

Energy-expending behaviour in frightened caribou when dispersed singly or in small bands

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Abstract: The behaviour of single, and small bands of caribou (*Rangifer tarandus groenlandicus*) when confronted by humans was compared with the energy-saving behaviour zoologists have ascribed to caribou in encounters with non-hunting wolves (*Canis lupus*). When confronted by me, or upon getting my scent, caribou ran away on all occasions. Their flight was occasionally interrupted by short stops to look back in my direction, but would continue on all occasions until they were out of sight. This behaviour is inconsistent with the one ascribed to caribou by zoologists when the intruder is a wolf instead of a human. In their view, the caribou stop their flight soon after the wolf gives up the chase, and accordingly save energy owing to their ability to distinguish between hunting and non-hunting wolves. However, small bands of caribou, as well as single animals, have never been observed to behave in this manner. On the contrary, the behaviour of caribou in such encounters is known to follow the same pattern as in their encounters with humans. Energy-saving behaviour is, however, sometimes observed when caribou become inquisitive about something in their surroundings. They will then readily approach as well as try to get down-wind of the object. When the object does not induce fear, it may simply be ignored, or charged before the caribou calm down. The effect of this "confirming behaviour" is that energy which would otherwise have been spent in needless flights from non-predators is saved.

Key words: *Rangifer*, wolves, anti-predator behaviour, energy expenditure, Greenland.

Introduction

Blehr (1990) discussed different techniques traditionally used by hunters of caribou and wild reindeer (*Rangifer tarandus*). The efficiency of hunting techniques was evaluated in terms of the evolutionary adaptation of caribou/wild reindeer to predation by wolves (Mech, 1970; Bergerud, 1974). This includes the way in which caribou frequently stop to look back during flight from their traditional enemy. This behaviour was explained by the fact that a wolf cannot catch a healthy animal (Pruitt, 1965; Mech, 1970), and so caribou/wild reindeer stop at intervals to check whether they are still being pursued, because they apparently want to save energy (Blehr, 1990).

Since my ethnological studies have been in areas where wolf is not part of the fauna, I have not personally had the opportunity to observe how caribou behave toward this predator. Nevertheless, I wish in the following seriously to question the existence of the energy-saving behaviour in caribou that Pruitt and Mech claim to exist. A claim that I took at face value when I wrote the above article. I have repeatedly observed single animals and small bands of caribou which have been frightened and have started to run away, only to make frequent stops to look back in my direction. But, crucial for our discussion here, the flight would continue after each stop until the animals were out of sight, even on the occasions when I stood quite motionless. The caribou's behaviour toward me thus differs

radically from the apparently energy-saving strategy that Pruitt and Mech believe it to adopt when confronted with a non-hunting wolf.

Study area

The study was carried out in the high density caribou area located in the inland region north and northeast of Kangerlussuaq air port (ca. 67°N; 50°W), Sisimiut municipality, in the low Arctic area of West Greenland, roughly 700 km² (Fig. 1). Geomorphically it is rather uniform, with gentle east-west trending mountain ridges, valleys and lakes. In the north and east the mountain formations reach 550-650 m above sea level.

Dwarf scrub heaths, meadows, steppe and grassland characterize the vegetation. A notable feature are the innumerable caribou trails between the coast and the Inland Ice. The climate is continental, average January -18°C for January, and July +10,5°C. The annual precipitation is less than 200 mm, whereof half falls between July and October (Bøcher, 1980).

Methods

Data on energy-saving behaviour of frightened caribou was looked for during ethnoarchaeological surveys throughout June in five consecutive years, 1985 to 1989, and a three week period in May/June 1991, by one obser-

