

Tail-flagging and other antipredator signals in white-tailed deer: new data and synthesis

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We present a series of predictions concerning the costs and benefits of antipredator behavior in ungulates and then test them with data on white-tailed deer reacting to a human on foot. Costs of tail-flagging were apparently low and no data supported the idea that flagging serves as a warning signal to conspecifics, in either this or in other studies. Flagging deer fled at greater speeds than nonflaggers, indicating that flagging could possibly signal prey's ability to escape. Dropping the tail at the end of the flight may additionally have made deer inconspicuous. Snorting did not appear directed at conspecifics, and comparative data suggest that it signals that the predator has been detected. In contrast, foot-stamping was effective in alerting other deer to the observer's presence. Deer may have bounded to clear obstacles along their flight path. These preliminary data indicate that several aspects of antipredator behavior in white-tailed deer may be pursuit-deterrent signals, and they therefore highlight the necessity of observing natural predators' reactions to signals given by deer in future studies. *Key words:* antipredator behavior, bound, foot-stamp, *Odocoileus virginianus*, pursuit deterrence, signals, snort, tail-flag, tail-flick, white-tailed deer. [*Behav Ecol* 6: 442–450 (1995)]

Theoretical interest in animal signaling (Grafen, 1990; Guilford and Dawkins, 1991; Maynard Smith, 1991; Zahavi, 1975) is directly relevant to many areas of behavioral ecological research: signaling of status (Whitfield, 1987) or intent during combat (Enquist, 1985); the criteria on which females choose mates (Vehrencamp et al., 1989); parent-offspring conflict (Godfray, 1991); and antipredator behavior (Hasson, 1991). Currently a body of empirical data is growing to support and redirect theory in relation to signaling between conspecifics, but there is still remarkably little observational or experimental information on signals that pass between prey and predators.

To date, most empirical work on antipredator signaling has been carried out on ungulates, which display a diverse array of auditory, olfactory, and visual behavior patterns in the face of danger (see Caro, 1994 for a review). Critical testing of hypotheses about the adaptive significance of ungulate antipredator behavior has proved exceptionally elusive, however, as signals are usually received by both predators and conspecifics. This makes it imperative to state competing predictions about adaptive hypotheses clearly and to use multiple tests to support or refute hypotheses. An additional problem is the relatively few systematic observations of ungulates signaling to free-living predators (see FitzGibbon and Lazarus, 1995) and the natural reluctance to use trained live predators against deer or antelopes (but see Lingle, 1992).

Tail-flagging in white-tailed deer (*Odocoileus virginianus*) is, perhaps, the best known ungulate antipredator behavior. Yet despite a number of papers on its adaptive significance (Bildstein, 1983; Coblenz, 1980; Hirth and McCullough, 1977; LaGory, 1987; Muller-Schwarze, 1991; Smith, 1991; Smythe, 1970, 1977), it is still unclear to whom tail-flagging is directed, and there is no consensus among biologists, naturalists, or

hunters about its functional significance. In an attempt to reach a consensus about antipredator behavior in white-tailed deer, we reexamine the adaptive significance of tail-flagging and other antipredator behaviors in this species by presenting new observational data and synthesizing our results with those of others. First, however, we present a scheme of the costs and benefits of putative antipredator behavior in ungulates that sets out testable predictions [see Caro (1986a) and Hasson et al. (1989) for similar approaches].

An important issue in studies of antipredator behavior is whether behavior carries a substantial cost: if costs are high, the circumstances in which a behavior occurs can give a clue to its function (Cyger, 1990). For example, if a costly antipredator behavior pattern is more likely in the presence of kin, its design features suggest that it warns kin of danger, but if it carries no cost, it may also be given by solitary individuals despite having been selected to warn kin. Unfortunately, a priori judgements about the magnitude of costs are problematic since there are potential time, energetic and survivorship components. For example, bounding is likely to be more costly in energetic terms than tail-flagging, but the latter may carry hidden survivorship costs by attracting a predator's attention or enabling it to be followed more easily.

Antipredator behavior patterns in ungulates can be divided into three major categories: (1) those that act as signals (sensu Markl, 1985) to conspecifics, (2) those that signal to the predator, and (3) those that simply help the animal to escape (Table 1) (Caro, 1986a, 1994). Signals directed at conspecifics could be maintained through kin selection by warning descendant or other kin of danger that they might not have seen (Sherman, 1977). Therefore, if groups contain kin, one might expect individuals in groups to perform such behavior more than single individuals, at least when knowledge of the whereabouts of conspecifics is perfect (Hasson, 1989). Alternatively, signals could be maintained through individual selection, inviting other individuals to bunch together before or during flight (Hirth and McCullough, 1977) in order to accrue benefits derived from dilution or hiding behind conspecifics

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Table 1
Costs and benefits of antipredator behavior in ungulates

