ALARM WALKING IN COLUMBIAN BLACK-TAILED DEER: ITS CHARACTERIZATION AND POSSIBLE ANTIPREDATORY SIGNALING FUNCTIONS

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Many antipredator behaviors advertise honestly an individual's health and awareness of predators, reducing the probability of further attack. We presented full-sized models of felid predators to Columbian black-tailed deer (*Odocoileus hemionus columbianus*) and observed a unique conspicuous gait pattern, the alarm walk, which has not been described in the literature. We conducted frame-by-frame analyses of gait timing and leg movement from video recordings of alarm walking and normal walking. Compared with normal walking, contact durations of all legs during alarm walking were greater and deer lifted their foreleg carpal joint higher off the ground, suggesting that alarm walking requires a level of control and flexibility in leg movement not possible in arthritic or lame individuals. Although phases of limb movement (i.e., midtime lag between fore and hind legs) were reliably different, there was no difference in the angle of foreleg lifting between the 2 walking styles. Performance of alarm walking was correlated with foot stamping, and was observed more often when the predator model was out of view. Although there was no direct evidence supporting any 1 function of alarm walking, available evidence suggests that alarm walking might have the dual function of signaling to a stealthy predator that it has been detected and that the displaying deer is healthy and capable of escaping, both of which should deter further pursuit.

Key words: alarm walking, antipredator behavior, black-tailed deer, gait analysis, *Odocoileus hemionus columbianus*, prancing, pursuit deterrent

Animal species have evolved a wide array of behavioral adaptations to aid in avoiding predation (reviewed in Caro 2005; Langerhans 2007). Before flight, prey may emit alarm vocalizations to warn conspecifics (e.g., Sherman 1977), perform visual displays to deter further approach by the predator (e.g., Caro et al. 2004), or physically fight off the predator (e.g., Lingle and Pellis 2002; Owings et al. 2001; Smith 1987). Finally, during escape, many species perform costly (in terms of time and energy) behaviors to demonstrate their health and ability to effectively avoid capture by the predator (e.g., Caro 1986a, 1986b; Caro et al. 1995; FitzGibbon and Fanshawe 1988). Clearly, the ability of prey to advertise honestly to onlooking predators that any further attempt at capture would be futile is mutually adaptive and would be favored by natural selection because of the potential energetic costs of failed pursuits and the likely loss of use of a favored hunting area.

During a previously reported experiment (Stankowich and Coss 2007a) that exposed models of predators to Columbian black-tailed deer (*Odocoileus hemionus columbianus*), we observed and documented deer performing an unusual and conspicuously fluid, high-stepping gait, with a much slower speed than that of a prancing horse, during alarm responses to life-sized models of felid predators. This "alarm walking" behavior was previously observed in Rocky Mountain mule deer (*O. h. hemionus*—V. Geist, University of Calgary, pers. comm.) in response to predatory encounters and appears to be similar to the "high-step warning gait" of elk (*Cervus elaphus*) mentioned by Altmann (1963) and Geist (2002), but it has never been fully described in print. Alarm walking occurred most frequently and with shorter reaction times in response to more provocative models (e.g., puma [*Puma concolor*]) than to

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less provocative models (e.g., mule deer—Stankowich and Coss 2007a). Similar results were found for snorting and foot-stamping behaviors performed during the same trials. Alarm walking occurred when animals did not immediately flee from the predator, but instead when they were highly aroused, alert, and scanning the surrounding vegetation for threats. Our goal in this paper, is to formally characterize the fluidity and high-stepping movement of the alarm-walking gait as unique from normal walking styles, and to provide an argument for its potential as a pursuit-deterrent antipredator signal of individual health and ability to escape an attack.

Pumas, wolves (*Canis lupus*), and coyotes (*C. latrans*) select prey disproportionately if they appear impaired by poor nutritional condition, age, and disease (Gese 1999; Husseman et al. 2003; Mech et al. 1995; cf., Pierce et al. 2000). Although puma predation is rarely observed (Beier et al. 1995; Smallwood 1993), coyotes make opportunistic attempts on hobbled individuals (Gese and Grothe 1995; Lingle 1998) and prefer to attack outlying individuals in groups (Lingle 2001) and nonalerted groups (Lingle and Wilson 2001). Wolves preferentially kill prey in poorer condition (elk—Huggard 1993; moose [*Alces alces*]—Mech 1970) and have been observed to select caribou (*Rangifer tarandus*) in moving herds that appear conspicuous because of their arrhythmic leg motion (Crisler 1956). As noted by Crisler (1956:343): "If that rhythm of the legs is off, how one's eye flies to it." Fluidity of leg motion can be compromised by degenerative arthritis of the spine and joints in older prey and by a common bacterial infection from *Erysipelothrix insidiosa* that produces rheumatoid arthritis; Sikes et al. (1972) reported that approximately 30% of white-tailed deer (*Odocoileus virginianus*) from the southeastern United States exhibited low titers for *E. insidiosa*. Selection of prey crippled by arthritis is an ancient process: 19% of lower Pleistocene deer fossils in Spain that appeared to be killed by carnivores exhibited osteopathology (e.g., metacarpal arthrosis), which would limit running ability (Palmqvist and Arribas 2001). Horses with arthritis in the carpal joints show moderate lameness while walking, significant lameness while trotting, and further increased lameness after forced carpal flexion of the afflicted joint (e.g., Hewes et al. 2005). Stotting behavior by mule deer (their primary escape style) requires great elastic strain energy with large impact forces (Lingle 1993); therefore, any arthritis that limited carpal or limb performance would hinder escape ability and the afflicted animal would be more vulnerable to capture by attacking predators. If alarm walking carried a cost and was an honest signal of condition (Zahavi 1977), then individuals in poor condition would be less capable of alarm walking, which illustrates the potential utility of alarm walking to signal prey condition to the predator.