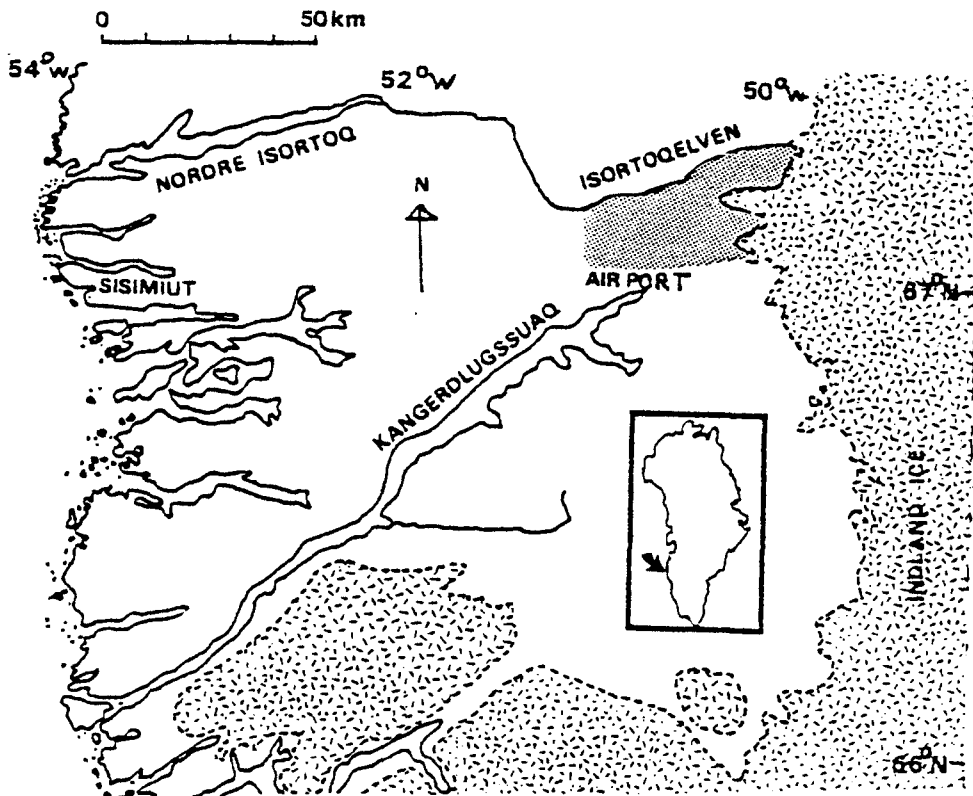


Fig. 1. The area of study (shaded) north of Kangerlussuaq airport, West Greenland.

ver travelling on foot looking for exceptions to the stereotypical flight behaviour. On the one occasion when an animal did not follow this pattern, the deviant behaviour was documented in detail (see Blehr, 1997). All encounters during the period June 15 to June 30, 1989 were recorded in order to provide an idea of the size and composition of the caribou bands during this period of the year.

Results and discussion

The fieldwork was carried out at a time of the year when most of the caribou were scattered throughout the area singly, or in bands with less than ten members (Table 1). My encounters with animals were therefore numerous. During a two week period in June 1989, I encountered totally 420 animals, not counting neonates (cf. Blehr, 1991). Average encounters a day were 8.3, with an average band size of 3.4 caribou.

Such small bands are typical of the ones found each spring before the forming of the large post-calving aggregates at the end of June or beginning of July. Bands of up to 30-40 animals were also occasionally encountered not deviating in flight behaviour from the one I detected in smaller bands. This number is the upper limit for what I will label "small bands" although de Vos (1960)

Table 1. Age and sex composition of the groups of caribou encountered between June 15 and June 30, 1989. N: number of groups, M: all males, FFX: females/yearlings and females with neonates, MX: mixed groups (i.e., some mature males as well as mature females), Y: all yearlings.

Group Type	Number of animals		
	median	range	<i>n</i>
M	1	1-3	12
FFX	3	1-26	66
MX	8	5-11	2
Y	1	1-4	44
			124

found that the activity pattern in bands with less than 50 individuals appeared to be more closely coordinated than in larger bands.

The behaviour of caribou towards man in terms of flight or flushing distance are considered to vary considerably both within and between populations (Kelsall, 1957; de Vos, 1960; Lent, 1966; Bergerud, 1974; Bubenik, 1975). I have estimated this distance to be roughly 200-400 m. during my walkabouts. However, like Kelsall (1957), I found that the distance could vary

considerably. Obviously, the conspicuous lack of contextual data of relevance for the flushing distances given by the different authors means that their findings should be used with the utmost caution for comparative purposes. Be this as it may, what is of crucial importance here is what the caribou do after the initial flight. Do they stop "to save energy" when no longer pursued, or do they keep on fleeing until they are out of sight?

Leaving aside for the moment variations in the caribou's behaviour due to their age or sex, I found that their reactions to my presence, on the occasions when they were unable to scent me, usually followed the same general pattern. If I kept on walking after having been spotted, the caribou would immediately take fright and make a short run before stopping to look back. While facing me some would urinate, while others would move slowly back and forth on the same spot, or towards me, with a characteristic high-stepping gait. Then, sooner or later, one or more of the caribou would panic and dash off, followed, usually in tight formation, by the others. Though they would stop one or more times to look back, and their speed would eventually slow down to an easy trot, their flight would always continue until they were out of sight. This even proved to be the case when I was moving away from them.