Prediction	Reasoning
Is antipredator behavior costly?	
Time cost	
1. Production before flight takes time and delays onset of flight.	Flight delay makes capture more likely.
2. Production during flight takes time and reduces flight speed.	Reduced flight speed makes capture more likely.
Energy cost	
1. Behavior before or during flight is energetically costly.*	Lowered stamina makes capture more likely.
Survivorship cost	
1. Performer attracts predator's attention, which results in predator chasing that individual.*	Predator notices prey because of behavior or searches out oddity.
Benefits: Behavior aimed at conspecifics (assumes some cost)	
General predictions	
1. Solitary individuals will not signal.	Conspecifics do not need to be warned as absent.
2. In groups, signal will be directed at conspecifics.	Conspecifics must see signal.
3. Signal will alert conspecifics.	Signal required only if others are unaware of predator.
Behavior warns offspring or other kin	
1. Females are more likely to signal than males.	Does but not bucks are accompanied by kin.
2. Females are more likely to signal in presence of kin and if more kin are present.	There is a greater benefit as risk of kin being captured is greater if more kin are present.
Behavior manipulates group members	
1. Group members will bunch together as they flee.	Individuals stay close to accrue group benefits.
Benefits: Behavior aimed at predator (assumes some cost)	
Behavior startles the predator	
1. Onset of chase is delayed or chase abandoned.*	Signal surprises predator (flash hypothesis).
Behavior deters further pursuit	
General prediction	
1. Hunting predators usually give up on seeing signal.*	Signaling that success is unlikely is usually honest, but predators may be very hungry.
by advertising alertness	
1. Signals will occur far from predator (either before or during flight).	This is more likely to dissuade predator when success rate is low.
by advertising condition	
1. Individuals in poor condition will not signal.*	Poor condition signallers lose more than they gain by signaling.
2. Individuals that are likely to outrun the predator will signal.	Signalers gain more by deterring predator's approach than by fleeing.
Behavior causes predator to lose contact	
1. Conspecifics will signal simultaneously or in rapid sequence.	Predator cannot follow a single individual and abandons chase (confusion hypothesis).
2. Signal stops suddenly after flight.*	Termination of signal enhances crypticity, and predator loses sight of prey.

Table 1, continued

Prediction	Reasoning
Behavior has no signal function	
1. Behavior is more prevalent when terrain is difficult to negotiate.	This carries prey over obstacles or helps it make quick turns.

Note that hypotheses can rarely be refuted with a single test.
* Not tested in this study.

(Hamilton, 1971). Such behavior is most likely when group membership is stable and individuals can interact repeatedly (Boyd, 1992).

If signals are directed at the predator, they might startle it, thus causing it to hesitate momentarily (Edmunds, 1974). Alternatively, signals might convey information about the predator's chances of capturing the prey. The signal could inform the predator that it has been seen (advertising alertness) and has thus lost the element of surprise that is critical when stalking or ambushing (Hasson, 1991), or the signal could inform the predator that the prey is in a sufficiently healthy state to outrun the predator (advertising condition; FitzGibbon and Fanshawe, 1989), important in relation to coursers. Signals carrying such information can only evolve if they benefit both prey and predator and must therefore be maintained through honesty (Caro, 1994; Vega-Redondo and Hasson, 1993; but see Johnstone and Grafen, 1993).

Signals could also cause a predator to lose contact with the prey either by confusing the predator (Jarman, 1974) or by making the prey additionally cryptic once signals cease, resulting in the predator losing sight of the quarry (Edmunds, 1974).

Finally, antipredator activities might not be signals at all; they could simply facilitate efficient flight by carrying the animal over obstacles or increasing its maneuverability (Lingle, 1993).

METHODS

We undertook a study of white-tailed deer antipredator behavior in the Edwin S. George Reserve in southeast Michigan, USA, between 5 September 1988 and 6 October 1989. The 464-ha reserve, surrounded by a high deer fence, is characterized by open fields with tussocks of tall grass, oak-hickory woods, and temporary and permanent swamps separated by steep topography [see Cantrall (1943) and Coblentz (1970) for a description of the plant communities]. The deer population of the George Reserve has been the subject of ecological (McCullough, 1979) and behavioral (Beier and McCullough, 1990; Hirth, 1977) research including an earlier study of tail-flagging (Hirth and McCullough, 1977). As a result of an annual deer cull begun in 1934 (O'Roke and Hamerstrom, 1948), the George Reserve deer are wary of humans, orienting towards and fleeing from them as they do from natural predators.

In our study, a single observer on foot (T.M.C., L.L., or A.W.G.) approached deer during daylight between 0700–1000 and 1630–1930 h, the times that deer were most active (Beier and McCullough, 1990). Data were collected in all weather except torrential rain. We encountered deer alone or in small groups, defined as collections of individuals less than 5 m from their nearest neighbor (LaGory et al., 1981); mean group size was 2.6 animals (range 1–19, $N = 648$ individuals or groups).

Once we sighted a single deer or a group, one individual

Table 2
Definitions of behavior patterns recorded in the study

Behavior	Definition and comments
Behavior patterns performed either before or after a flight but not while fleeing	
Foot-stamp	Lifting of the foreleg and suddenly striking the ground with the hoof one or more times. Usually only one foreleg was involved.
Snort	A low frequency barking sound resulting from a sharp expelling of air through the nostrils. It could be heard over 100 m away.
Tail-flick	Moving the tail to one side while it was held vertically downwards. This usually occurred repeatedly and to both sides of the body.
Behavior patterns performed during flight	
Tail-flag	Lifting the tail to a vertical up position. Occasionally animals might lift their tail while standing still.
Bound	A long jump that carried the deer over at least double the distance covered by one galloping stride.

