circumstances. In response to coursers, for example, the gazelles may be informing the predators of their ability to outrun them (Zahavi, in Dawkins 1976). If that were the case, stotting should occur as an honest and graded signal, its intensity closely linked to individual differences in stamina and/or running speed. If not, cheaters will arise during the course of evolution, exaggerating their ability to escape. Predators will then be selected to abandon stotting as an assessment criterion. Honest signals investigated so far have been involved in the assessment of fighting ability between conspecifics (Davies and Halliday 1978; Clutton-Brock and Albon 1979).

In this paper we consider the incidence of stotting by adult Thomson's gazelles in response to a coursing predator, the wild dog, and test the hypothesis that stotting is an honest signal, informing predators of a gazelle's ability to outrun them. Additional data on gazelles stotting in response to a stalking predator, the cheetah, and to a second coursing predator, the spotted hyaena *Crocuta crocuta*, are presented for comparison. The three predator species were chosen because Thomson's gazelles constitute a large part of their diet in the study area (Schaller 1972; Borner et al. 1987), allowing the effect of predator hunting technique on the incidence of stotting in a single prey species to be investigated.

Methods

Thomson's gazelles and their predators were observed on the long, intermediate and short-grass plains of the Serengeti National Park, Tanzania between March 1985 and April 1987. Wild dogs were observed for approximately 1000 hours and during this time they were seen to chase adult Thomson's gazelles on 125 occasions. In addition, 1752 hours of cheetah observations were made and data from 133 hunts of adult gazelles were collected. All the data were collected during daylight hours (approximately 6.30 am to 7 pm). Observations were made through 10 × 50 binoculars from a Landrover and recorded onto tape for later transcription to data sheets.

Behaviour of predators

The hunting strategies of the predators were categorised as coursing or stalking (Kruuk 1972; Schaller 1972; see introduction). During their encounters with gazelles, the predators' behaviour was described as approaching or hunting. Approaching predators moved towards the gazelles but did not subsequently stalk or chase them whereas hunting predators did stalk and/or chase the prey group. If the predators killed a gazelle, then the hunt was considered successful; if no kill was made, the hunt was unsuccessful. Unsuccessful hunts were further divided between those in which the predators chased a group, but did not appear to pursue a specific individual and those in which they did focus on one gazelle, but failed to capture it. In the latter case, the predators followed the flight path of a particular animal, rather than those of other group members. Usually, the chased gazelle split away from the rest of the herd.

Behaviour of the prey

Since we were only concerned with the function of stotting in adult Thomson's gazelles (aged 16 months – approximately 12 years, as categorised by Walther 1973), only data from adults were used in the analyses. Stotting in immature gazelles probably has a different function, informing their mothers that they have been disturbed and are in need of defence (Caro 1986b).

The herds of Thomson's gazelles in the study area were mainly mixed sex groups (Walther 1964), containing an average of 56 gazelles (range 1–250). At the beginning of their flights from the wild dogs and hyaenas, we recorded the number of adult gazelles in the group which fled, as well as the number of fleers which stotted. This was later calculated as the percentage of fleers that stotted. If at least one adult gazelle stotted, the group was described as "stotting". The proportion was noted at the start of flights because initial observations suggested that a large number stotted when wild dogs and hyaenas first chased a group, but that once the predators had selected a gazelle the other members of a group ceased stotting. The total number of stots made to cheetahs were counted, because earlier observations had revealed that gazelles rarely performed more than a few stots in response to these predators.

Detailed observations of stotting were only made in response to the coursing wild dogs. The rate of stotting, in stots per second, was measured by counting between ten and thirty stots onto a tape recorder as they occurred. The number of stots was then divided by the time taken to perform them (rather than the total flight duration as used by Caro 1986b). We felt that an accurate measure of rate could not be relied upon when calculated from a small number of stots, so the rate was only measured if the gazelles stotted more than ten times. Where-

ever possible, the rate was recorded at the start since it could have varied during the chase, and comparable measures from different individuals were required. On the thirty occasions when the stot rate of the same individual was sampled more than once during a chase only the first record was used in the analysis. The duration for which gazelles continued to stot was also measured to the nearest second, and the distance from the predator when they ceased stotting was estimated. It is probable that gazelles also adjust the height of their stots, in addition to their rate, but because this variable proved impossible to record accurately, it could not be used as a measure of stotting.