Given the high incidence and detrimental effects of gait maladies in ungulates, we 1st quantified the footfall patterns and leg-lifting behavior during alarm walking to distinguish it from normal walking patterns. We then briefly examined the potential signaling functions of alarm walking, using available data to attempt to provide support for several predictive hypotheses. Alarm walking could have 1 or more functions including warning conspecifics, drawing attention away from

vulnerable fawns, signaling alertness to the predator, and signaling condition to the predator. Because we did not design this study to test these alternative hypotheses, we can only examine the incidence of alarm walking and perform post hoc tests of potential function. We directly test the conspecific warning hypothesis as a singular function by comparing alarm walking in solitary deer and deer displaying alarm walking in the presence of conspecifics and fawns, and correlating the performance of alarm walking with other antipredator behaviors whose functions have been tested directly. We then discuss other potential circumstantial evidence of pursuit deterrence or invitation.

MATERIALS AND METHODS

Description of field trials.—All trials were performed between June and September in 2004 and 2005 on free-living deer in coastal, open-terrain, grassy–scrub environments at 2 field sites in northern California: Point Reyes National Seashore and the Bodega Peninsula. Full descriptions of the field sites, natural densities of predators, construction of predator models, procedures for exposure of models, quantification of behavior, and color images of the models have been reported elsewhere (Stankowich and Coss 2007a). Four animal models were constructed out of full-sized poster prints of laterally facing quadrupeds (puma, tiger [*Panthera tigris*], leopard [*P. pardus*], and mule deer) on matte paper and mounted on foamboard silhouettes that folded in the middle to allow concealment of the images. Models were presented from 0700 to 1200 h and 1600 to 2000 h from behind bushes and hillsides to groups of deer 15–70 m away (in order to avoid simply startling the deer due to the sudden appearance of an object, but close enough to discern the shape and color pattern of the model), and a focal individual was selected for observation and filming. Such model-presentation distances are well beyond those of rarely observed successful puma attacks (<5 m—Beier et al. 1995), but far enough away so that the simple motion of the model appearing does not startle the deer. Models were exposed up to 4 times for 30 s per exposure with 1 min between exposures, and 18 or 19 trials were conducted per model. A 2nd observer, positioned well beyond flight-initiation distances of black-tailed deer (Stankowich and Coss 2006, 2007b), used a Panasonic model PV-DV601D mini digital video camera (Matsushita Kotobuki Electronic Industries Ltd., Osaka, Japan) to record the responses of the focal individual during presentations of models. All procedures followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Quantification and analysis of behavior.—After each trial, we recorded distance between the model and focal deer at the time of each exposure, group size and composition, presence of fawns, environmental factors (weather and wind speed and direction), and presence of snorting by the deer group heard during the course of the trial. From videotapes, we recorded presence of foot stamping, tail flagging, and alarm walking. Bouts of typical alarm walking were located on the videotapes using the appearance of the general movement pattern (i.e., not

a specific motor-pattern feature) and the duration of each bout was recorded in relation to the timing of model exposure and concealment. Previously reported results showed that deer alarm walked more often and with shorter reaction times in response to the puma and tiger models than to the leopard and deer models (Stankowich and Coss 2007a).

We further examined the effect of solitary or grouped individuals, group size, presence of fawns, and distance to the model as a function of the presence or absence of alarm walking using binary logistic regression, and the proportion of total time spent alarm walking while in camera view (arcsine transformed) using analysis of covariance (ANCOVA). Because there were only 6 trials with solitary individuals (single adult), we classified single adults with 1 fawn as "solitary" individuals for logistic regression and ANCOVA analyses, and included "presence of fawns" as a factor. Total time spent alarm walking with the model erected in view in each trial was compared with the total time spent alarm walking with the model out of view using a paired-samples *t*-test. Because total time with the model exposed was significantly less than total time out of view, we also calculated the total time spent alarm walking in the 30 s after the model was concealed for each exposure (during the 1-min interval between exposures), to provide a matching amount of time available to alarm walk (i.e., each 30-s exposure would have a matching 30-s period of nonexposure immediately after it). Total time alarm walking during the 30-s exposures was compared with the total time alarm walking in the 30 s after exposures using a paired-samples *t*-test.

Deer typically exhibited more than 1 action pattern after detection of predator models. The interrelationships of the dichotomous presence or absence of alarm walking, foot stamping, snorting, and tail flagging (side-to-side movement of the tail; cf., tail-flicking—Lagory 1981) during presentations of predator models were examined by tetrachoric correlations and binary item factor analysis (Waller 1994) of 51 deer for which all data were available. Significance was reached at $\alpha = 0.05$, and all analyses were conducted with SPSS 10.0 except tetrachoric correlations and factor analyses, which were performed with NOVAX 1.3 (Waller 1994). Because of mislabeling in SPSS (Levine and Hullett 2002), all effect sizes, reported as η^2, for significant factors for all analyses, were calculated by hand according to Cohen (1973).

