

American black bears and hair snares: a behavioral analysis

Authors: Gurney, Steven M., Smith, Jennifer B., Etter, Dwayne R., and Williams, David M.

Source: Ursus, 2020(31e9): 1-9

Published By: International Association for Bear Research and

Management

URL: https://doi.org/10.2192/URSUS-D-18-00020.2

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

American black bears and hair snares: a behavioral analysis

Steven M. Gurney¹, Jennifer B. Smith^{1,3}, Dwayne R. Etter², and David M. Williams¹

¹Boone and Crockett Quantitative Wildlife Center, Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, East Lansing, MI 48824, USA

²Michigan Department of Natural Resources, Wildlife Division, 4166 Legacy Parkway, Lansing, MI 48911, USA

Abstract: Despite the widespread use of noninvasive hairsampling for American black bear (Ursus americanus) population monitoring, there is no explicit analysis of black bear behavior at hair snare sites. During 2016, we deployed hair snares and camera traps at 40 sites across the northern Lower Peninsula of Michigan, USA, and collected 560 video recordings of black bear activity. Our objectives were to develop an ethogram of bear behaviors at snare sites and quantify their occurrence. We found that bears allocated their time consistently when they were physically inside or outside of the snare, but they divided their time among multiple behaviors when crossing the wire. The inconsistencies in wire crossing revealed unexpected behaviors with important implications for study design. Our findings explicitly describe how black bears interact with hair snares, provide recommendations for addressing the influence of behavior on sampling efficiency, and establish a foundation for further study of animal behavior at hair snares.

Key words: American black bear, behavior, detection, ethogram, hair snare, mark-recapture, Michigan, noninvasive, *Ursus americanus*

DOI: 10.2192/URSUS-D-18-00020.2 *Ursus 31:article e9 (2020)*

Accurate estimates of population size drive conservation priorities and are the cornerstone for effective management of large mammal populations (Karamanlidis et al. 2015, Mumma et al. 2015). However, population estimates can be difficult to obtain, especially for cryptic species or mammals that occur at low densities and across large spatial scales (Beier et al. 2005, Long et al. 2007, Wilton et al. 2014). Noninvasive sampling

³ email: jbartonsmith@gmail.com

techniques are often used to estimate population size and characteristics of such species. For example, hair snares are an established noninvasive method for obtaining capture—mark—recapture data for ursid populations (Augustine et al. 2014). Compared with live-trapping, hair sampling can produce larger sample sizes and survey larger geographic areas (Mowat and Strobeck 2000, Dreher et al. 2009), which can improve accuracy in abundance estimates (Boersen et al. 2003). However, these benefits are only realized when detection rates are sufficiently high (Mills et al. 2000, Tredick et al. 2007, Augustine et al. 2014).

Successful detection of animals from hair sampling requires multiple events to occur: animals must encounter the trap and deposit samples, which must be successfully collected, and DNA from collected samples must amplify (Goossens et al. 1998, Lamb et al. 2016). Animal behavior at traps influences capture probability for multiple reasons. For instance, the design of baited noninvasive hair snares is intended to prompt a specific behavior in which the animal deposits hair (Kendall and McKelvey 2008). This hair deposition behavior is often specific to the study species; for example, American black bear (Ursus americanus; hereafter, black bear) hair snares require the animal to cross a strand of barbed wire (Woods et al. 1999), whereas wolverine (Gulo gulo) hair snares require the animal to climb a post (Mulders et al. 2007). Once the hair deposition behavior has occurred, additional patterns of behavior at or around the snare further influence the quantity and quality of collected samples (Long et al. 2007, Marucco et al. 2010, Latham et al. 2012, Sawaya et al. 2012). Studying patterns of behavior at traps can identify actions affecting capture probability and may provide valuable guidance for modifications to study designs to improve detection.

Remote cameras (hereafter, camera traps) are a versatile device well-suited to collecting animal behavior data (O'Connell et al. 2011). Camera trap footage allows us to observe and identify behaviors affecting hair deposition and, by extension, capture probability (Wilton et al. 2016). These behavioral data can be compiled into an ethogram (Altmann 1974) and quantified into an activity budget (Ransom and Cade 2009). An ethogram is a formal description of a species' behavior; it can be a comprehensive inventory of behaviors or focus on a category of behaviors (Grier 1984).