Some behavior patterns were first recorded after the study had begun, which produced slightly different sample sizes.

was assigned as the focal deer, usually the nearest group member. Next the observer tried to make a concealed approach as closely as possible in an effort to behave like an advancing predator. Nevertheless, deer were often already watching the observer before we noticed them, and this was recorded. It was easy to determine when a deer was watching the observer as it stood in a stiff, upright posture with ears forward, staring directly at the observer for some time (Linsdale and Tomich, 1953). As soon as the focal deer had detected the observer or as soon as we noticed deer that were already aware of us, we stopped, started a stopwatch, and made a mental note of the grass tussock or bush where the focal deer stood. The number and age-sex class of the deer and the habitat in which they stood were then recorded. We classified deer as adults (of full body size), yearlings (young of the previous year which were smaller than adults), and fawns and neonates (young of the current year); we combined the first two age-classes in many of the analyses. We also classified deer according to whether they were male or female or of unknown sex; males could be identified by antlers and/or testes. Habitats were broadly categorized as open (open fields with bunchy grass tussocks), open and bush (fields with tall, scattered bushes), wood (trees of varying density), and forest (densely packed trees that were difficult to penetrate), vegetation types representing increasingly closed habitats; marshy vegetation (waterlogged soil or surface water) was recorded as well.

We recorded the number of times the focal deer foot-stamped, flicked its tail from side to side, or snorted. (see Table 2 for definitions) and noted the number and identity of other group members performing these activities. The observer then recorded whether none, some, or all of the other group members were alerted to our presence as a result of any of these activities or whether they were all alerted already. Being alerted was defined as staring at us in the upright posture described above. It was easy to record the occurrence of these three antipredator behaviors and conspecifics' responses to them because they occurred infrequently and rarely at the same time and because deer usually stood still at this stage.

When these records had been collected, the observer

walked directly towards the focal animal and counted paces. As soon as the focal animal fled, the observer stopped walking, reset the stopwatch, and observed the group's flight until the deer stopped. Often deer ran (A) directly way from the observer but on many occasions at (B) an oblique or (C) right angle to our advance, which was noted. The observer recorded the number of times the focal deer bounded and the position of its tail (vertically up, horizontal, or down) during flight (Table 2) and again made a mental note of the animal's exact location at the end of the flight. If the deer tail-flagged, the direction the underside of the tail faced was noted and a small diagram was drawn of the positions of other group members in relation to the flagging focal deer. Later, a perspex cross was superimposed on this diagram with its main axis being the deer's flight path. From the focal deer's perspective, we could classify each conspecific into one of four positions: (a) behind the focal animal, defined as 45° either side of the flight "wake" where it could easily have seen the white underside of the focal animal's tail, (b) behind but between 45–90° of the focal individual's flight wake where it would be more difficult to see the tail, (c) in a broad 180° arc in front, or (d) actually directly in front of the focal deer's flight path. In the latter two positions, it would have been impossible to see the white underside of the focal deer's erect tail. We also scored the number and identity of other group members fleeing, tail-flagging, and bounding.

Once the flight was over, the observer stopped the watch and walked toward the original location of the focal deer, again counting paces. We measured observers' strides at regular intervals throughout the study and converted them to meters. The distance at which the deer first detected the observer was calculated by adding this figure to the number of paces already counted. From the original location of the focal deer, the observer then paced a straight line to the position of the focal deer at the end of its flight. This yielded a minimum flight length. Dividing flight length by flight time gave flight speed. Finally, we noted whether group members stayed roughly the same distance from each other during flight, bunched together, or made off in different directions; and whether any deer that had not been in the original group joined the group in flight.

Since the population contained approximately 200 animals that were not recognized individually, some deer were encountered more than once. However, we assumed that their behavior would have depended more on the nature of the contact with the observer, on local ecological circumstances, and on the proximity of other deer, than on individual differences in antipredator behavior that might bias results. Previous studies of antipredator behavior in ungulates have invariably used populations where individuals were not recognized. In any case, observers took care to walk different routes on consecutive days to minimize the likelihood of encountering the same individuals close in time; we recorded between one and six flights on each day of observations. Using SPSS/PC (4.1), we analyzed data with nonparametric statistics (Siegel, 1956) since many variables were discrete, and variables that were continuous were not normally distributed and could not be normalized using standard transformations. Statistical tests were two-tailed, and null hypotheses were rejected at the 0.05 level.

RESULTS

Are antipredator behaviors costly?

While watching the observer, deer sometimes foot-stamped, tail-flicked, or snorted before fleeing. Latencies between detecting the observer and fleeing were longer when the focal deer foot-

stamped or tail-flicked than when it did not (stamp: $N = 48$ instances in which they stamped prior to flight, and $N = 148$ in which they did not, $\bar{X}_s = 60.7, 28.3$ s respectively, Mann-Whitney U tests, $z = -4.957, p < .0001$; flick: $N = 19, 33$ flights respectively, $\bar{X}_s = 65.8, 34.7$ s, $z = -2.493, p = .013$; taking only those flights in which the observer saw the deer before it saw the observer). Latencies did not differ according to whether the focal deer snorted or not prior to fleeing ($N = 17, 176$ flights respectively, $\bar{X}_s = 42.6, 32.7$ s, $z = -1.452$, ns).

Foot-stamping and tail-flicking may have delayed flight or, alternatively, may have been performed in relaxed situations where deer did not need to flee quickly. Tail-flicking, at least, was observed when deer were at greater distances from the observer ($N_s = 19, 34$ flights when flicks, respectively, did and did not occur, $\bar{X}_s = 57.9, 48.2$ m, Mann-Whitney U test, $z = 2.055, p = .04$), and subsequent flights were slower if the focal animal had foot-stamped or tail-flicked immediately before the flight than if it had not (stamp: $N_s = 71, 431$ flights respectively, $\bar{X}_s = 4.5, 5.4$ m/s, Mann-Whitney U tests, $z = -3.030, p = .002$; flick: $N_s = 39, 121$ flights respectively, $\bar{X}_s = 4.8, 6.3$ m/s, $z = -3.564, p = .0004$; snort: $N_s = 36, 460$ flights respectively, $\bar{X}_s = 5.5, 5.3$ m/s, $z = 0.049$, ns). Both facts suggested that stamping and flicking were associated with relatively relaxed situations rather than that they imposed a time cost on performers.