Analysis of data on footfalls.—To quantify the gait pattern and durations of footfalls we selected the 10 best bouts of alarm walking and 10 best bouts of normal walking (all from different individuals) from the digital video according to the following guidelines: the subject was walking in very low or no vegetation to achieve high accuracy in selecting the video frames (30 frames/s) in which each foot struck and left the ground, and at least 4 full gait cycles (beginning with the landing of the left forefoot and ending with the next landing of the left forefoot) were performed sequentially without a noticeable pause or change in speeds. As described by Hildebrand (1965, 1966, 1976), the starting point for each sequence was defined by the frame where the left hind foot hit the ground; the ending point was the frame where the left hind foot hit the

ground to start the next sequence, and we recorded the frames in which every foot subsequently struck and left the ground for up to 4 full gait cycles. Therefore, data consisted of contact durations for each foot during the sequence with 4 full stride durations for the left hind foot and 3 full stride durations for the other 3 feet. Initial examination of the contact durations of the forefeet and hind feet revealed that their contact durations were unequal. Following Hildebrand (1976), we calculated and defined the following timing variables for both the left and right pairs of feet: stride duration (duration of time between landings of the hind foot), midtime (the halfway point in the contact duration for a single foot), midtime lag (the percent of stride duration that the forefoot midtime follows hind foot on the same side: $100\% \times$ [(forefoot midtime − hind-foot midtime)/stride duration]), and hind contact duration (percent of stride that the hind foot is on the ground: $100\% \times$ (hind-foot contact duration/stride duration)).

Differences between alarm walking and normal walking in contact durations of all 4 feet were analyzed using repeated-measures analyses of variance with walking type as the between-subjects factor and stride number (number of complete contact durations analyzed per sequence [i.e., subject]: left forefoot = 4, left hind foot = 5, right forefoot = 3, right hind foot = 4) as the repeated within-subjects factor. Gait graphs were produced, correlating midtime lag (y) and hind contact duration (x; after Hildebrand [1976]). Before analysis, midtime lag and hind contact duration for both sides of the body were arcsine square root transformed because they were proportions. Following Lingle (1992), differences between alarm walking and normal walking in midtime lag and hind contact duration were analyzed for each side of the body (left and right) using repeated-measures multivariate analyses of variance (MANOVAs), with walking type as the between-subjects factor and stride number as the repeated within-subjects factor. When the assumption of sphericity was violated, the Greenhouse–Gessier method, which adjusts degrees of freedom to achieve a more accurate *P*-value and is more conservative than alternative corrections, was used to calculate results in within-subjects tests, and these instances are noted in the text. Because of insufficient numbers of alarm-walking sequences of suitable quality on video, we were not able to compare alarm walking between older and younger deer. Significance was reached at $\alpha = 0.05$ and all analyses were conducted with SPSS 10.0.

Analysis of leg lifting.—To quantify the height and angle of foreleg lifting during alarm and normal walking, we selected the 6 best bouts of alarm walking and 6 best bouts of normal walking from the video record according to the following guidelines: the subject was walking with its flank facing the camera view so that lateral views of the leg angles remain the same throughout the sequence, and at least 3 full gait cycles (beginning with the landing of the left forefoot and ending with the next landing of the left forefoot) were performed sequentially without noticeable pause or change in speeds. Video sequences were converted to QuickTime video (Apple Inc., Cupertino, California) and quantified using Graphclick (Bovet 2006), a motion-analysis video software program. For each
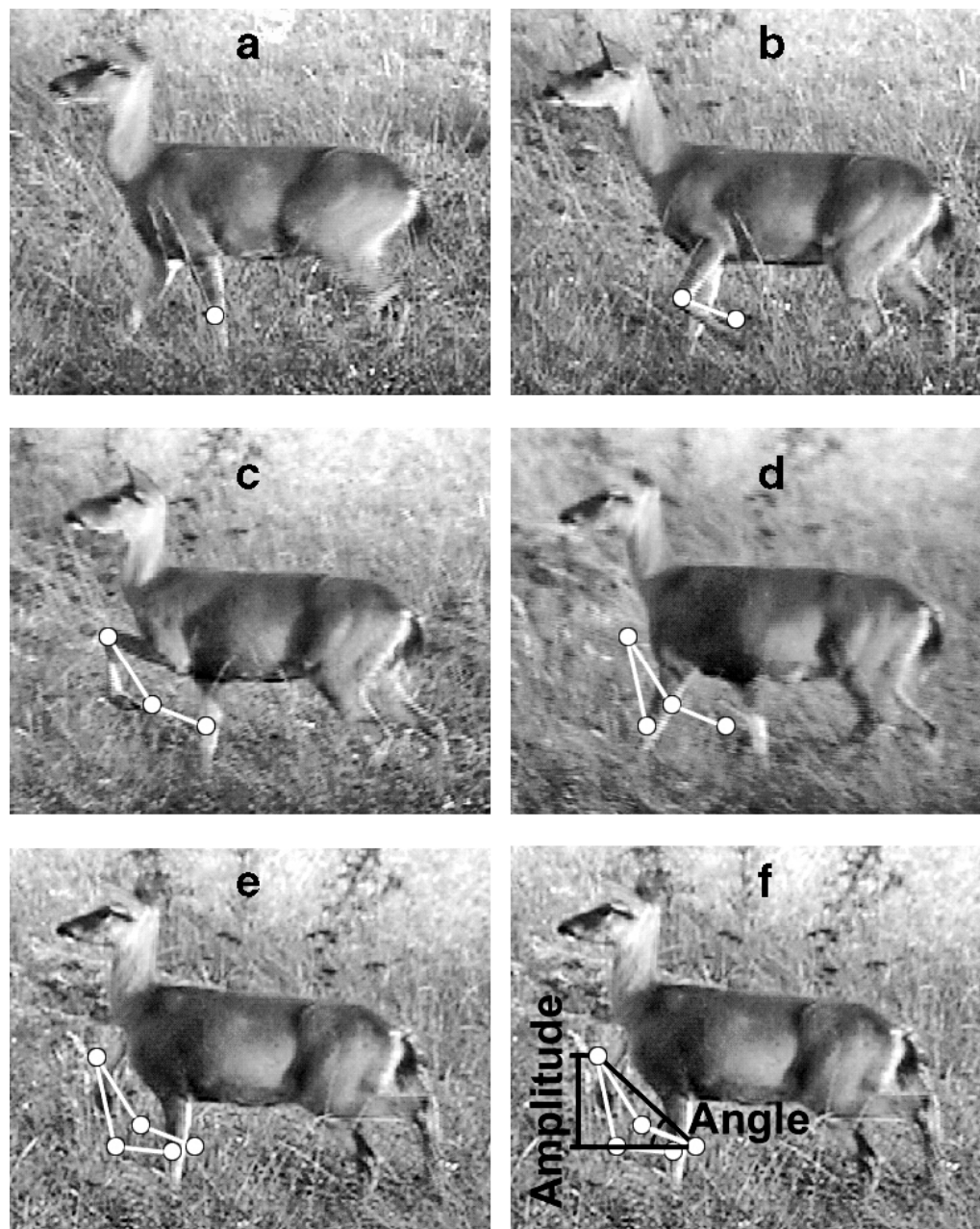
Fig. 1.—Five selected frames from a video sequence of alarm walking, illustrating various stages in 1 gait cycle. a–e) White dots indicate the digitized point of the carpal joint in each picture; path of the dots relative to the body of the deer is traced from picture to picture. f) Image shows the measurements (amplitude and angle) taken from digitized sequences.