In the northern Lower Peninsula (NLP) of Michigan, USA, barbed-wire hair-snare corrals (hereafter, hair

snares) have been used as part of a population monitoring program for black bears since 2003. However, capture probability of this population via hair snares is notably low (e.g., 0.02; Dreher et al. 2007). Whereas multiple studies recognize that bear behavior can affect hair sampling (Boulanger et al. 2004, Gardner et al. 2010, Marucco et al. 2010, Wilton et al. 2016), to our knowledge there is no explicit analysis of black bear behavior at hair snares. In 2016, we placed trail cameras at 40 hair snares in the NLP of Michigan to record video of black bears at the snare sites. Our objectives were to develop an ethogram of bear behaviors at snare sites and quantify the occurrence of those behaviors. Our findings provide insight into how black bears respond to and interact with these snares, and identify individual behaviors that affect hair deposition.

Study area

We established hair snare traps in the NLP of Michigan; most sites were in the Manistee National Forest and the Roscommon State Forest, which are adjacent to the Cadillac and Houghton Lake areas, respectively (Fig. 1). These areas are predominantly forested, managed primarily for timber and recreation, and are fragmented by roads, oil pipeline access paths, private property, agricultural fields, and human developments. The topography around Cadillac consists of glacial moraines, sandy hills, and moderate to steep slopes, whereas the landscape surrounding Houghton Lake is relatively flat. The study area is considered a northern lacustrine-influenced ecotone; its forests include northern hardwoods, upland-conifers, pine barrens, and a mix of hardwood and conifer swamps (Albert 1995). Bound by Lake Michigan to the west and Lake Huron to the east, the NLP has greater exposure to lake-effect weather conditions than the southern Lower Peninsula (Barnes and Wagner 2004), resulting in cooler temperatures and a shorter, more variable, growing season.

Methods Site selection

We deployed hair snares and trail cameras in 2 grids ($10 \text{ km} \times 18 \text{ km}$) spaced 46 km apart. Each grid consisted of 20 snares configured into 5 clusters; each cluster consisted of 4 snares, spaced approximately 1.6 km apart (Fig. 1). Sites were located on public land and were selected based on the presence of high-quality black bear habitat and on anecdotal knowledge of previous bear locations from the Michigan Department of Natural

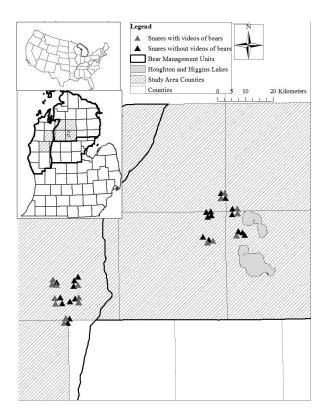


Fig. 1. Study area in the northern Lower Peninsula of Michigan, USA, depicting locations of grids of hair snares in 2016. Remote cameras placed at each hair snare were used to study behavior of American black bears (*Ursus americanus*) while visiting the snares.

Resources. We avoided sites near motorized vehicle trails or roads and maintained a 500-m buffer between snare sites and human developments to minimize the likelihood of human—bear conflict.

Hair snares

We visited snares at 6–7-day intervals for 6 consecutive weeks (sampling occasions) in June and July 2016. This temporal sampling frame coincides with the spring molt and is ideal for maximizing sample size (Wegan et al. 2012, Yamauchi et al. 2014, Wilton et al. 2016). We constructed snares by encircling a baited location with 2 strands of barbed wire. We strung wires around 3–5 trees at uniform heights of 20 cm and 50 cm (Dreher et al. 2007). Variation in site characteristics (e.g., topography, vegetation) dictated that the size of the enclosed area ranged from approximately 9 to 28 m². We placed a scent lure (attractant) and a food bait within each snare. Attractants were either cherry syrup or black bear scat collected from captive individuals at the Binder Park Zoo

in Battle Creek, Michigan. Food baits consisted of either a mixture of peanut butter and oats or pig jowls (bacon). We suspended 2 food baits over the center of the snare at different heights: we hung a larger food bait (454 g [16 oz] bacon or 226 g [8 oz] peanut butter–oat ball) approximately 3 m in the air, and a smaller food bait (28 g [1 oz] of either bacon or peanut butter-oat ball) approximately 1.2 m above the ground. The higher bait was intended to attract animals over the entire sampling period, whereas the lower bait was intended to encourage bears to cross the snare wire. We placed one attractant at each hair snare; we suspended the cherry syrup attractant with the larger food bait, whereas we placed the bear scat attractant on the ground in the center of the snare. We randomly assigned bait and attractant pairings to a snare location within a cluster and assignments were uniform among all 10 clusters (e.g., snares located in the northeast corner of each cluster were assigned bacon food bait and bear scat attractant).