To compare the stotting rates of gazelles selected by the wild dogs with those they did not select (but which appeared to be similarly positioned and available), the rates of the chased gazelle and of an adult gazelle running alongside it were measured at the beginning of chases. If there were no gazelles alongside, then the rate and sex of the nearest adult in the group were recorded.

Finally, the flight distance of the group and the length of the chase were measured. The flight distance was the distance between the predator and the nearest gazelle when the prey group first fled. It was estimated to the nearest 10 m if the distance was less than 100 m and to the nearest 50 m if greater. The observers' accuracy at estimating distances were regularly checked against objects placed at known distances. The chase length was the interval, measured to the nearest second, between the time when the prey group fled and the time when the predators either killed a gazelle or abandoned the chase.

Results

The occurrence of stotting in response to wild dogs

Gazelle groups were more likely to stot in response to wild dogs that hunted them than to those that approached but did not subsequently chase them ($\chi^2 = 27.20$, $df = 1$, $P < 0.0001$, Table 1). They were also more likely to stot if they fled from close to the wild dogs than if they fled from further away: there was a negative correlation between flight distance and the percentage of fleers stotting ($r_s =$

Table 1. The number of groups in which at least one gazelle stotted when fleeing from three species of predator. The data from hunting and approaching predators are compared

	Stotting groups	(% of total)	Non- stotting groups	(% of total)	Total
Wild dog					
hunting	118	(78.1)	33	(21.9)	151
approaching	115	(47.7)	126	(52.3)	241
Cheetah					
hunting	12	(9.0)	121	(90.9)	133
approaching	2	(3.0)	64	(97.0)	66
Hyaena					
approaching	15	(35.7)	27	(64.3)	42

–0.366, $n=252$, $P<0.0001$). The size of the group affected the likelihood of stotting: if data from both hunts and approaches were combined, single gazelle were more likely to stot (81.4%, $n=140$) than groups (51.2%, $n=252$, $\chi^2=34.9$, $df=1$, $P<0.0001$).

Individual gazelles that were selected and chased by wild dogs normally stotted at the start of chases (84.3%, $n=106$), although there was considerable variation in the duration for which they continued to stot (see also below). On some occasions they performed as many as 100 stots, stotting throughout most of the chase, and only stopping when the dogs got too close. The mean distance at which they abandoned stotting was 38 m ($n=29$). Although the stot rate of an individual did sometimes vary during the chase, it did not consistently decline or increase – on the thirty occasions when an individual was sampled more than once, the second rate was greater than the first on fifteen occasions, lower on twelve and unchanged on three.

The effect of stotting on prey selection and hunting success of wild dogs

When hunting a group, wild dogs selected and concentrated their chases on gazelles that stotted at lower rates (Mann-Whitney U -test, $z=-3.172$, $n=120$, $P<0.005$). The mean rate of those chased was 1.64 stots/second (SD=0.31, $n=82$) and of those not chased 1.86 stots/second (SD=0.35, $n=38$). When the stotting rate of a selected gazelle was compared with that of another running at approximately the same speed alongside, there was also a significant difference (Wilcoxon matched pairs, $z=-2.600$, $n=26$, $P<0.01$). The mean rate of those chased in these cases was 1.5 stots/second and of those not chased 1.8 stots/second. Two possible reasons for this difference might be suggested; either the dogs choose gazelles which stot at a lower rate than others nearby, or the gazelles reduce their stotting rate when seriously chased. In the eight cases when gazelles were observed both before they were selected and while being chased, four animals increased their stotting rate when selected while four decreased it. This implies that the gazelles are as likely to decrease their stotting rate on being hunted as they are to increase it and that the dogs are selecting on the basis of stotting rate. In addition, wild dogs were seen to change the focus of a hunt from one stotting gazelle to another on five occasions and on four of these the gazelle preferred was stotting at a lower rate (Table 2).