video sequence, we plotted 4 series of points on a coordinate axis to track the movement of each point during the course of the walking bout. The 4 points and rationale for using them were: 1) the dorsal surface of the base of the tail where the tail meets the body—this point served as an anchor or origin for the other points to correct for any movement of the body image of the deer between video frames; 2) the leading surface of the carpal joint of the facing forelimb (because deer walked in different directions across the camera view in different video sequences, data from left and right forelimbs were pooled)— this point was chosen to characterize the movement of the forelegs because it was the point of greatest amplitude during

the leg lift (Fig. 1); 3) and 4) the tip of the nose and the lacrimal point of the eye—the coordinate distance between these 2 points was calculated to serve as a scaling factor to determine the absolute distance the leg travels. Video frames with 0.1-s intervals were chosen for quantification (i.e., 10 frames/s) and 60 frames per sequence were analyzed; this frame rate allowed 3 full gait cycles of alarm walking to fit in the 60 video frames.

Coordinates for the carpal joint (point 2) were reset using the base of the tail (point 1) as the origin (0, 0), and a scalar was calculated by dividing 15 cm (approximate distance between the eye and nose on a live deer) by the coordinate distance between the nose and eye points. We examined plots of the y-

coordinate versus time of the carpal joint, recorded the highest (peak: Fig. 1c) and lowest (Fig. 1d) points of the joint in each cycle, and calculated the difference between these points in centimeters; this value is the amplitude of the joint (shown in Fig. 1f). We next examined plots of x- versus y-coordinates of the carpal joint, which illustrated the profile of the leg movement in time and space (Fig. 1e). We then selected the points representing the moment where the leg was on the ground but furthest back in the cycle, just about to leave the ground (Fig. 1a); and the point where the carpal joint was at its peak (Fig. 1c). We calculated the horizontal and vertical distances between these points and used geometry to calculate the angle of the step (shown in Fig. 1f). This process was repeated for all 3 cycles per bout of walking. Differences between alarm and normal walking in both amplitude and angle were analyzed together with a repeated-measures MANOVA, with walking type as the between-subjects factor and stride number as the repeated within-subjects factor. Significance was reached at $\alpha = 0.05$ and all analyses were conducted with SPSS 10.0.

RESULTS

Analysis of footfalls.—Contact durations for all 4 feet were longer during alarm walking than during normal walking (Fig. 2; repeated-measures MANOVA; analyses of variance; $n_{\text{left forefoot}} = 16$ subjects, $n_{\text{left hind foot}} = 14$, $n_{\text{right forefoot}} = 21$, $n_{\text{right hind foot}} = 16$, all $P < 0.02$, all $\eta^2 > 0.299$). There were no reliable within-subjects effects of stride number (all $P > 0.05$). There was a statistically significant interaction between stride number and walk type in the left forefoot (within-subjects effects, Greenhouse–Geisser method; $F = 5.135$, $n = 21$, $d.f. = 1.612$, 30.635, $P = 0.017$, $\eta^2 = 0.201$), where contact duration increased in successive strides during alarm walking while contact duration decreased in successive strides during normal walking; all other stride × walk type interactions were not statistically significant ($P > 0.05$).