Trail camera setup and sample collection

We placed 1–2 trail cameras (Bushnell ® 12MP Trophy Cam HD Essential, Overland Park, Missouri, USA) at every snare location. Camera settings (e.g., recording time and interval length) balanced battery longevity with maximum data collection. Cameras were motionactivated and recorded either still photos or 20-second videos at 15-second intervals. We positioned cameras to view the entire trap and immediate surroundings (realized field of view ranged approx. 1-3 m beyond edge of snare). We placed an additional camera (positioned opposite from the existing device) during the second sampling occasion if a site was visited by black bears during the first week. We were unable to deploy secondary cameras simultaneously or at all locations on account of logistical constraints. Instead, we added cameras opportunistically as we confirmed bears had visited sites. During each sampling occasion, we downloaded camera data, collected all deposited hairs, and replaced the baits and attractant.

Ethological data collection and analyses

We reviewed video footage from successful hair snares (i.e., snares that collected supposed black bear hair) and developed an ethogram of frequently occurring behaviors. We regarded behaviors as instantaneous events and recorded them at the moment of their onset (e.g., the animal assumes a seated position; Altmann 1974). We assigned each behavior to 1 of 3 classes reflecting where the behavior occurred: outside of snare (OS), inside of snare (IS), or wire crossing (WC). We could not definitively identify individuals because bears were not marked and

Table 1. Total time, percentage of total time, total number of events (behaviors recorded instantaneously at moment of onset), and percent frequency of events of each class of American black bear (*Ursus americanus*) behavior in the northern Lower Peninsula of Michigan, USA, 2016.

Behavioral class	Total time (sec)	Percent time	Total no. of events	Percent frequency
Outside of snare	5,443	50	475	46
Inside of snare	4,590	42	409	39
Wire crossing	854	8	151	15
Total	10,887	100	1,035	100

collected hair samples were not genotyped. Therefore, we distinguished unique visits if the interval between camera observations of a bear at a snare was ≥30 minutes (Wilton et al. 2016). When multiple individuals were present in a single video, we recorded behavior data separately for each adult bear (i.e., we recorded multiple visits; Altmann 1974). We recorded number of events and time spent on each defined behavior relative to the total number of events and observed time of its corresponding class, respectively. We used these values to characterize activity budgets (overall percentage of events and time) and visit profiles (average no. of events and time per visit) of black bears at the hair snares. We reviewed and identified video footage of consecutive clips showing a bear outside the snare, then inside the snare, with no recorded wire crossing. We used this approach to estimate the number of times a bear crossed the wires per visit.

Results

We collected camera data for 240 snare-weeks (sampling occasion per snare). Twenty-seven of the 40 snares collected supposed black bear hair. Seventeen of the 27 successful snares were equipped with video cameras; these 17 cameras (Fig. 1) collected data for 49 snareweeks, corresponding to 560 video clips of black bears exhibiting 1,035 behavioral events (Table 1). We defined 6 distinct behaviors within the OS behavioral class, 6 within the IS behavior class, and 9 within the WC class. Three of the defined behaviors occurred in multiple classes: bipedal, bait-tugging, and climbing a snare tree (a tree to which the snare is attached) occurred both outside and inside of the snare. Each behavior is defined in detail in our ethogram (Table 2). We identified 148 unique visits, of which 100 (68%) included bears displaying WC or IS behaviors (i.e., bear entered the snare). On average, bears that entered the snare spent more time at the trap

Table 2. An ethogram of frequently occurring American black bear (Ursus americanus) behaviors observed at hair-snare sites in the northern Lower Peninsula of Michigan, USA, 2016.

