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Aposematic Behaviour in the Striped Skunk, *Mephitis mephitis*

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Abstract

From April to August, 1993 to 1995, we studied the aposematic behaviour patterns of striped skunks, *Mephitis mephitis*, incidentally while ground-tracking radio-marked animals. During 2668 h of tracking, 207 defensive postures were displayed by 34 radio-collared (27 females, 7 males) and 21 unidentified skunks. Skunks most often advertised their noxiousness using Tail-up (69.1 % occurrence) and Stomp (17.4 %). Encounters were frequently (42.5 %) terminated by the skunk running away from the source of disturbance. Most warning behaviour was directed at radio-trackers (95.7 %), and the remainder was displayed to a variety of predatory and non-predatory animals or objects. Stomp occurred more frequently in taller vegetation, where visual advertisement was limited. Reaction distance of skunks disturbed by observers (median = 6 m) was not affected by wind, movement or vegetation height. The small awareness circle and high tolerance of skunks to disturbance are consistent with the life history traits of aposematic animals.

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Introduction

All prey are not of equal value to predators. Some prey may be considered unprofitable because of chemical defence (WHITTAKER & FEENY 1971), ability to afflict physical injury to predators (EDMUNDS 1974), or ability to escape following discovery (BAKER & PARKER 1979). Species relying on chemical defence often advertise their noxiousness through visual (COTT 1940), auditory (DUNNING & KRUGER 1995), or olfactory cues (EISNER & GRANT 1981; CAMAZINE 1985). The advertisement of noxiousness through morphological or behavioural traits is referred to as aposematism. Aposematism not only benefits the prey by reducing the frequency of predatory attacks, but may also benefit the predator by reducing the amount of time devoted to noxious prey (BROWER 1969).

Aposematic coloration is a well-studied example of morphological advertisement (COTT 1940; EDMUNDS 1974; CLOUDSLEY-THOMPSON 1980; ORTOLANI & CARO 1996). Simple configurations of highly contrasting colours facilitate recognition and learning by

predators (GITTLEMAN & HARVEY 1980; GITTLEMAN et al. 1980) and, in some cases, trigger innate avoidance reactions (SMITH 1977; SCHULER & HESSE 1985). However, no defence is perfect, and aposematically coloured prey may occasionally be tested by inexperienced or juvenile predators, or predators mistakenly identifying prey (COTT 1940; CLOUDSLEY-THOMPSON 1980). The efficacy of warning coloration is directly dependent on visibility. Thus, most aposematically coloured species are diurnal (COTT 1940). Aposematically coloured animals active in periods of low light, at night, or in conditions of low visibility should benefit from advertising their noxiousness through non-morphological means (SILLÉN-TULLBERG & BRYANT 1983; ENGEN et al. 1986).

Striped skunks, *Mephitis mephitis*, rely on chemical defence to deter predators. They are equipped with two musk glands located on each side of the anus. Upon provocation, musk is sprayed at the predator. The strong-smelling substance is composed primarily of butane and methane compounds (WOOD 1990) and may cause temporary blindness and vomiting if received in the eyes or mouth (CUYLER 1924).

Striped skunks are aposematically coloured. Their coloration is black with two white stripes running down the back. The stripes unite on the shoulders and continue to the top of the head. A single narrow white stripe is also present on the bridge of the nose. An equal mixture of white and black hairs characterizes the bushy tail (WADE-SMITH & VERTS 1982). The combination of black and white is one of the most conspicuous colorations in nature (COTT 1940).

The striped skunk is active primarily at night and frequently utilizes habitats with tall and dense understory vegetation (VERTS 1967; S. LARIVIERE and F. MESSIER, unpubl. data). Under these conditions, warning coloration may not always be conspicuous, and skunks may perform aposematic behaviour to identify themselves to potential predators.

Incidental reports of the defensive behaviour of the striped skunk include erection of the tail, stomping of the front feet, hissing, clicking of the teeth, charging, handstands, fleeing, hiding, denning, aiming and spraying (CUYLER 1924; LAUN 1962; VERTS 1967). Although the efficiency of these behaviour patterns in deterring predators has been reported (WALTON & LARIVIERE 1994), the importance and sequence of display of each respective behaviour remains undescribed. Herein, we report the sequence of defensive displays used by striped skunks facing potential threats and examine the following predictions: 1. Considering that visual displays will not be efficient in tall vegetation, we predict that auditory warnings (e.g. feet stomping) should occur more frequently in taller vegetation; and 2. Considering that skunks appear to be nearsighted (VERTS 1967) and make primary use of olfaction and audition (LANGLEY 1979; NAMS 1991), we predict that defensive behaviour should occur at longer distances when the skunk is downwind from the source of disturbance (Wind effect), in shorter vegetation (Cover effect), and when the disturbing animal is moving (Movement effect).