Walk type had a statistically significant multivariate effect on hind contact duration and midtime lag in the right pair of legs (repeated-measures MANOVA, multivariate between-subjects effects: $F = 7.439$, $n = 20$, $d.f. = 2$, 17, $P = 0.005$), but the effect did not reach statistical significance for the left pair ($F = 3.380$, $n = 20$, $d.f = 2$, 17, $P = 0.058$). There was no reliable multivariate within-subjects effect of stride or stride × walk type for either pair of legs (all $P > 0.05$). There were no differences between walk types in hind contact duration (x) for either the left or the right pair of legs (Figs. 3a and 3b; repeated-measures MANOVA, univariate between-subjects effects; right side: $F = 1.408$, $n = 20$, $d.f. = 1$, 18, $P = 0.251$; left side: $F = 0.037$, $n = 20$, $d.f. = 1$, 18, $P = 0.849$). However midtime lag (y) was significantly greater during normal walking compared with alarm walking in both the left and right pairs of legs (Figs. 3a and 3b; repeated-measures MANOVA, univariate between-subjects effects; right side: $F = 13.709$, $n = 20$, $d.f. = 1$, 18, $P = 0.002$, $\eta^2 = 0.440$; left side: $F = 6.280$, $n = 20$, $d.f. = 1$, 18, $P = 0.022$, $\eta^2 = 0.259$). There was no reliable univariate within-subjects effect of stride or
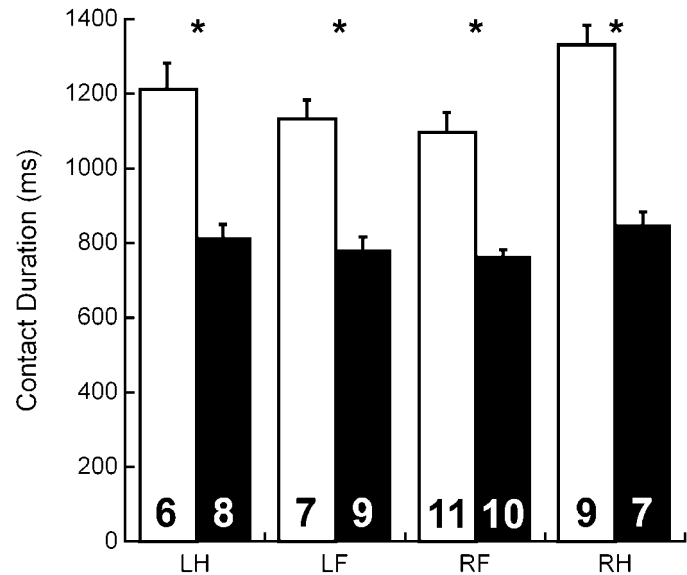

FIG. 2.—Mean ($\pm$ *SE*) contact durations (ms) for each foot during alarm walking and normal walking. White bars indicate alarm walking and black bars indicate normal walking. LH = left hind foot; LF = left forefoot; RH = right hind foot; RF = right forefoot. Sample sizes for each walk type for each foot are labeled in each bar. Differences between alarm and normal walking styles were statistically significant for all feet (* $P < 0.02$).

stride × walk type on hind contact duration or midtime lag for either pair of legs (all $P > 0.05$).

Analysis of leg lifting.—Walk type and stride number had statistically significant multivariate effects on angle and amplitude of leg lifting (repeated-measures MANOVA, walk type: $F = 5.388$, $n = 12$, $d.f. = 2$, 9, $P = 0.029$; stride: $F = 6.103$, $n = 12$, $d.f. = 4$, 7, $P = 0.019$), but there was no statistically significant interaction between these factors ($F = 2.007$, $n = 12$, $d.f. = 4$, 7, $P = 0.198$). Amplitude of leg lifting during alarm walking was significantly greater than during normal walking (Fig. 4; between-subjects effects: $F = 11.964$, $n = 12$, $d.f. = 1$, 10, $P = 0.006$, $\eta^2 = 0.545$); amplitude tended to be greater in earlier strides and lower in later strides of a single bout, but this difference did not reach statistical significance (within-subjects effects, Greenhouse–Geisser method: $F = 4.042$, $n = 12$, $d.f. = 1.277$, 12.768, $P = 0.058$, $\eta^2 = 0.264$), and there was no reliable interaction effect between stride and walk type ($F = 1.253$, $n = 12$, $d.f. = 1.277$, 12.768, $P = 0.298$). There was also no reliable difference in the angle of leg lifting between walking styles (repeated-measures MANOVA, between-subjects effects: $F = 2.372$, $n = 12$, $d.f. = 1$, 10, $P = 0.155$), but angles were greater during earlier strides and lower during later strides of a single bout (within-subjects effects: $F = 5.189$, $n = 12$, $d.f. = 2$, 20, $P = 0.015$, $\eta^2 = 0.307$). The interaction between stride and walk type for leg-lifting angle was not statistically significant ($F = 1.728$, $n = 12$, $d.f. = 2$, 20, $P = 0.203$).