On those occasions when I stood motionless, the initiative to flee would be taken by the animal that had become aware of me. The lag between alert and flushing time was also somewhat longer when I stopped walking once I had been spotted. Apparently less alarmed, they would run off in a looser formation (cf. de Vos, 1960). It also happened that when only a single animal discovered my presence both it and the rest of the band simply drifted away while grazing, looking back in my direction now and then until they disappeared out of sight. Let me add that this reaction to my presence was very rare. In most cases, the uneasiness indicated by the alarm pose of the caribou that had first sighted me would communicate itself to other animals which would then become aware of me. Despite the fact that I stood motionless, they would bunch together, and take flight followed by the rest of the band.

Except for cows with neonates, the caribou often tried to get down-wind of me after their initial scare. As a rule, one or more of them would succeed in this, but usually only after several fruitless attempts, as they tended to turn back too early. The first animal to reach a down-wind position would normally make one or two excitatory jumps before it took flight in the customary manner.

While I have stressed the paramount role played by scent as a flight releaser in caribou that are both visually and olfactory aware of an intruder (cf. Murie, 1935; Bergerud, 1974), Kelsall (1968) has questioned their ability to perceive by smell alone. He regards each attempt the caribou make to go down-wind of whatever has alarmed them as successful. For him, their behaviour illustrates that caribou doubt the evidence presented by

their sense of smell.

Bergerud (1974) argues however that scent seemed to be the most discerning sense which could release immediate flight behaviour prior to visual contact (cf. Murie, 1935). This might be true on most occasions, but I have observed animals, which, having scented me hesitated uneasily for a few minutes before finally fleeing. When camping in topographical bottlenecks, I have also observed that the animals' urge to keep to their initial route of travel was apparently strong enough to overcome the fright induced by my scent. Once downwind of me, they would immediately stop in their path and stretch their heads forward into the wind to take in my scent better. After the usual high-stepping gait on the same spot, urinating, and more head stretching, the animals would inevitably back track for a distance of anywhere between five and a couple of hundred meters, only to return in order to take in my scent again. In this manner, the animals could trot back and forth undecidedly for up to 15-20 minutes, before finally galloping away at full speed through the area downwind of me. Once beyond my scent, they stopped occasionally to look back in my direction in the usual manner, but would keep on fleeing until they passed out of sight. Other situations have also been recorded when scent has not triggered flight behaviour (Kelsall, 1957; de Vos, 1960; Bubenik, 1975).

Occasionally, caribou would insist on keeping to their route of travel even when I encountered them outside bottlenecks. This occurred when they were visually aware of me, but did not have my scent. After the initial bunching together, and a rush, usually back along their route, they would return at full gallop, making only a small detour around me (cf. Kelsall, 1957). On the occasions when my appearance had split a band, and I was blocking their line of travel, only small detours were made around me when the stimulus to rejoin other members of the band became dominant.

Whereas small homogenous bands rarely split when confronted with humans, the opposite seemed to be the rule on the two occasions I encountered post-calving aggregates of 300-400 animals that had formed. In such a band, animals in some of the scattered groups at the outer fringe of the aggregate would be the first to become aware of my approach. Their alarm pose, followed by the usual bunching together and subsequent rush, served to trigger off flight behaviour among animals in the neighbouring groups (cf. Lent, 1966). Neonates and cows which had become separated from each other in the tumult, rushed back and forth searching for each other. In this manner, panic spread from group to group through the whole band, resulting in smaller or bigger aggregates of caribou running hither and thither, depending upon where they had received the flight stimuli, or, if they were calves or cows, where they had last had been together. Sometimes single animals or groups stopped to watch the behaviour of others, before they again panicked and rushed off.

The lack of organized action was conspicuous (cf. de Vos, 1960). Only when most of the animals had become aware of my whereabouts did their movements become coordinated and directed away from me. However, before this stage was reached the large group of yearlings, which are such characteristic feature of a post-calving aggregation, had focused all their attention on me. Seemingly unafraid, the 20-30 yearlings in such groups would repeatedly make runs towards me, first stopping when the distance separating us was down to 15-20 meters. If I then stopped walking, they would stand bunched together and watch me intensely for half a minute or more. Some of them would then take fright and make short hesitant rush away from me followed by the rest. On the occasions I kept on walking, their stops were shorter, but regardless of my behaviour they soon returned. In fact, it appeared as if they never got tired of following me in this manner. First when the other members of the band had coordinated their flight away from me did their urge to follow them take precedence, and I would be left alone. It is tempting to suggest that it was such large groups of yearlings that Kelsall (1968) had in mind when he assumed that caribou seem to doubt the evidence offered by their sense of smell.