Behavior	Definition			
Outside of snare				
Scan	Assessing the area for visual or olfactory cues and assuming an upright position with the weight of the body on 3 or 4 legs, ambulatory or stationary. Accompanied by head movement up and down or in multiple directions.			
Pacing	Ambulation following the outside perimeter of the snare. Slow, upright gait in a pronograde posture; 3 feet support the body at all times.			
Bipedal	Standing upright on hind legs, stationary or ambulatory.			
Bait-tugging	Biting and tugging a suspended bait to release it from the suspension string. This behavior was always initiated from inside the snare and may involve action in a quadrupedal, bipedal, sitting, or lying posture.			
Climb external tree	Climbing a tree external from the snare structure. All 4 feet completely leave the ground.			
Climb snare tree	Climbing a tree that the snare is attached to. All 4 feet completely leave the ground.			
Inside of snare				
Quadrupedal	Assuming an upright position with the weight of the body on 3 or 4 legs, ambulatory or stationary.			
Bipedal	Standing upright on hind legs, stationary or ambulatory.			
Sitting	Resting on the hocks and buttocks.			
Bait-tugging	Biting and tugging a suspended bait to release it from the suspension string. May involve action in a quadrupedal, bipedal, sitting, or lying position.			
Climb snare tree	Climbing a tree to which the snare is attached. All 4 feet leave the ground.			
Lying	Act of ventral or dorsal lying.			
Wire-crossing				
Step over	Stepping over both wires, one leg at a time. Three feet are always supporting the body.			
Jump over	With mostly hindlimb propulsion, leaping over both wires; the forelegs leaving the ground first, followed by the hindlegs.			
Unclassified	At least one forelimb steps over the wire, but video ends before a complete cross is observed.			
Paw wire	Lifting one forelimb and touching the wire with paw, or temporarily resting forelimb on wire. Animal does not completely cross the wires.			
Going between	Crossing between the upper and lower wires.			
Step on	Planting ≥1 forepaw on the upper wire and pushing it down, then stepping over both wires, one leg at a time. Hind paw often replaces the forepaw's pressure on the wire during crossing.			
Incomplete	Both forelimbs step over the wire, but bear then backs up and does not cross.			
Half-jump	Both forelimbs step over the wire first, then both hindlimbs leap over the wire.			
Cross via tree	Using a tree to which the snare is attached to cross over the wires by climbing up and then down the tree.			

 $(\bar{x} = 405 \pm 96)$ [95% CI] sec) than did bears that did not enter ($\bar{x} = 83 \pm 56$ sec).

Overall, black bears spent most of their time outside of the snare (50% of observed time; Table 1) and were typically scanning or pacing in this location (59% and 32% of observed time, respectively; Fig. 2A). Within a given visit, the most frequently occurring OS event was scanning ($\bar{x} = 2.00 \pm 0.27$ events/visit; range = 0–8; Fig. 3A), suggesting that bears investigate the trap before further interacting with it. Bears observed inside of the snare spent the most time engaged in quadrupedal or sitting behaviors (55% and 19% of observed time, respectively; Fig. 2B). The most frequent IS events were quadrupedal $(\bar{x} = 2.30 \pm 0.45 \text{ events/visit; range} = 0-11; \text{ Fig. 3B})$ and bipedal ($\bar{x} = 1.10 \pm 0.24$ events/visit; range = 0-5; Fig. 3B). These and all other behaviors inside of the snare involved efforts to retrieve or consume the bait. Over half of the observed time within the WC class was dedicated to either stepping over the wire (36%) or crossing in a way

considered unclassifiable (18%; Fig. 2C). We estimated that bears crossed the wires an average of 3.00 ± 0.37 times/visit (range = 1-14), but observed bears crossing the wires an average of 2.00 ± 0.37 times/visit (range = 1-11; Fig. 3C), primarily by stepping over the wire $(\bar{x} = 0.62 \pm 0.21 \text{ events/visit; range} = 0-6; \text{Fig. 3C})$. We also observed WC behaviors that likely compromised deposition of hair (i.e., evasive behaviors), which included jumping over the wire ($\bar{x} = 0.33 \pm 0.14$ events/visit; range = 0-3; Fig. 3C), stepping on the wire ($\bar{x} = 0.16 \pm 0.11$ events/visit; range = 0-2; Fig. 3C), and climbing trees $(\bar{x} = 0.03 \pm 0.04 \text{ events/visit; range} = 0-1; \text{ Fig. 3C}).$