Factors influencing alarm walking.—Influence of model type on performance of alarm walking has been reported and
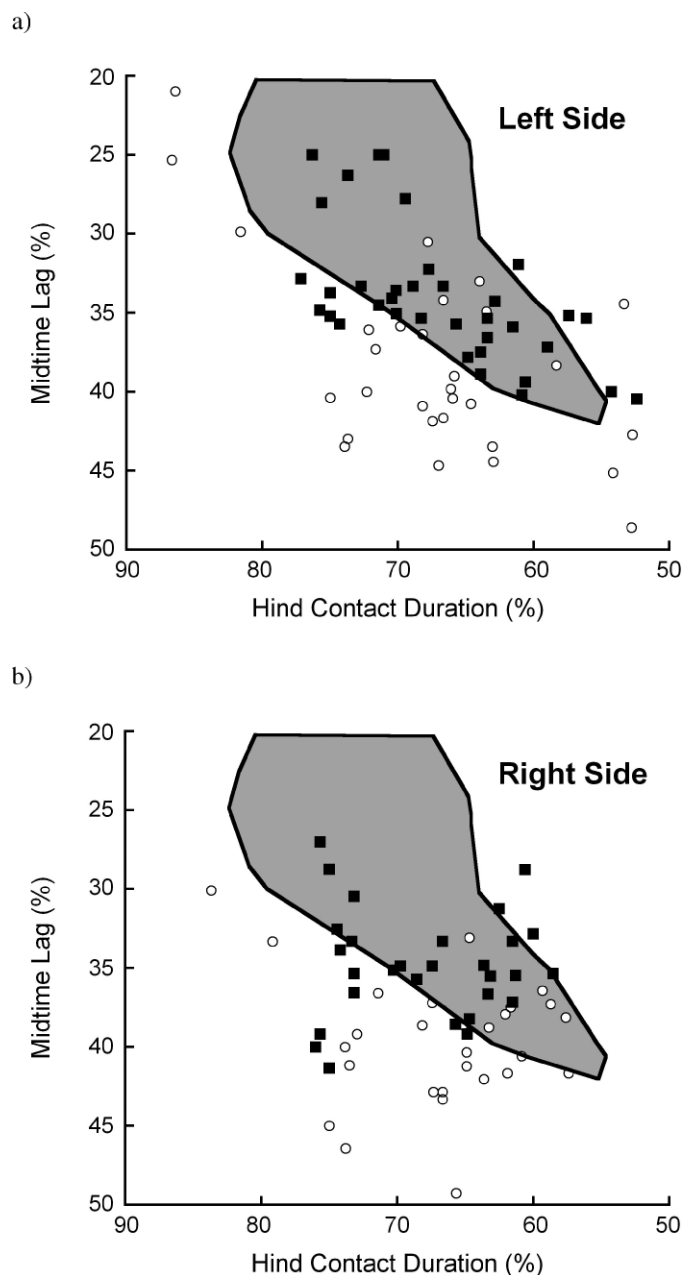
a)

b)

FIG. 3.—Gait diagrams showing midtime lag and hind contact duration for each stride measured for the a) left and b) right pairs of legs. White circles (○) indicate alarm walking and black squares (■) indicate normal walking. Both axes are reversed following Hildebrand (1976). The gray polygon plotted on each graph signifies the approximate area occupied on a gait diagram by the general cervid gait as reported by Hildebrand (1976:226). Note: Outliers are not shown for graphical clarity; there are 6 points that fall outside of the scale of a) and 1 point that falls outside of the scale of b) further to the right on the x axis.

discussed elsewhere (Stankowich and Coss 2007a). Deer alarm walked on all terrain types and in both short and tall vegetation. In the analyses of presence/absence of alarm walking and proportion of total time in camera view spent alarm walking, there were no statistically significant effects of sex of the focal animal (logistic regression of presence/absence: Wald = 0.057,
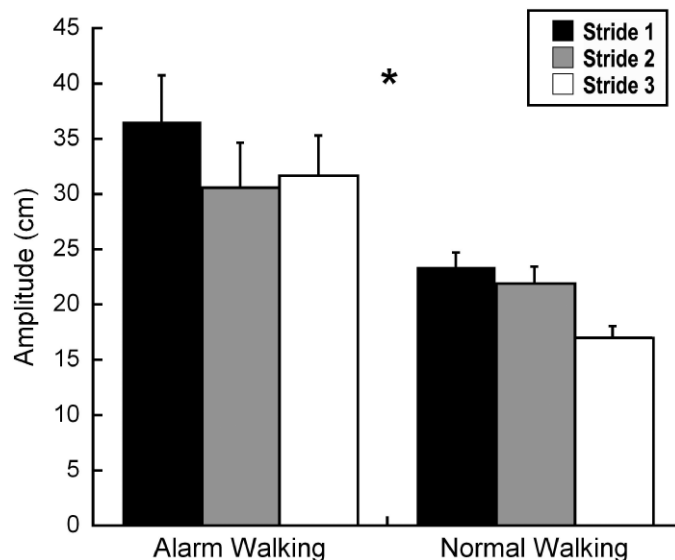

FIG. 4.—Mean ($\pm$ SE) amplitudes of the foreleg carpal joint during leg lifting in each of 3 consecutive strides of normal and alarm walking. Sample sizes for all strides in both walk types are equal: $n = 6$ for all bars. Alarm-walking carpal-joint amplitudes are significantly greater than normal-walking amplitudes (* $P = 0.006$).