Methods

This study was conducted in the aspen parkland region of central Saskatchewan (52°N, 107°W), Canada. From Apr. to Aug., 1993 to 1995, striped skunks were captured, anaesthetized and radio-collared as

part of an ecological study on their space-use patterns in relation to waterfowl nest predation. Radio-tracking was performed on foot from 1800 to 0600 h. Observations at night were enhanced by the use of night-vision goggles (AN-PVS 5, Bill's Electronics, Mildmay, Ontario).

During radio-tracking sessions, observers recorded any sudden change of behaviour by skunks that was distinctly defensive and identified the source of disturbance. Observers remained motionless throughout the defensive display. Following departure of the skunk from the immediate vicinity, observers recorded the reaction distance (m, Distance) between the skunk and the source of disturbance when first detected, time, and characteristics of the disturbance. Defensive behaviours were characterized in 10 exclusive categories and were recorded as absent or present for the entire encounter event: Tailup (sudden vertical erection of the tail), Stomp (stomping of both front feet simultaneously on the ground), Charge (short rapid run towards the source of disturbance), Scratch (rapid backward movement of the skunk while dragging front legs on the ground), Run (rapid movement away from the source of disturbance), Hide (attempt to be cryptic by remaining motionless and lying on the ground with tail down), Den (avoidance of encounter by retreating into a burrow and cessation of activity), Hiss (vocalization while facing the source of disturbance), Aim (anal region fully exposed and directed towards the source of disturbance, skunk looking over shoulder), Spray (discharge of musk). Other variables included Wind (skunk upwind, downwind, sidewind of source of disturbance, or no wind), Movement (observer stationary or moving when detected, both skunk and observer moving, unknown), and Cover (height of herbaceous vegetation: <0.5 m, 0.5–1 m, or >1 m). The numbers of displays within each defensive posture were recorded, and the defensive posture was considered terminated when the skunk resumed foraging or moving normally.

One-way ANOVA was used to determine the effect of sex on the dependent variable Distance. A three-way ANOVA with interactions was used to investigate the effects of Wind, Cover and Movement on Distance. Chi-square tests were used to assess variations in Stomp among Cover classes. All statistical calculations were performed using the SAS statistical package for microcomputers and two-tailed probability levels. Probability values ≤ 0.05 were considered significant.

Results

During 2668 h of radio-tracking, a total of 207 defensive postures were displayed by 34 radio-collared skunks (27 females, 7 males) and 21 unidentified skunks. Defensive postures were observed during 100 tracking sessions totalling 1083 h of tracking (average = 10.83 h/session); the median number of defensive postures per session was 2 (range = 1–5). The median number of observed defensive displays by animals was 4 for radio-collared animals (n = 34, range = 1–14). All encounters involved solitary skunks.

On 26 occasions (12.6 %), the encounter was limited to a cessation of movement and a subsequent change of direction by the foraging animal, without any obvious sign of alarm or display of the previously defined defensive behaviour. Because of the slight change in behaviour, they were nonetheless considered as disturbance events. During a single disturbance event, skunks exhibited a median of 2 different defensive behaviour patterns (range = 0–6, n = 207).

In all, 198 defensive behaviour patterns (95.7 %) were directed at observers, while the remaining 9 (4.3 %) were directed at coyote (*Canis latrans*, 1/207, WALTON & LARIVIERE 1994), dog (*Canis familiaris*, 2/207), white-tailed deer (*Odocoileus virginianus*, 1/207), porcupine (*Erethizon dorsatum*, 1/207), muskrat (*Ondatra zibethicus*, 1/207), red-winged blackbird (*Agelaius phoeniceus*, 1/207), unidentified passerine (1/207), and an inanimate object (observer's backpack, 1/207). Because the type of disturbance may have an effect on reaction distances and chronology of warning displays, further analyses were limited to disturbance induced by observers.

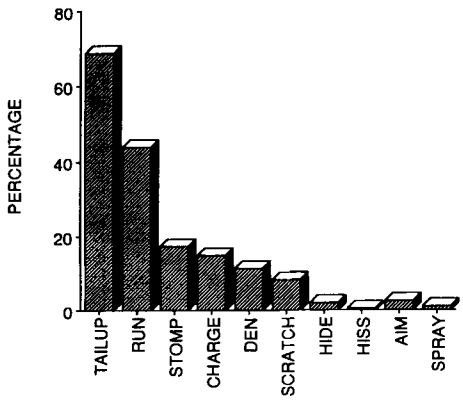

Fig. 1: Frequency of display of specific defensive behaviour by striped skunks disturbed by humans (n = 198 defensive behaviours)

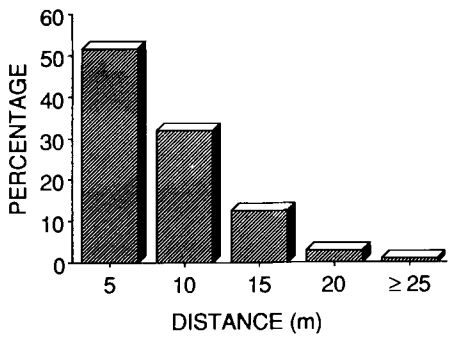

Fig. 2: Distribution of reaction distances of striped skunks disturbed by humans (n = 198 defensive behaviours). Data are reported in 5-m categories, 1–5, 6–10, 11–15, 16–20, and 21–25

On 11 occasions, reaction distance was not estimated. No differences in reaction distance were detected among males, females, and unidentified skunks ($F_{2, 192} = 1.74$, $p = 0.18$). All defensive postures were pooled for subsequent analyses.