Discussion

Black bears allocated their time consistently when they were inside or outside of the snare (e.g., typically quadrupedal when inside), but they divided their time among multiple behaviors when crossing the wire. The

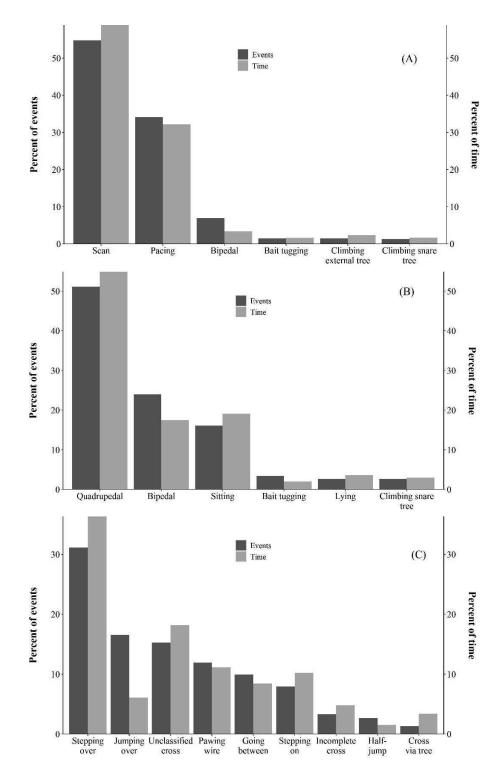


Fig. 2. Activity budgets of American black bears (*Ursus americanus*) within 3 different classes of behavior observed at hair snares in the northern Lower Peninsula of Michigan, USA, 2016. Behaviors were classified by their location: (A) outside of snare, (B) inside of snare, and (C) wire crossing. Percent of events (behaviors recorded instantaneously at moment of onset) and time represented by dark gray and light gray, respectively.

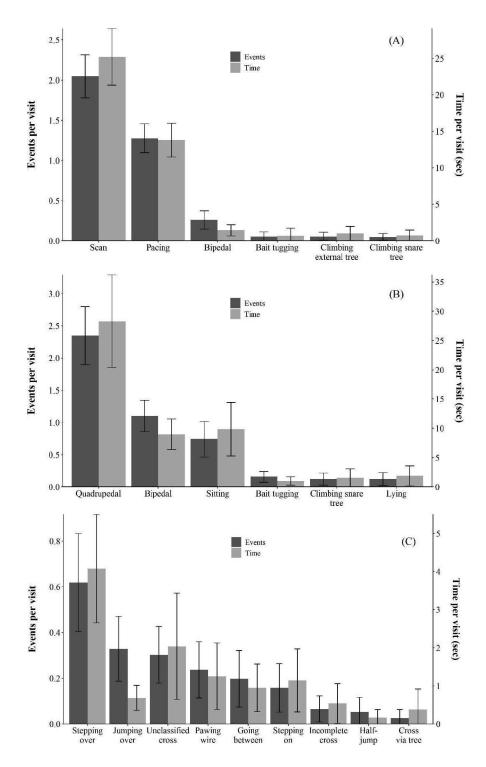


Fig. 3. Visit profiles of American black bears (*Ursus americanus*) within 3 different classes of behavior observed at hair snares in the northern Lower Peninsula of Michigan, USA, 2016. Behaviors were classified by their location: (A) outside of snare, (B) inside of snare, and (C) wire crossing. Events (behaviors recorded instantaneously at moment of onset) per visit is in dark gray and time per visit is in light gray. Error bars indicate 95% confidence limits.

variation in wire-crossing behaviors revealed evasive behaviors with important implications for study design. Although most visits resulted in a wire-crossing event, 32% did not. Moreover, specific behaviors clearly resulted in contact with the snare wire, whereas other behaviors increased evasion. Our findings suggest that factors other than bear presence, including behavior, influenced the deposition of hair samples.