$n = 73$, d.f. = 1, $P = 0.812$; ANCOVA of proportion of time spent alarm walking: $F = 0.016$, $n = 35$, d.f. = 1, 31, $P = 0.901$), group size (Wald = 1.043, $n = 73$, d.f. = 1, $P = 0.307$; $F = 0.688$, $n = 35$, d.f. = 1, 31, $P = 0.414$), solitary versus grouped status (Wald = 0.043, $n = 73$, d.f. = 1, $P = 0.835$; $F = 1.860$, $n = 35$, d.f. = 1, 31, $P = 0.184$), presence of fawn (Wald = 0.586, $n = 73$, d.f. = 1, $P = 0.444$; $F = 0.167$, $n = 35$, d.f. = 1, 31, $P = 0.686$), and distance to the model on either variable (Wald = 0.360, $n = 73$, d.f. = 1, $P = 0.548$; $F = 0.923$, $n = 35$, d.f. = 1, 31, $P = 0.325$). Completely solitary deer (i.e., without any fawns; solitary versus grouped in previous analysis) alarm walked in 2 of 4 trials when models of felids were used and in 0 of 2 trials when the model of a deer was used. Deer spent more time alarm walking while the model was out of view than in view during the period of the trial when exposures were occurring (paired-samples t-test: $t = -5.724$, d.f. = 37, $P < 0.001$), but there was no reliable difference between the time spent alarm walking while the model was in view and during the 30-s interval after each exposure ($t = -0.741$, d.f. = 37, $P = 0.463$).

The co-occurrence of alarm walking and foot stamping by the same deer (Table 1) generated the largest correlation coefficient (0.784) followed by the correlation coefficient of foot stamping and tail flagging (0.626). Two factors were extracted using common factor analysis with promax rotation (Widaman 1993), yielding an interfactor correlation of 0.565. Alarm walking generated a very high loading on the 1st factor, whereas the relatively high loadings for foot stamping were distributed about equally on both factors, the 2nd of which was dominated by snorting and tail flagging (Table 1). Although alarm walking is not uncoupled sequentially from foot stamping as a single latent variable, it is apparent from the

pattern of factor loadings that the tendency to alarm walk during model presentations was not linked cohesively with conspicuous displays, such as snorting and tail flagging.

DISCUSSION

Alarm walking was quantitatively different in form from normal walking in deer. Deer performing the alarm walk had reliably longer contact durations for all feet and a greater difference in amplitude of the foreleg carpal joint than deer performing the normal walk. The phases of contact of fore and hind limbs also were different between walking styles, as indicated by shorter midtime lags during bouts of alarm walking (Figs. 3a and 3b). We interpret these differences to mean that the alarm walk is a slower, more deliberate style of walking where deer lift their forelegs higher in the air, causing more flexion of their carpal joints.

Although the amplitude of leg lifting during alarm walking was greater than during normal walking, there was no difference in the angle of leg lifting, suggesting that the 2 walking styles are qualitatively the same in form, but the stepping motion is simply prolonged and exaggerated during alarm walking. In this sense, alarm walking is similar to but much slower than the "prancing" behavior of many African bovids. Prancing is an antipredator behavior described as "pronounced and exaggerated high steps made at a slow trotting speed" (Caro et al. 2004:206), is performed after flight at safe distances, and likely signals the performer's alertness to the predator (Caro 1994). We can also distinguish alarm walking from the "stiff-legged walk" described by Cowan and Geist (1961) during mule deer aggression and during alarm reactions of mule deer (Bowyer et al. 2001) and mountain goats (*Oreamnos americanus*—Singer 1978): stiff-legged walking is slow and stiff, with the head held down in line with the rest of the body (Cowan and Geist 1961), whereas alarm walking is slow and fluid, with great flexion of the carpals and the head held upright and alert. Plots of normal walking (Fig. 3) generally fell within Hildebrand's (1976) characterization of the general cervid gait (which included 26 plots from *Odocoileus*), whereas most plots of alarm walking fell outside this region. Clearly, there is a gradation between plots of normal and alarm walking on the gait diagrams; however, differences between the 2 gait styles in contact duration for each foot and leg-lifting amplitude are distinct and non-overlapping.

The slower nature of alarm walking is largely because of a noticeable pause in the gait when the forelimb carpal joint is at its peak amplitude. An individual's ability to maintain balance with high leg amplitude during this period suggests a high level of control of the limbs, fluidity of movement, joint mobility, and flexibility. Precise control and superior flexibility may be a signal that the deer's joints are healthy and disease-free, and the individual is capable of rapid acceleration and high agility during escape, should there be an attack. As noted above, the fluid property of alarm walking, coupled with high leg lifting were clearly conspicuous to human observers, which aided in our selection of gait sequences for video quantifica-

TABLE 1.—Tetrachoric intercorrelation coefficients of 4 behavioral measures exhibited by 51 Columbian black-tailed deer (*Odocoileus hemionus columbianus*) exposed to models of felid predators. Factor loadings were generated by principal axes factor analysis with promax rotation.

	Intercorrelations				Factor loadings	
	Alarm walk	Foot stamp	Tail flag	Snort	1	2
Alarm walk	1.000				1.085	−0.188
Foot stamp	0.784	1.000			0.553	0.564
Tail flag	0.262	0.626	1.000		−0.067	0.777
Snort	0.237	0.611	0.549	1.000	−0.108	0.805

tion. It is not unreasonable to argue that alarm walking is also conspicuous to predators scanning for the highly contrasting, stiff, arrhythmic gaits indicative of injured prey. If recognition by predators of the varying gaits of deer employs a bell-shaped generalization gradient (e.g., Ghirlanda and Enquist 2003) centered on the average (normal) gait, then alarm walking and limping might characterize opposite gait-recognition categories.