Table 2. The stotting rate (in stots/s) of gazelles originally chased and of those that the dogs switched to in the same group. The sex of each gazelle is also indicated

	First chased		Second chased	
	Rate	Sex	Rate	Sex
case 1	1.4	♀	1.1	♂
case 2	1.8	♂	1.4	♂
case 3	2.0	♂	1.8	♂
case 4	1.8	♂	1.3	♂
case 5	1.5	♀	1.6	♀

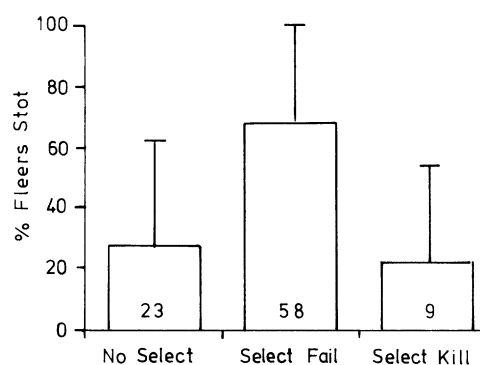


Fig. 1. The mean percentage of fleers stotting in groups from which dogs did not select a vulnerable animal to chase (no select); were able to select a gazelle but were unable to outrun it (select fail) and for groups from which the dogs successfully made a kill (select kill). Numbers in columns refer to sample sizes and standard deviations are shown by bars

Whether the proportion of the group stotting had any effect on the predators' selection of prey is unclear. Analysis of variance techniques revealed that the percentage of fleers stotting was higher when dogs selected an animal than when they did not do so, the proportion of gazelles stotting having been adjusted to take account of significant effects of group size and flight distance ($F=15.97$, $df=1,65$, $P<0.001$, No select vs Select fail in Fig. 1).

The percentage of fleers stotting also appeared to affect whether or not a selected gazelle was killed. The percentage of fleers which stotted was lower when the dogs killed a member of the group than when they abandoned the chase, the data having been adjusted to take account of significant effects of group size and flight distance as above (ANOVA, $F=4.87$, $df=1,54$, $P<0.05$, Select fail vs Select kill in Fig. 1).

Individual gazelles which were selected but which then escaped were more likely to stot during the chase than those which were unable to outrun the wild dogs. Of escapees, 89% stotted, while only

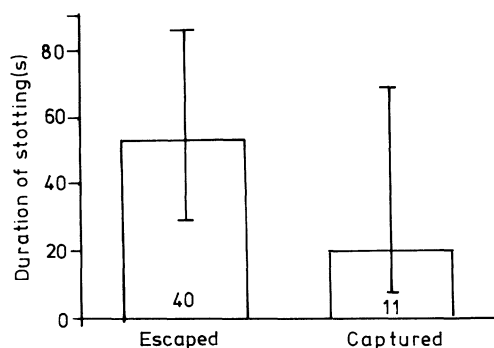


Fig. 2. The median duration of stotting (in seconds) of gazelles which escaped once chased and of those killed by wild dogs. Numbers in columns refer to sample sizes and interquartile ranges are shown by bars

74% of those captured did ($\chi^2 = 4.08$, $df = 1$, $n = 103$, $P < 0.05$). Gazelles that escaped also stotted for longer durations during the chase (Mann-Whitney U -test, $z = -1.982$, $n = 40, 11$, $P < 0.05$; Fig. 2). This was true despite the fact that chases which resulted in kills were far longer than those which were abandoned (Mann-Whitney U -test, $z = -4.024$, $n = 24, 70$, $P < 0.0001$). A comparison of stotting rate between gazelles that escaped and those that were captured at the end of the chase was not possible since only four of those gazelles for which stotting rate could be measured were then killed by the dogs.

If stotting is a measure of a gazelle's ability to outrun predators, wild dogs might be expected to abandon chases earlier against gazelles stotting at higher rates than against those stotting at lower ones. In fact, there was no such relationship (correlation between unsuccessful chase length and stotting rate, $r_s = -0.02$, $n = 69$, NS). In addition, dogs did not catch up more quickly on gazelles that stotted at higher rates compared with those that stotted at lower rates ($r_s = -0.117$, $n = 60$, NS).