The snares employed in this study are designed to capture hair samples when black bears cross the wires (Woods et al. 1999), but bears also made contact with the wire from a variety of other behaviors once inside the snare. Nearly all these productive IS behaviors involved the bear obtaining the food (e.g., tugging the bait). For instance, when bears tugged the bait ($\bar{x} = 0.16 \pm$ 0.08 events/visit; range = 0-2), they often bumped into the wires or forcefully pulled the suspended bait outside of the snare, resulting in an additional wire crossing. It is worth noting that the cameras in our study did not record continuous video; consequently, all behavioral events were not observed (i.e., imperfect detection). Therefore, the values portrayed in our visit profiles are likely representative, but may be biased low. Behaviors in the wire-crossing class were responsible for the majority of bear contact with the wire, supporting the assumption that wire crossing is important for maximizing sample size and should be the targeted hair-deposition behavior. However, the specific method bears use to cross the wire likely affected hair deposition.

Black bears occasionally avoided contact with the barbed wire (and presumably avoided depositing hair) when crossing the wire. Notably, these evasive behaviors included jumping over the upper wire of the snare. To our knowledge, black bears had not been documented jumping over hair-snare wires prior to our study (though Johnson [2018] recently documented bears jumping over electrical fencing), yet this behavior accounted for 17% of WC events. Bears also stepped on the wires (8% of WC events) during wire-crossing. This behavior commonly has been observed in ursids (Kendall and McKelvey 2008, Wilton et al. 2016) and is considered an avoidance behavior because contact between the underside of a paw and the wire is unlikely to deposit numerous or high-quality hairs. It is possible that stepping on the wire is a learned behavior stemming from interacting with a snare multiple times (Wilton et al. 2016). Although uncommon, bears were also observed climbing trees to evade the wires (1% of WC events). In addition to these wire-avoidance behaviors, perhaps the most obvious, yet pernicious, behavior influencing detection was individual aversion to hair snares.

Ursus 31:article e9 (2020)

Low detection estimates from existing spatial markrecapture models of hair snare data in the NLP raised formative questions about how often black bears were in proximity to a hair snare, but never entered or interacted with the snare (D. M. Williams, unpublished data). Those questions were motivational for our efforts here to characterize and evaluate behavior around snares. According to our visit definition, 32% of visits in our data included a bear approaching, but not entering, a snare, and therefore constituted undetected encounters. Similar to bears that entered, bears that did not enter were typically scanning or pacing outside of the snare (58% and 37% of observed time, respectively). Sampling design, including time since bait and attractant was refreshed, absence of bait, sampling occasion, and number of previous visits, may also affect bear behavior and likelihood of wire crossings. Moreover, bears likely encountered > 1 site or encountered the same site multiple times. Trap aversion could be driven by previous negative experience with hair snares (Boulanger et al. 2008) or a preoccupation with breeding (Rogers 1987, Noyce and Garshelis 1997, Boulanger et al. 2004). Regardless of the reason, it is troubling that 32% of visits did not include a bear entering the snare, especially in conjunction with our finding that 26% of the observed WC events consisted of behaviors that likely compromise deposition of bear hair (and thus a capture event) at snares. These findings emphasize the role individual capture heterogeneity plays in detecting bears (Boulanger et al. 2004), and the value of explicitly quantifying patterns of behavior at traps.

Our results suggest variation in black bear behavior is relevant to sampling efficiency. The utility of hair samples as a noninvasive sampling technique is dependent on capture probability, which in turn is influenced by the behavior of the target species (Kendall and McKelvey 2008). Evaluating the behavioral response of animals to traps provides an opportunity to increase capture probability, maximize the benefits of noninvasive studies, and ultimately to improve the accuracy and precision of population estimates. Our study provides the first formal description and quantification of how black bears behave at barbed-wire hair-snares. Although our study focused on black bears, analyzing video footage of behavior at traps is a versatile approach for seeking to understand sources of variation in capture rates of any species (Marucco et al. 2010).

Management implications

Modifications to the design of black bear hair-snare studies could address both the positive and negative influences of bear behavior on capture probability. Whereas any bait may lure a bear, its location within the snare influences contact between a bear and the wire after the wire has been crossed. For managers using bait, we recommend a design that includes suspending bait within reach of a bear inside the snare to improve the likelihood of collecting additional hair samples after the bear crosses the wire. However, this increase in samples may come with an increase in capture heterogeneity; and that heterogeneity must be accounted for in models of abundance estimation. Finally, some bears stepped on or jumped over the wire to avoid contact when entering or exiting the snare. We did not observe any adults or yearlings attempt to evade the wire by crawling under the lowest wire. Thus, in future studies, researchers could raise the height of the wires in the 2-strand design or add a third strand of barbed-wire to determine whether either modification can reduce the frequency of the evasive stepping-on and jumping behaviors.