The two behaviors performed during flight, tail-flagging and bounding, did not reduce flight speed. In fact, focal animals fled at considerably greater speeds if they flagged than if they did not ($N_s = 537, 82$ flights respectively, $\bar{X}_s = 5.6, 3.8$ m/s, Mann-Whitney U test, $z = 6.192, p < .0001$). Bounding had no effect on flight speed ($N_s = 121, 460$ flights respectively, $\bar{X}_s = 5.8, 5.3$ m/s, $z = 1.740$, ns).

We were unable to measure the energetic cost of the five behavior patterns. Nevertheless, it seems reasonable to assume that stamping, flicking, and flagging the tail demanded little energy expenditure. Snorting may have imposed slight energetic costs on individuals (Caro, 1994), while bounding almost certainly required somewhat more energy than a flat run.

The survivorship cost of each behavior could not be measured as natural predators were not observed in this study.

Benefits

Are behaviors aimed at conspecifics?

Focal individuals in groups did not perform any type of behavior more often than solitary individuals; indeed, bounds were more likely in flights of solitary deer (focal deer found in groups stamped prior to 15.9% of 295 flights versus 12.1% of 215 flights in which they were found alone, $\chi^2 = 1.198$, ns; flick: prior to 25.3% of 95 group flights versus 25% of 68 solitary flights, $\chi^2 = 0$, ns; snort: prior to 7.6% of 290 group flights versus 6.5% of 217 solitary flights, $\chi^2 = 0.101$, ns; flag: during 88.0% of 382 group flights versus 85.3% of 252 solitary flights, $\chi^2 = 0.713$, ns; bound: during 17.2% of 349 group flights versus 26.3% of 243 solitary flights, $\chi^2 = 6.694, p < .01$).

Tail-flagging seemed directed primarily at the observer rather than at conspecifics. In 542 flights in which it was recorded, the underside of the erect tail was either directly (category A, see Methods, 30.3%) or almost directly (category B, 62.2%) facing the observer; in only 7.6% of flights was it definitely facing elsewhere (category C). In the 255 flights when the focal deer was in a group and flagged its tail, an average of only 39.4% of conspecifics were in the 180° arc behind the focal animal (categories a and b). In the other flights (categories c and d) it would be extremely difficult for conspecifics to see the focal deer's white anal hairs during flagging.

Furthermore, we found no strong evidence that tail-flagging alerted conspecifics. In 42.8% of the 285 flights when the fo-

Table 3
Mean percentage of focal individuals that exhibited antipredator behavior

	Stamp	Flick	Snort	Flag	Bound
Adult females	17.9 (190)	25.0 (76)	9.6 (187)	85.7 (217)	19.0 (200)
Adult males	8.7 (23)	23.1 (13)	4.2 (24)	88.9 (27)	33.3 (24)
Yearlings	12.8 (187)	29.4 (51)	4.9 (185)	86.6 (232)	20.7 (222)
Fawns and neonates	13.2 (68)	19.0 (21)	4.5 (67)	87.4 (87)	20.2 (84)

Yearlings, and fawns and neonates combined include deer of both sexes. Number of flights is shown in brackets.

cal animal flagged, all other group members were already aware of the observer's presence. In the remaining 163 flights when they were not, the focal individual caused all (55.8% of cases) or some (24.5%) of the group members to become aware of the observer, but it was not possible to determine whether this was due to the focal animal flagging or simply fleeing. The effect of snorting was more equivocal and the sample size was small. In seven out of 21 cases, all the other group members were aware of us already, while snorting alerted all (seven cases), some (three), or none (four) of the group members in the remaining 14 cases.

In contrast, foot-stamping was more effective in alerting conspecifics to danger. In only 21.2% of 33 instances were conspecifics aware of us before the focal animal stamped, and in the remaining 26 cases, stamping alerted all (61.5% of cases), some (26.9%), or none (11.5%) of the group members to us. In short, it warned others of danger in 69.7% of instances. A focal deer was more likely to stamp its feet if we came upon it suddenly before it noticed us (24.4% of 197 focal deer foot-stamped when the observer saw them first versus only 7.1% of 268 when they noticed us first, $\chi^2 = 26.095, p < .0001$, an effect unlikely due to us missing this behavior since deer often foot-stamped repeatedly). Also, focal deer were more likely to foot-stamp in open habitats where sound carried well than in closed habitats (17.2% of 371 flights in open, and open and bush habitat combined versus 9.6% of 166 flights in woodland and forest combined, $\chi^2 = 4.485, p = .034$).

No measures were taken of whether conspecifics were alerted as a result of tail-flicking. However, deer were more likely to flick their tails if we saw them first (35.8% of 53 focal deer tail-flicked when the observer saw them first versus 18.5% of 97 when they noticed the observer first, $\chi^2 = 4.624, p = .032$). Since deer repeatedly flicked their tails in bouts lasting up to 2 min, this result was unlikely due to our having missed the behavior.