Stotting as an indicator of physical condition

Without shooting or immobilizing individual gazelles, it was not possible to directly relate their stot rates to physical condition. Some indirect evidence was collected, however, based on the fact that gazelles are likely to be in worse condition in the dry season than in the wet. Reduced fat reserves, which are generally associated with poor condition in ungulates (Sinclair and Duncan 1972; Brooks et al. 1977), may not alter a gazelle's ability to outrun predators, but there is some evidence that ungulates on reduced food supplies may lose skeletal muscle as well (Torbit et al. 1985; Tyler 1987). Thus, the seasonally reduced food supply

Table 3. The mean rate of stotting (in stots/second) and the mean proportion of fleers stotting in groups fleeing from wild dogs in the wet and dry season

Season	Stot rate means \pm SD	(%) of fleers stotting means \pm SD
Dry	1.4 \pm 0.3 (n = 13)	36.9 \pm 41.3 (n = 42)
Wet	1.7 \pm 0.3 (n = 107)	66.9 \pm 44.0 (n = 48)

may affect a gazelle's ability to outrun predators and/or stot. When compared with the wet season data, the proportion of a group stotting was lower in the dry season, the proportion of gazelles stotting having been adjusted to take account of significant effects of group size, hunt outcome and flight distance (ANOVA, $F = 6.61$, $df = 1, 68$, $P < 0.02$; Table 3). In addition, when gazelles did stot, dry season stotting rates were significantly lower than wet season ones, taking into account the sex of the stotter and the hunt category (whether individuals were chased or not, ANOVA, $F = 11.57$, $df = 1, 81$, $P < 0.001$; Table 3).

While these results do suggest that gazelles are stotting less when they are in poor physical condition, there could be other explanations. The vegetation type, for example, may be different in the two seasons, although possible differences were minimised by collecting all the data from wild dogs on the short-grass plains where the vegetation is rarely higher than 10 cm.

Comparing the stalking and coursing predators

Although cheetahs do sometimes hunt like coursers, trotting towards their prey in full view (Kruuk and Turner 1967), this rarely occurs unless the vegetation is too short for stalking (Schaller 1968; Eaton 1974). In this study, cheetahs were mainly observed in higher grass where they almost invariably stalked. Since they rely on surprise, they are rarely successful against groups that have been alerted to their presence (Eaton 1970). In comparison, the wild dogs usually ran towards their prey in full view and in all the hunts, the gazelles detected them well before the chase began ($n = 125$). Hyenas are thought to course in a similar manner (Kruuk 1972), while the hunting technique of lions resembles that of cheetahs (Schaller 1972).

The incidence of stotting in response to the various predators appeared to reflect these differences in predator hunting strategies (Table 1). Data from both approaches and hunts revealed that gazelle groups were far more likely to stot in response to wild dogs than they were to cheetahs ($\chi^2 = 166.8$,

$df=1$, $P<0.0001$; Table 1). Groups stotted in 59.4% of flights from wild dogs but in only 7.0% of flights from cheetahs. The number of stots performed in response to cheetahs (mean = 4.3, $n=12$) also appeared to be lower than to wild dogs (as found by Caro 1986b). Since no data were collected in response to hunting hyaenas, the incidence of stotting to this predator approaching was compared to that of approaching wild dogs and cheetahs only. Hyaenas caused gazelle groups to stot much more often than cheetahs did ($\chi^2=20.8$, $df=1$, $P<0.001$), but less often than wild dogs ($\chi^2=3.9$, $df=1$, $P<0.05$). Casual observation of gazelles responding to lions confirmed an earlier observation that they rarely stot to these predators (Schaller 1972).

In response to cheetahs, gazelles were more likely to stot when they were actively hunting rather than just approaching but not significantly so ($\chi^2=1.94$, $df=1$, NS, Table 1). When a gazelle was actually selected and chased by cheetahs it rarely stotted (on only 2.3% of 133 occasions), unlike gazelles chased by wild dogs (see above) and hyaenas (Kruuk 1972, p.196).

Discussion

The prey is healthy hypothesis (Caro 1986a), first suggested by Zahavi (in Dawkins 1976), states that by stotting gazelles inform predators that they are healthy enough to outrun them. In this definition it is assumed that a gazelle's physical condition directly affects its ability to outrun predators. In this paper we suggest that gazelles stot in order to advertise their ability to outrun predators and assume that physical condition is one important influencing factor. Any gazelle stotting at a higher rate than those nearby signals that it will be more difficult to catch. Variation in the rate of stotting could allow predators to assess the ability of potential prey to escape. If stotting is to be maintained as a stable strategy in this way, several conditions need to be fulfilled.