Acknowledgments

We thank the Michigan Department of Natural Resources, U.S. Fish and Wildlife Service Federal Aid in Wildlife Restoration W-155-R, College of Agriculture & Natural Resources, Department of Fisheries & Wildlife, and the Boone & Crockett Quantitative Wildlife Center at Michigan State University for funding and project support. Special thanks to N. Fowler for insightful feedback and T. Rodriguez for statistical programming advice. Finally, we thank the Associate Editor, an anonymous reviewer, and J. Boulanger for their constructive comments and suggestions on earlier drafts of this manuscript.

Literature cited

- ALBERT, D.A. 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: A working map and classification. North Central Forest Experiment Station General Technical Report NC-178. U.S. Forest Service, St. Paul, Minnesota, USA.
- ALTMANN, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49:227–266.
- AUGUSTINE, B.C., C.A. TREDICK, AND S.J. BONNER. 2014. Accounting for behavioural response to capture when estimating population size from hair snare studies with missing data. Methods in Ecology and Evolution 5:1154–1161.
- BARNES, B.V., AND W.H. WAGNER. 2004. Michigan trees: A guide to the trees of the Great Lakes Region. University of Michigan Press, Ann Arbor, Michigan, USA.
- BEIER, L.R., S.B. LEWIS, R.W. FLYNN, G. PENDLETON, AND T.V. SCHUMACHER. 2005. A single-catch snare to collect

- brown bear hair for genetic mark–recapture studies. Wildlife Society Bulletin 33:766–773.
- BOERSEN, M.R., J.D. CLARK, AND T.L. KING. 2003. Estimating black bear population density and genetic diversity at Tensas River, Louisiana using microsatellite DNA markers. Wildlife Society Bulletin 31:197–207.
- BOULANGER, J., G. STENHOUSE, AND R. MUNRO. 2004. Sources of heterogeneity bias when DNA mark—recapture sampling methods are applied to grizzly bear (*Ursus arctos*) populations. Journal of Mammalogy 85:618–624.
- ——, G.C. WHITE, M. PROCTOR, G. STENHOUSE, G. MACHUTCHON, AND S. HIMMER. 2008. Use of occupancy models to estimate the influence of past live captures on detection probabilities of grizzly bears using DNA hair snagging methods. Journal of Wildlife Management 72:589–595.
- DREHER, B.P., G.J.M. ROSA, P.M. LUKACS, K.T. SCRIBNER, AND S.R. WINTERSTEIN. 2009. Subsampling hair samples affects accuracy and precision of DNA-based population estimates. Journal of Wildlife Management 73: 1184–1188.
- ——, S.R. WINTERSTEIN, K.T. SCRIBNER, P.M. LUKACS, D.R. ETTER, G.J. ROSA, V.A. LOPEZ, S. LIBANTS, AND K.B. FILCEK. 2007. Noninvasive estimation of black bear abundance incorporating genotyping errors and harvested bear. Journal of Wildlife Management 71:2684–2693.
- GARDNER, B., J.A. ROYLE, M.T. WEGAN, R.E. RAINBOLT, AND P.D. CURTIS. 2010. Estimating black bear density using DNA data from hair snares. Journal of Wildlife Management 74:318–325.
- GOOSSENS, B., L.P. WAITS, AND P. TABERLET. 1998. Plucked hair samples as a source of DNA: Reliability of dinucleotide microsatellite genotyping. Molecular Ecology 7:1237–1241.
- GRIER, J.W. 1984. Biology of animal behavior. Times Mirror/ Mosby College Publishing, St. Louis, Missouri, USA.
- JOHNSON, B.J. 2018. Permeability of three-strand electric fences by black bears and grizzly bears. Thesis, Montana State University, Bozeman, Montana, USA.
- KARAMANLIDIS, A.A., M.G. HERNANDO, L. KRAMBOKOUKIS, AND O. GIMENEZ. 2015. Evidence of a large carnivore population recovery: Counting bears in Greece. Journal for Nature Conservation 27:10–17.
- KENDALL, K.C., AND K.S. MCKELVEY. 2008. Hair collection. Pages 141–182 in R.A. Long, P. MacKay, W.J. Zielinski, and J.C. Ray, editors. Noninvasive survey methods for carnivores. Island Press, Washington, DC, USA.
- LAMB, C.T., D.A. WALSH, AND G. MOWAT. 2016. Factors influencing detection of grizzly bears at genetic sampling sites. Ursus 27:31–44.
- LATHAM, E., J.B. STETZ, I. SERYODKIN, D. MIQUELLE, AND M.L. GIBEAU. 2012. Noninvasive genetic sampling of brown bears and Asiatic black bears in the Russian Far East: A pilot study. Ursus 23:145–158.
- LONG, R.A., T.M. DONOVAN, P. MACKAY, W.J. ZIELINSKI, AND J.S. BUZAS. 2007. Comparing scat detection dogs, cameras,