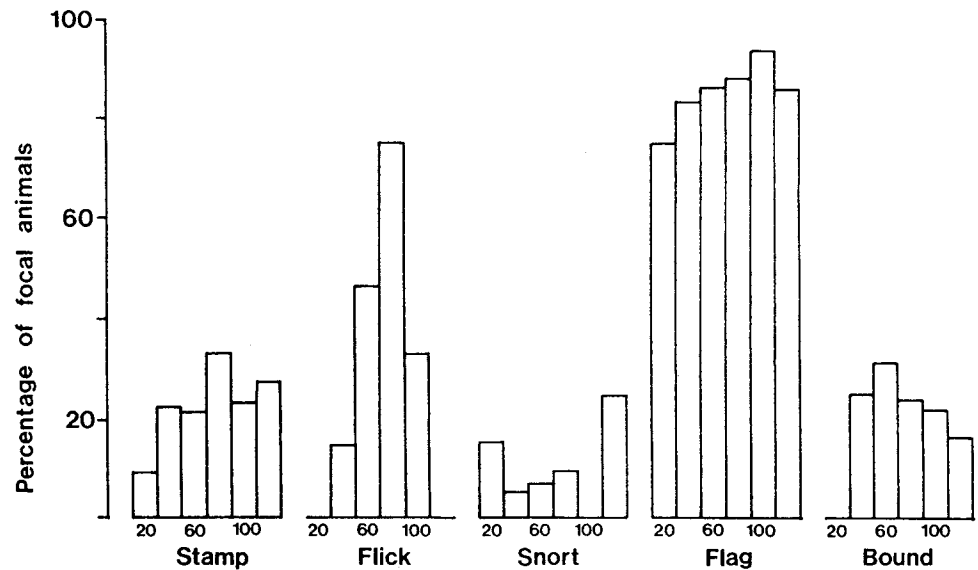
Do behaviors warn kin?

Female white-tailed deer are philopatric and often live with dependent offspring while males live alone or with unrelated males (Hawkins and Klimstra, 1970). Therefore, females might be expected to show a greater predisposition to signal if a signal's function was to warn kin of danger. Table 3 shows that the proportion of focal adult females and males showing each sort of behavior differed little (Fisher's Exact tests, all ns).

Furthermore, focal adult females were no more likely to perform these behavior patterns if either neonate, fawn, or yearling females were present than if they were not (stamp: 22.5% of 80 flights when kin were present versus 14.5% of 110 when kin were absent, $\chi^2 = 1.40$, ns; flick: 25.0% of 36

Figure 1

Percentage of focal animals that exhibited antipredator behavior before or during the flight separated by the distance that they detected the observer. From left to right for each behavior: 0–20 m, 21–40 m, 41–60 m, 61–80 m, 81–100 m, >101 m. *N*s: foot-stamp, 11, 57, 57, 33, 17, 18 flights, respectively; tail-flick, 6, 16, 15, 8, 6, 2; snort, 13, 59, 57, 31, 15, 16; flag, 16, 61, 60, 35, 17, 22; bound, 11, 55, 57, 33, 18, 18. Data were restricted to flights in which the observer saw the deer before the deer saw the observer.



versus 25.0% of 40 respectively, $\chi^2 = 0$, ns; snort: 12.7% of 79 versus 7.4% of 108 respectively, $\chi^2 = 0.905$, ns; flag: 87.1% of 93 versus 84.7% of 124 flights respectively, $\chi^2 = 0.095$, ns; bound: 10.8% of 83 versus 24.8% of 117 respectively, $\chi^2 = 5.561$, $p = .022$).

Do behaviors manipulate group members?

We found no evidence that foot-stamping or snorting by any group member before a flight or that tail-flagging or bounding by any group member during a flight caused other group members to bunch together and so enable the signaller to benefit from being in a tight group (stamp: 30.4% of 56 groups bunched together if any stamping had occurred versus 31.4% of 309 groups when it has not, $\chi^2 = 0$, ns; snort: 23.8% of 21 versus 31.7% of 344 respectively, $\chi^2 = 0.264$, ns; flag: 30.4% of 345 versus 45.0% of 20 respectively, $\chi^2 = 1.251$, ns; bound: 27.0% of 89 versus 32.6% of 276 respectively, $\chi^2 = 0.752$, ns; similar data were not collected for tail-flicking).

If antipredator behaviors served to invite other deer to join the signaller, solitary deer might be more likely to perform such behavior providing other deer could see them. However, data presented earlier showed that, except for bounding, solitary animals were no more likely to perform antipredator behaviors than those in groups. Indeed, extragroup individuals rarely joined fleeing groups and were no more likely to join if any group member performed a behavior pattern than if none did so (stamp: others joined a group in which stamping occurred on 5.5% of 55 occasions versus 4.3% of 422 occasions when no stamping occurred; snort: 7.1% of 28 versus 4.2% of 449 respectively; flag: 4.4% of 425 versus 5.8% of 52 occasions respectively; bound: 7.1% of 98 versus 3.7% of 379 occasions respectively, Fisher's Exact tests, all ns; similar data were not collected for tail-flicking).

Are behaviors aimed at the predator?