Considering the gregarious nature of the caribou, the flight pattern described above for post-calving bands appears mainly to be the result of the numerous contradictory stimuli the animals receive from their fellow-members when they are together in such large aggregates. No wonder, then, that this pattern differs from the one found in small bands where the situation is more easily surveyed, and thus makes the stimuli the animals act upon more congruent.

Since my field work was carried out for the most part in the period prior to post-calving aggregates, one could argue that the characteristic behavioural pattern I observed largely reflected the flight pattern of cows with neonates, which are known for their wariness at this time of the year. But apart from the fact that they never dared to approach me or go downwind of me before fleeing, and that they were the first animals in mixed bands actually to take flight (cf. Kelsall, 1957; de Vos, 1960; Lent, 1966; Bergerud, 1974), their behaviour when it comes to energy expenditure did not otherwise deviate from the general pattern I have described above. Another possible objection to the general conclusions I draw from my observations could be that they are based solely on the flight behaviour the caribou exhibit in June. Yet, observations by others confirm the general validity of my findings (Kelsall, 1957; Lent, 1966). In fact, caribou in summer and autumn may even be more easily frightened by humans than I have maintained (Kelsall, 1957).

That cows with neonates in mixed bands were the first to flee was not the only behavioural difference related to sex and age. Yearlings, who had just been left by their mothers upon the births of the new calves, would occasionally come trotting all the way up to me. But for this to

happen I had to be downwind of them and take care to stay motionless after having been spotted. As for cows, they are on most occasions significantly more wary than bucks (Murie, 1935; Bergereud, 1974). Nonetheless, I have experienced situations when the caution of lone adult bucks has surpassed that of cows (cf. Kelsall, 1957).

It should be emphasized strongly that though differences were found in the caribou's behaviour pattern in the initial phase of their encounter with me, depending on their age and sex, these differences are of no relevance for my argument here. Of paramount importance, however, is what the caribou actually did after their initial rush away from me: And on this point, as we have seen, I found a clear pattern: Regardless of their age and sex I found that the single animals and small bands would eventually save themselves by flight. A flight only occasionally interrupted by short stops to look back in my direction. Even yearlings, who I found to display the most erratic behaviour of all age groups in the initial phase of their encounters with me, ended up by adopting the same stereotypical flight pattern as their elders.

How does this flight pattern accord with, or differ from the way caribou behave towards wolves which are not stalking or pursuing them? Amazingly, few first hand observations of such confrontations are documented in the literature. Yet, thanks mainly to the observations of Crisler (1956), I believe we are able to answer this question. Among her observations of wolf-caribou interactions in the Brooks Range of Alaska in 1953-54 was one where the wolf immediately stopped and sat down as soon as the cow checked her flight to take a look back at her pursuer. The caribou's behaviour may appear suicidal, but as a wolf apparently "prefers not to be eyed when approaching its prey" (Crisler, 1956:340), it stops its stalking once the caribou has sensed it. And also, since the wolf depends on the stimulus of a running animal before making a rush for it (Mech, 1970), the initiative is left with the caribou. This is obviously to the latter's advantage, since it means that the distance between wolf and caribou is frozen up to the moment when the caribou decides to flee. Thus, when the cow took off again, with the upward launch so characteristic of frightened caribou, the wolf followed it. Crisler repeatedly observed the caribou behave in this hesitating manner in encounters with wolves, a behaviour which is identical with the one the caribou generally display when scared by a human they cannot scent. Furthermore, the episode referred to above is also of special interest since the upward launch with which the cow took off tells us that it was really scared. Having taken real fright, its behaviour was no longer hesitant: It kept on running, even after it was no longer pursued. This was not an unique occurrence. On the same day, Crisler had twice observed other single cows which kept on running steadily in the same manner, even after their pursuers had given up the chase (Crisler, 1956).

From Crisler's documentation, it appears that single caribou are quite unable to distinguish between wolves

that are exhibiting appetitive searching behaviour and those that are not. The general validity of Crisler's findings is supported by Murie's observations of the flight behaviour of caribou in small bands on Mount McKinley in June 1939 and 1940 (Murie, 1944). In terms of energy expenditure the flight pattern of caribou in such bands, when confronted with non-hunting wolves, is identical to that displayed when they confront humans (Kelsall, 1957; Lent, 1966).