Tailup was observed in 68.7 % of defensive postures induced by humans and was the most frequently displayed behavioural warning (Fig. 1). Run and Stomp occurred in 43.9 % and 17.2 % of cases, respectively. Hide, Spray and Hiss were performed least (2.0 %, 1.0 % and 0.5 % of encounters, respectively; Fig. 1).

In all, 102 (51.5 %) defensive postures occurred when the observer was within 5 m of the skunk. Only 8 defensive postures (4.0 %) were recorded when the observer was more than 15 m from the skunk (Fig. 2).

There was a difference in frequency of Stomp among cover classes ($\chi^2 = 9.2$, $df = 2$, $p = 0.01$), with more stomping occurring in taller vegetation. We did not find

any effect of Wind ($F_{3, 157} = 1.22$, $p = 0.30$), Movement ($F_{3, 157} = 2.25$, $p = 0.08$) or Cover ($F_{2, 157} = 0.34$, $p = 0.71$) on the dependent variable Distance (full model, $F_{31, 157} = 0.88$, $p = 0.66$). There were no interactions between independent variables ($F < 1.00$ for all interaction terms, $p > 0.43$).

Skunks often displayed the same warning behaviour more than once during a disturbance event. Most often, the same behavioural warnings would be repeated 2–4 times. Fleeing skunks frequently stopped 2–10 m away and looked over their shoulders. Disturbance events lasted from 0.1 to 2 min. In most instances, the skunk was observed to resume foraging within 2 min after the disturbance.

Discussion

Our observations of the defensive behaviour of striped skunks are consistent with the general life histories of aposematic species in that: 1. Striped skunks use a series of warning displays to advertise their presence and only use chemical defence as a last resort (Fig. 1); 2. Displays are only used when disturbances occur in close proximity (Fig. 2) and skunks do not appear to differentiate between potential threats and non-predatory disturbances; 3. Auditory warnings are displayed more frequently in low-visibility conditions; and 4. Skunks resume normal activities rapidly (within 2 min) after a disturbance event.

None of the variables tested (Wind, Cover, Movement) had an impact on the propensity of skunks to react to sources of disturbance. Because chemical defence is effective mainly at close distances, aposematic animals should ignore predators that are too far away to perceive the warning coloration or displays. Also, the display of defensive behaviour to non-predatory species such as deer, muskrat, and bird species suggest that skunks may use quick behavioural warnings such as Tailup, even when unable to assess predation risk related to a specific disturbance.

Defensive displays by skunks emphasized visual cues (Tailup), auditory cues (Stomp, Hiss), or both visual and auditory cues (Charge, Scratch). The remaining defensive behaviour consisted of avoiding confrontation altogether (Run, Hide, Den), or at last resort chemical defence (Aim, Spray). In this study, observers acted as 'experienced' predators as they were instructed to remain immobile throughout the sequence of defensive displays. Thus, the observed frequency of spraying may have been lower than what would occur during encounters with naive predators.

In areas where visual advertisement could not be perceived, striped skunks advertised more frequently using auditory cues (e.g. Stomp). This may prevent the skunk from being attacked by experienced predators mistakenly identifying the skunk as other prey. Alternatively, defensive behaviour leading to the avoidance of confrontation (Run, Hide, Den) may be used by skunks as protection against inexperienced predators which may ignore the warnings and still attack. Innate avoidance reactions of aposematic prey have occasionally been demonstrated (SMITH 1977; SCHULER & HESSE 1985) but are believed to be rare (MALLET & SINGER 1987). Avoidance of an encounter may represent the best defensive strategy.

Olfactory advertisement of noxiousness could not be quantified in this study. However, observers could on occasion detect the presence of the skunk by smell when

within 10 m and downwind from the animal. Thus, it is likely that skunks are easily detected by predators relying on olfaction for hunting. Moreover, a faint skunk odour could sometimes be detected in the grass following the passage of a skunk. It is possible that the normal body odour of skunks may also act as an advertisement of noxiousness, hence further facilitating recognition by predators.

Advertising noxiousness through behavioural warnings would represent an energetically economical way to prevent unnecessary and risky physical encounters with predators (GUILFORD 1986). Skunks can only spray successively 5–6 times (CAHALANE 1961:210), and animals using chemical defence benefit from using the strict minimum to avoid complete depletion of the defence system (EISNER & MEINWALD 1966; DEAN 1979), and to reduce energetic costs associated with the production of the chemical compounds. Therefore, warning displays complement the effects of coloration in reducing the need for chemical defence. This may have evolved as a way of dealing with frequent encounters with predators, or predators travelling in pairs or packs such as coyotes.

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