Alarm walking in black-tailed deer is an indication of recognition of danger (Stankowich and Coss 2007a) and is correlated with increased fearfulness of and attentiveness to a predatory threat (Stankowich 2006). Using the predictions by Caro and colleagues (1995) regarding the functions of ungulate antipredator behavior, if alarm walking served only to warn conspecifics of danger, alarm walking should have increased with group size and been absent in solitary animals. There was no effect of group size or the presence of fawns on the probability or duration of alarm walking, and alarm walking was performed by both solitary and grouped individuals. However, this lack of significance does not rule out conspecific warning as an "effect" ("function" per Williams [1966]) of alarm walking. A conspicuous display by 1 member of a social group becomes immediate public information for assessment by nearby conspecifics and the predator that elicited the display. However, although other antipredator behaviors such as snorting and foot stamping were contagious within groups, the quiet nature of alarm walking typically did not attract the attention of other deer in the immediate area (T. Stankowich, in litt.). Nevertheless, alarm walking may have dual effects that benefit solitary animals as well, and we cannot exclude the possibility that conspecifics may benefit from this apparent signal.

Performance of alarm walking was highly correlated with the presence of foot stamping, an auditory and visual signal (Caro et al. 2004) that may have dual functions of warning conspecifics and deterring pursuit. Foot stamping in white-tailed deer is effective in alerting conspecifics to danger (Caro et al. 1995), but is performed in both grouped and solitary individuals, suggesting multiple functions. Within the factor analysis, snorting, tail flagging, and foot stamping showed high loadings on the 2nd factor that did not include alarm walking. We propose that, although it may have other antipredatory effects (e.g., warning conspecifics), alarm walking in association with foot stamping functions to alert a stealthy predator

that it has been detected and to signal the performer's ability to escape with agility and speed.

If an individual signals to a predator that the predator has been detected, the predator should be more likely to give up their hunt on that individual or group; but the only means of directly testing this function is to observe the responses of predators to the performance of these behaviors. Ambushing predators (e.g., leopards) can be dissuaded from attacking by revealing that their attempt to be stealthy has failed (Zuberbühler et al. 1997, 1999). Because actual predation attempts on *Odocoileus* by stealthy predators are rarely observed in the wild (Beier et al. 1995; Smallwood 1993), this hypothesis is nearly impossible to test directly. However, an advertisement of alertness to a stealthy predator might result in a higher probability of signaling when prey are farther from the predator than during the urgent situation when the predator is within striking range (Caro et al. 1995). Although distance to the model predator had no effect on the performance of alarm walking, the minimum distance of model presentation was 15 m and successful ambush attacks occur when the predator is able to approach unnoticed within 5–10 m of the prey (puma—Beier et al. 1995; lion [*Panthera leo*]—Stander 1992). Therefore, alerted deer were likely outside the range of danger for a successful ambush attack by a felid, which agrees with the prediction (Caro 1994) that signals of awareness should be performed in dangerous situations but not the most dangerous (i.e., inside the attack range of the predator).

Deer spent more time alarm walking when the predator model was out of view, concealed behind cover ($P < 0.001$), and more time stationary and alert while the predator was in view. Alarm walking deer often approached the area of the model to further inspect the threat and walked with their flank facing the location of the model (T. Stankowich, in litt.), allowing full side display of the leg movement from the perspective of the hidden predator. These observations suggest that when the stealthy predator is concealed and potentially preparing to pounce, deer attempt to signal to the predator that it has been detected and an attack would be unsuccessful. Stealthy predators usually do not attack from the open (Beier et al. 1995), and a concealed predator would likely monitor the prey, possibly readying itself to pounce; such anticipation of a predatory attack from a predator that disappeared from view heightens the need for prey to display and demonstrate their awareness and ability to effectively escape an attack.

Although the presence of fawns did not influence the probability of alarm walking, alarm walking may have the effect of pursuit invitation to the hidden predator to deflect attention away from their fawns when fawns are present (Smythe 1970; but see Coblentz 1980; Hirth and McCullough 1977), or demonstrate that they are strong and able to defend both themselves and their fawns should there be an attack; indeed, mule deer females effectively defend their fawns against coyote attacks (Lingle et al. 2005, 2007a, 2007b).

To summarize, we found alarm walking to be a highly conspicuous gait that is performed reliably in the presence of stealthy predators and is correlated with antipredator behaviors known to be visual signals aimed at predators to deter further pursuit. As a slower, but much higher-stepping gait than normal walking, alarm walking requires deliberate coordination of the limbs, the combination of which likely prompts higher-order inferences by the predator about prey youthfulness and agility associated with better escape ability. Although most tests of the predictions of potential functions for alarm walking were inconclusive, alarm walking was most common when the predator was concealed, a property that could signal to the predator that the prey is prepared for the predator's attack. Although we did not directly test the effect of alarm walking on predator attack probability, we suggest that alarm walking functions as a signal of awareness of the predator and of escape ability, meant to deter further pursuit, but it may also have other antipredator effects as well (e.g., conspecific warning or protection of fawns). Future studies of alarm walking should focus on measuring alarm-walking ability in all ages of deer, determining if older, hobbled, or arthritic deer are even capable of performing the behavior, because this would indicate that alarm walking is an honest signal of the strength and agility of the performer, and testing predator responses to video playbacks of deer walking in normal and alarmed states.

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