As we did not observe hunting attempts by natural predators, it was difficult to test directly hypotheses concerning signaling to predators. However, we tested the following four hypotheses indirectly (Table 1). First, if a behavior is relatively cost free and advertises that the prey has seen the predator, it should be more effective at deterring pursuit when the prey is far away. At close distances, hunting success is likely greater and, in addition, success rate is less likely affected by prey's level of alertness, making pursuit deterrent signaling less ef-

fective and hence less likely attempted nearer the source of danger (Lazarus J, personal communication). Antipredator behaviors were exhibited throughout the range of distances that deer detected us (Figure 1), although tail-flicking was more likely to occur when deer detected us from farther away as described earlier (stamp: $N = 46$ in which deer stamped prior to flight, and $N = 147$ in which they did not, \bar{X} s = 62.7, 55.2 m respectively, Mann-Whitney U tests, $z = 1.614$, ns; snort: N s = 16, 175 flights respectively, \bar{X} s = 66.3, 54.4 m, $z = 0.721$, ns; flag: N s = 181, 30 flights respectively, \bar{X} s = 59.0, 48.8 m, $z = 1.722$, ns; bound: N s = 47, 145 flights respectively, \bar{X} s = 56.1, 57.9 m, $z = -0.029$, ns).

Second, if behavior were a signal of the prey's condition, it should have been exhibited only by individuals that could outrun or outmaneuver a predator. Although we took no measures of body condition, we found that, in each age class, individuals that tail-flagged ran away from the observer at greater speeds than those that did not flag (Figure 2). This was true both of focal animals found in groups and those found alone when possible confounding effects of conspecifics' speeds were absent. Flagging, therefore, might have provided a signal that the individual would run fast.

Third, if behavior served to confuse a predator, then one would expect a number of individuals to perform it simultaneously or in rapid sequence. However, we found no significant associations between the number of deer fleeing in a group and the number of individuals flagging their tails or bounding (flag: $N = 328$ flights, $r_s = -.0227$, ns; bound: $N = 314$ flights, $r_s = -.0522$, ns). This is a surprising result as one would expect a significant positive correlation between group size and the number of individuals performing the behavior. Negative correlations suggest that being in a larger group inhibits these behaviors.

Fourth, if signals were designed first to draw attention to the prey simply to exaggerate its crypticity once the signal stopped, signals might be expected to occur during flight but be curtailed suddenly at the end of it. Only tail-flagging conformed to these design criteria as other behaviors occurred before or only intermittently during flight. Signals should be terminated more in wooded areas since the additional crypticity gained by terminating a signal would be more beneficial in woods than in open areas where deer would be conspicuous anyway. This was supported because the proportion of flagging focal deer that suddenly dropped their tails was high

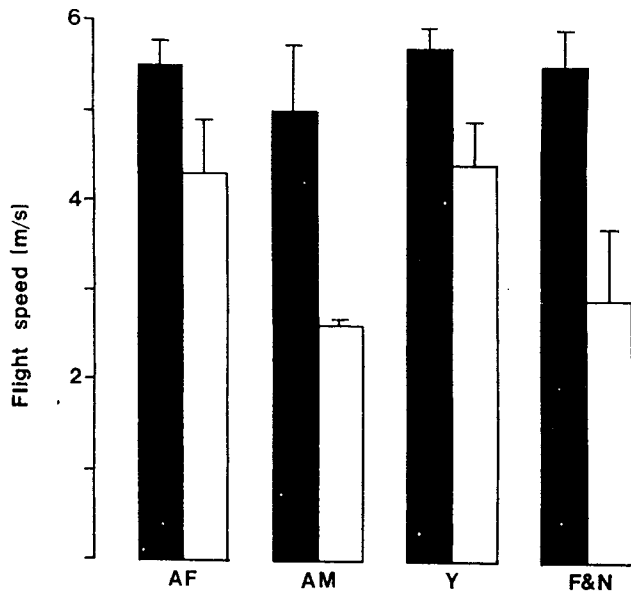


Figure 2
Mean (and SE) flight speeds in solitary individuals that did (solid bars) and did not (open bars) tail-flag. AF: adult females, $N_s = 72$, 13 flights respectively, Mann-Whitney U tests, $z = 2.028$, $p = .043$; AM: adult males, $N_s = 15$, 3, $U = 9$, ns; Y: yearlings, $N_s = 82$, 14, $z = 2.224$, $p = .026$; F&N: fawns and neonates, $N_s = 26$, 4, $z = 2.259$, $p = .024$.

when their flight finished in wood habitats: adults, 78.5% ($N = 65$ flights); yearlings, 90.2% ($N = 61$); and fawns and neonates 100.0% ($N = 15$); parallel data were not recorded in open habitats.

Does behavior facilitate flight?

Could some of these behaviors simply have helped deer escape from us? Behaviors occurring before flight and tail-flagging could not have provided mechanical advantage during flight which left bounding as the only possibility. Although bounding did not affect flight speed, it might have enabled deer to clear obstacles. Focal animals were more likely to bound in open habitats from which they ran directly towards cover than in closed habitats where they maneuvered between thickets and trees during flight (23.6% of 377 flights in open, and open and bush habitat combined versus 14.6% of 198 flights in woodland and forest combined, $\chi^2 = 5.834$, $p = .016$).

DISCUSSION

Tail-flagging

Results of this and earlier studies on tail-flagging are summarized in Table 4. Our study demonstrated that flagging did not reduce flight speed; time costs were not examined in other studies. Energetic costs of flagging are likely negligible. However, it is unknown whether flagging increases or decreases the probability of attack by predators, and observations of deer flagging in response to natural predators are needed. If survivorship is increased by flagging, it is likely a signal to the predator; if it is decreased, it is likely a signal to conspecifics.