As Lent (1966) has pointed out, there seems to be no indication that the escape reactions of caribou differed according to the species causing the alarm (cf. Kelsall, 1957). This view is also confirmed by my observation of caribou-muskox interaction in 1991. In that year, the caribou north of Kangerlussuaq for the first time had regular contact with animals from the muskox population which had been introduced in the neighbouring area to the south in the 1960's. On three occasions I had the opportunity to witness these encounters and observe how the caribou behaved in precisely the same energy-expenditure manner towards muskox as they did in their encounters with me. I also had my first opportunity regularly to meet with bands of caribou that were fleeing apparently for no obvious reason. However, on the occasions when I backtracked along their path, I inevitably met with the new ungulate, which indicate that the caribou kept on fleeing long after they had lost sight of the muskox.

Taking into consideration the evolutionary adoption of the caribou to predation by wolves it should come as no surprise that the flight behaviour of the former is found to be the same towards humans and other species that cause alarm as it is towards the wolf. Accordingly, the energy-saving behaviour Pruitt (1965) and Mech (1970) ascribe to caribou in encounters with non-hunting wolves seems not to rest on empirical foundations.

But how are we to interpret statements that seem to support energy-saving behaviour? For example by Murie (1944), who maintain that caribou generally seem not to be worried much by wolves unless chased? Since we do not know all the stimuli influencing the escape behaviour of caribou, we cannot adequately explain all their reactions when face-to-face with a predator (cf. Lent, 1966). But if we wish to explain as many of these reactions as possible, we might start by differentiating between the content and magnitude of the stimuli they receive in different contexts. From my own experience an obvious distinction is between animals in large and small bands. Surprisingly, although band size is regarded as relevant in other contexts (Kelsall, 1957; de Vos, 1960; Bergerud, 1974; Whitten & Cameron, 1986), it has been ignored when it comes to the study of the caribou's flight behaviour. This is also true in Murie's work, but thanks to his documentations we are able to ascertain whether differences in behaviour were the result of membership of large or small bands (Murie, 1944). The statement above from Murie (1944) was synthesized from observations of cari-

bou that are members of large bands where the flight stimuli they receive from other caribou are either lacking or inconsistent. If this is correct, then the hesitant behaviour observed among caribou in large bands in the presence of wolves cannot be interpreted as support for the energy-saving hypothesis. Instead, it must be seen as generated from the numerous contradictory stimuli the animals receive from their fellow-members when they are together in such large aggregates.

Finally, although Kelsall and I disagree as to the relative importance of the sense of smell as a flight releaser, we do agree as to why a caribou readily approaches, as well as tries to get down-wind of an object that arouses its curiosity. Such behaviour obviously indicates that it wants to investigate. Should the object turn out to be harmless, then it can be chased away, or simply be ignored. The effect of this "confirming behaviour" is that energy which would otherwise have been wasted in headless flights away from non-predators is saved. In July 1978, during an earlier visit to the area, I witnessed how a small band of seven caribou grazing on a mountainside stampeded when a hare (*Lepus arcticus*) suddenly appeared at very close range. When they stopped after a short run, one of them came back and charged the intruder, which ran away. The caribou then resumed grazing (cf. Thomson, 1975). Thus, the frightened caribou does indeed exhibit energy-saving behaviour. But, as this example illustrates, the situations when such behaviour result in energy actually being saved are quite different from the ones found when they are facing wolves.

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Editorial to Blehr's conference article with appendix

As an anthropologist, Blehr has been studying for years the relationship between caribou as a prey animal and man as a predator. A relationship that, besides the weapon technology of the hunter, has been determined by the possibilities and limitations inherited in the flight behaviour of the caribou. While carrying out an ethnoarcheological survey in a caribou high density area in West Greenland, Blehr used the opportunity to study flight behaviour of caribou as well.

On the basis of his findings, Blehr wrote the article «Energy-expending behaviour in frightened caribou when dispersed singly or in small bands», which to his amazement he found impossible to get published in a zoological journal. The referees were almost unanimous in their denouncement of the article as anecdotal, and thus, in their view the article was without scientific value. Provoked by

this he wrote «In defence of «anecdotal data». A case study from a caribou area in West Greenland» presented as a lecture in Fairbanks.

When *Rangifer* now chose to publish not only the latter paper that Blehr presented at the 2nd IAU conference in Fairbanks in 1995, but also in an appendix the article that gave the background for his conference lecture, it is in the belief that *Rangifer* as a journal should be more open for scientists other than biologists (cf. text on the journal's last cover page). This attitude is in accordance with what the Nordic Council for Reindeer Research wants the journal to be. Therefore, *Rangifer* is in certain cases open for papers not following the accepted or common natural scientific style. The Blehr case (shortened lecture article and appendix) gives an additional opportunity to illustrate the research method he pleads. His contribution will probably incite the discussions on both scientific method and editorial style.