Firstly, stotting must be honest, the performance (be it the height, rate or duration) closely related to the gazelle's ability to outrun a predator. Gazelles which were chased and killed by the wild dogs were less likely to stot during the hunt and, when they did, stotted for shorter periods than those which escaped. Wild dogs were also more successful at killing gazelles from groups that had a low proportion of stotters at the beginning of flights. Such groups might be expected to contain more vulnerable gazelles. Moreover, gazelles in the

dry season were less likely to stot and, when they did, stotted at lower rates than they did in the wet season. One reason for this difference could have been that the gazelles were in poorer physical condition in the dry season. During these months, the supply of food declines, resulting in the utilization of fat reserves (Bradley 1977; Stelfox and Hudson 1986) and probably also protein from skeletal muscle. However, without an independent measure of a gazelle's escape potential, a relationship between stot rate and ability to outrun predators cannot be confirmed.

One corollary of the honest signal principle is that gazelles should not be able to cheat successfully. Gazelles which are actually incapable of outrunning the predators, might try and deceive them by stotting at high rates, but should be unable to perform deceitfully for long. Dogs could check for such cheating by continuing to chase suspicious gazelles for a critical period. In addition, the duration of continuous stotting that a gazelle could maintain or the average height of its stots could be additional indicators of its ability to outrun predators, more difficult to bluff than the rate of stotting. This might explain why those gazelles which were unable to outrun predators stotted for shorter periods during chases than those which escaped.

The second requirement for stotting to be maintained, is that predators should select prey on the basis of their stotting behaviour (Harvey and Greenwood 1978). Gazelles chosen by the wild dogs were found to stot at lower rates than those which were ignored. In addition, when the dogs switched focal gazelles during a hunt, they usually changed to one stotting at a lower rate.

Gazelles rarely stotted in response to cheetahs. These predators, unlike wild dogs, were never seen to change the focus of their chase from one gazelle to another and are thought to select their prey before the chase begins, using features which allow them to stalk within reach, such as vigilance and proximity (personal observation). As a result, stotting is unlikely to affect a gazelle's chance of being selected by this predator. In contrast, wild dogs and hyaenas probably select their prey during the chase, choosing a vulnerable individual on the basis of its performance in flight (Estes and Goddard 1967; Kruuk 1972). Since they run down their prey in long chases, the prey's fitness and stamina may be important factors and stotting may enable predators to assess them.

If, by stotting, gazelles are attempting to alter the predator's choice of prey, they should do so when they are most at risk of being selected. Thus, gazelles were not only more likely to stot when

alone than when in groups, but were also more likely to stot in response to hunting rather than approaching predators. Further, a greater proportion of a group stotted when fleeing from dogs at close distances than when they fled further away. If gazelles only stot when the risk of capture is high, as they appear to, it might be assumed that there are energy costs associated with the behaviour. Energetically expensive but useless stotting can be avoided.

Although stotting may be energetically expensive, it does not appear to slow the gazelles down – wild dogs did not gain on gazelles stotting at higher rates more rapidly than those stotting at lower rates. It is possible that those gazelles which are able to outrun predators can ‘afford’ to spend time and energy in stotting at a high rate and still stay out of reach of the predators. Those in worse condition, on the other hand, cannot stot at a higher rate without slowing down or running out of energy.

While it is probable that predators benefit from being able to assess the ability of potential prey to outrun them, it is not clear what benefit gazelles gain from providing this information. The answer may be related to the wild dogs’ method of hunting. The outcome of their long chases probably depends on the relative stamina of predator and prey. In the absence of stotting, a dog might be forced to chase over a considerable distance in order to determine whether it can outrun and catch a gazelle. If gazelles signal their ability to escape at the start of hunts and wild dogs take account of this information when selecting prey, those gazelles with a good chance of escaping will not have to prove their physical fitness by outrunning the wild dogs in long, exhausting chases. Furthermore, any chase is likely to be dangerous, even for a healthy gazelle, because of the risk of injury, and because such long chases may leave them vulnerable to other predators that they encounter before having had time to recover.

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