Table 4 shows that no data supported the hypothesis that flagging signals to conspecifics since solitary deer flagged, flagging was not specifically directed at conspecifics, and deer were not alerted to a human observer as a result. In addition, most studies of tail-flagging in white-tailed deer failed to support the hypothesis that females signal to kin because they did

not flag more than males and were no more likely to flag if kin were present. Smith (1991) and Muller-Schwarze (1991) did report higher rates of flagging in females than in males, however. Furthermore, the social cohesion hypothesis, which states that flagging attracts conspecifics, was not supported because group members did not bunch in response to flagging; nor did extragroup members join the flagger. Although this hypothesis has received considerable attention (Hirth and McCullough, 1977; LaGory, 1987), it has been advanced only by eliminating competing hypotheses and until now has never been directly tested. Smith's (1991) finding that solitary deer flagged more than deer in groups (not corroborated here) does not by itself provide strong support for the cohesion hypothesis. In short, evidence from a number of populations is inconsistent with the hypothesis that tail-flagging is an alarm signal directed at conspecifics (see Table 4).

Unfortunately, the only viable alternative hypothesis, that flagging signals to predators, has never been systematically examined because observations of predators' responses to flagging are necessary to gauge its consequences, but, to date, studies have used only humans to elicit responses from deer. Nevertheless, deer that flagged dropped their contrasting tails at the end of flights, on occasions rendering them inconspicuous, at least to a human observer. The increasing propensity for younger deer to drop their tails might have reflected young ungulates' greater susceptibility to predation (Caro and FitzGibbon, 1992), but specific predictions about predators' inability to keep track of prey could not be tested.

Individuals that flagged ran faster than those that did not. In fallow deer (*Dama dama*), which also have a white underside to their tail, the proportion of time the tail is held erect also increases with flight speed (Alvarez et al., 1976). If predators find it difficult to judge their prey's flight speed as prey runs directly away from them, and hence make a decision to chase prey or not, an unequivocal signal such as tail-flagging could become established if it signalled the prey's ability or willingness to flee at high speeds. Flagging could signal either flight speed or an associated factor such as body condition. In both fallow deer and Thomson's gazelles (*Gazella thomsoni*; Caro, 1986b), the tail is held vertically, exposing its white underside while stotting, and in Thomson's gazelles, data from two sources indicate that stotting is an honest signal of condition (Caro, 1994; FitzGibbon and Fanshawe, 1989). Thus, there is a comparative basis, at least, for thinking that tail-flagging could signal the ability of the performer to outrun the predator.

In short, the hypothesis that tail-flagging in white-tailed deer has evolved as a signal to predators is supported by the elimination of competing hypotheses; Bildstein (1983) reached much the same conclusion in a similar fashion. In our study, preliminary data further suggest that tail-flagging either serves to make deer more cryptic or that it signals prey's ability to outrun a predator. These hypotheses now require testing by direct observations of natural predation attempts on white-tailed deer. Indeed, it is unlikely that studies using humans or domestic dogs as predators will further increase understanding of the adaptive significance of tail-flagging. Neither species has shared a long evolutionary history with white-tailed deer, and so it is unlikely that they have been selected to respond to antipredator signals appropriately.

Snorting

Few data are available on the costs of snorting in white-tailed deer, although it did not appear to delay the onset of flight unduly (Table 5). Snorting may impose an energetic cost on antelopes (Caro, 1994), but this was not examined in white-tailed deer.

Table 4
Summary of results found on tail-flagging in this and other studies

	Hirth and McCullough (1977)	Bildstein (1983)	LaGory (1987)	Smith (1991)	This study
Costs					
Time	—	—	—	—	—
Energy	—	—	—	—	No
Survivorship	—	—	—	—	—
Benefits: tail-flagging aimed at conspecifics					
General predictions					
Solitaries will not flag	—	No	No	No	No
Flag directed at conspecifics	—	No	—	—	No
Flag alerts conspecifics	—	No	—	—	No
Tail-flagging warns offspring or other kin					
Females flag more than males	No	No	No	Yes	No
Females flag if kin present	—	—	No	—	No
Tail-flagging manipulates group members					
Group members bunch together	—	—	—	—	No
Solitaries will flag more than group members	—	No	No	Yes	No
Extragroup members join flagger	—	—	—	—	No
Benefits: tail-flagging aimed at predator					
Tail-flagging startles the predator					
Onset of chase is delayed	—	—	—	—	—
Tail-flagging deters further pursuit					
General prediction					
Hunters abandon chase in response	—	—	—	—	—
by advertising alertness					
Signals occur far from predator	Intermed distance	Yes	—	—	No
by advertising condition					
Prey in poor condition do not signal	—	—	—	—	—
Individuals that run fast will signal	—	—	—	—	Yes
Tail-flagging causes predator to lose contact					
Conspecifics flag simultaneously or in rapid sequence	—	—	—	—	No
Signal stops suddenly	—	—	—	—	Yes

— indicates not tested.

In this and other studies, virtually no data suggest that snorting warns other deer of danger. On the contrary, solitary deer frequently snorted; in groups, snorting often occurred when conspecifics were already aware of danger; and even when they were aware, snorting was not particularly effective in alerting other deer to our presence. Although findings on sex differences in snorting are contradictory across studies (Table 5), Hirth and McCullough's (1977) finding that groups of females snorted more than groups of males may be an artifact of female groups being larger than male groups (LaGory, 1987) and, in any case, can only constitute weak support for an alarm function. Snorting did not cause group members to bunch during flight or cause extragroup members to join the focal animal.

By elimination, snorting, like tail-flagging, appears directed at the predator. LaGory (1987) reached a similar conclusion but again only by elimination. Against this, however, deer in our study snorted at all distances from the observer and in Hirth and McCullough's (1977) were prone to snort when they were surprised at close range. On the other hand, among African bovids, snorting appeared to signal that the observer had been seen, and crude experiments involving a human advancing or retreating from adult male topis (*Damaliscus kor-*

rigum) indicated that snorting informed the observer that he had been detected (Caro, 1994). Similar conclusions were reached by Yahner (1980) for barking in muntjacs (*Muniacus reevesi*) and by Tilson and Norton (1981) for alarm-duetting in klipspringers (*Oreotragus oreotragus*). Therefore, our working hypothesis is that snorting in white-tailed deer advertises alertness to the predator. However, detailed records of predators' responses to snorting are required.

Foot-stamping

Foot-stamping did not impose a substantial time cost in the sense of forcing deer to run quickly to make up for the delay in starting to flee. Indeed, deer usually flee at slower rates after stamping. Other costs were not measured, but it is difficult to imagine that stamping could be energetically costly.

Deer were more likely to foot-stamp in open habitats where sound carried well; they usually stamped when conspecifics were unaware of us; and stamping had a marked effect on alerting conspecifics to our presence. Thus, a strong prediction of the signaling to conspecifics hypothesis is supported by the data. Nevertheless, solitary deer as well as those in groups foot-stamped (12.1% and 15.9% of flights respective-

Table 5
Summary of results of snorting, foot-stamping, tail-flicking, and bounding

	Snort			Foot-stamp This study	Tail-flick This study	Bound This study
	Hirth & McCullough (1977)	LaGory (1987)	This study			
Costs						
Time	—	—	No	No?	No?	No
Energy	—	—	—	—	—	—
Survivorship	—	—	—	—	—	—
Benefits: behavior aimed at conspecifics						
Solitaries will not perform	—	No	No	No	No	No
Act directed at conspecifics	—	—	—	—	—	—
Act alerts conspecifics	—	—	No?	Yes	—	—
Behavior warns offspring or other kin						
Females act more than males	Yes	No	No	No	No	No
Females act if kin present	—	—	No	No	No	No
Behavior manipulates group members						
Group members bunch together	—	—	No	No	—	No
Solitaries will act more than group members	—	No	No	No	No	Yes
Extragroup members join actor	—	—	No	No	—	No
Benefits: behavior aimed at predator						
Behavior startles the predator						
Onset of chase is delayed	—	—	—	—	—	—
Behavior deters further pursuit						
General prediction						
Hunters abandon chase in response	—	—	—	—	—	—
by advertising alertness						
Signals occur far from predator	Yes	—	No	No	Yes	No
by advertising condition						
Prey in poor condition do not signal	—	—	—	—	—	—
Individuals that run fast will signal	—	—	No	No	No	No
Behavior causes predator to lose contact						
Conspecifics act simultaneously or in rapid sequence	—	—	—	—	—	No
Signal stops suddenly	NA	NA	NA	NA	NA	NA
Behavior facilitates escape						
Used in certain environments	NA	NA	NA	NA	NA	Open habitat

— indicates not tested, NA not applicable.

ly), and foot-stamping was not performed by females primarily in the presence of kin. These contradictory results question the way in which the behavior might be maintained in the population, although if foot-stamping carries little cost, it might not always be limited to adult females with kin. If foot-stamping simply served to warn others of danger, it was not surprising that deer did not bunch together or that other deer did not join the group. Little evidence could be marshalled to refute or support signaling to predators.

No other studies have examined the adaptive significance of foot-stamping, and our data are preliminary, but they suggest that foot-stamping may be a relatively cost-free alarm signal to conspecifics.

Tail-flicking

Flights preceded by tail-flicking were delayed, but since tail-flicking usually occurred far from the observer and was followed by a relatively slow flight, little cost seemed involved. It is difficult to imagine that flicking imposed a large energetic cost or that it attracted predators' attention.

LaGory (1981) found that tail-flicking in white-tailed deer occurred at the end of bouts of alertness but was never followed by flight. Contrary to our study, he suggested tail-flicking could act as a cue to conspecifics that no danger was nearby. In contrast, among fallow deer the rate of tail swaying was highest when the animal moved away from a source of alarm (Alvarez et al., 1976). These authors suggested that exposure of the white rump patch during tail-flicking serves as a warning device although they did not specify the intended receiver. In our study, predictions concerning tail-flicking as a signal to conspecifics were not met (Table 5). In addition, our finding that tail-flicking occurred far from the observer provides no more than weak support for a predator signaling function. At present, then, the function of tail-flicking remains an enigma.

Bounding

Bounding did not reduce flight speed. Since it did not occur in flights that started very close to the observer (Figure 1), some energetic cost may have been involved. We found no evidence that bounding was a signal to conspecifics, and it was

unlikely to be a condition-dependent signal to predators because it was not associated with flight speed. Deer bounded through open habitat, which in the George Reserve often consisted of tall tussocks of grass. Thomson's gazelles have similarly been recorded bounding more through tall vegetation (Caro, 1994). In both species, bounding may serve to minimize contact with the ground where predators might be lurking or to maximize vertical distance should any predator appear while the animals are traversing tall vegetation. Similarly, impalas (*Aepyceros melampus*) bound more when they run through bushes and hartebeests (*Alcelaphus buselaphus*) when they traverse slopes and rocks (Caro, 1994). Bounding, therefore, seems a mechanism to clear obstacles in these species.

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