- and hair snares for surveying carnivores. Journal of Wildlife Management 71:2018–2025.
- MARUCCO, F., L. BOITANI, D.H. PLETSCHER, AND M.K. SCHWARTZ. 2010. Bridging the gaps between noninvasive genetic sampling and population parameter estimation. European Journal of Wildlife Research 57:1–13.
- MILLS, L.S., J.J. CITTA, K.P. LAIR, M.K. SCHWARTZ, AND D.A. TALLMON. 2000. Estimating animal abundance using noninvasive DNA sampling: Promise and pitfalls. Ecological Applications 10:283–294.
- MOWAT, G., AND C. STROBECK. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark–recapture analysis. Journal of Wildlife Management 64:183–193.
- MULDERS, R., J. BOULANGER, AND D. PAETKAU, 2007. Estimation of population size for wolverines *Gulo gulo* at Daring Lake, Northwest Territories, using DNA based mark–recapture methods. Wildlife Biology 13:38–51.
- MUMMA, M.A., C. ZIEMINSKI, T.K. FULLER, S.P. MAHONEY, AND L.P. WAITS. 2015. Evaluating noninvasive genetic sampling techniques to estimate large carnivore abundance. Molecular Ecology Resources 15:1133–1144.
- NOYCE, K.V., AND D.L. GARSHELIS. 1997. Influence of natural food abundance on black bear harvests in Minnesota. Journal of Wildlife Management 61:1067–1074.
- O'CONNELL, A.F., J.D. NICHOLS, AND K.U. KARANTH, editors. 2011. Camera traps in animal ecology: Methods and analyses. Springer Science & Business Media, Tokyo, Japan.
- RANSOM, J.I., AND B.S. CADE. 2009. Quantifying equid behavior—A research ethogram for free roaming feral horses: U.S. Geological Survey Techniques and Methods 2-A9, Reston, Virginia, USA. https://pubs.usgs.gov/tm/02a09/ pdf/TM2A9.pdf. Accessed 31 Jan 2020.
- ROGERS, L.L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monographs 97.

- SAWAYA, M.A., J.B. STETZ, A.P. CLEVENGER, M.L. GIBEAU, AND S.T. KALINOWSKI. 2012. Estimating grizzly and black bear population abundance and trend in Banff National Park using noninvasive genetic sampling. PLoS ONE 7:e34777. doi:10.1371/journal.pone.0034777.
- TREDICK, C.A., M.R. VAUGHAN, D.F. STAUFFER, S.L. SIMEK, AND T. EASON. 2007. Sub-sampling genetic data to estimate black bear population size: A case study. Ursus 18: 179–188.
- WEGAN, M.T., P.D. CURTIS, R.E. RAINBOLT, AND B. GARD-NER. 2012. Temporal sampling frame selection in DNAbased capture–mark–recapture investigations. Ursus 23: 42–51.
- WILTON, C.M., J. BERINGER, E.E. PUCKETT, L.S. EGGERT, AND J.L. BELANT. 2016. Spatiotemporal factors affecting detection of black bears during noninvasive capture–recapture surveys. Journal of Mammalogy 97:266–273.
- ——, E.E. PUCKETT, J. BERINGER, B. GARDNER, L.S. EGGERT, AND J.L. BELANT. 2014. Trap array configuration influences estimates and precision of black bear density and abundance. PLoS ONE 9:e111257. doi:10.1371/journal.pone.0111257.
- WOODS, J.G., D. PAETKAU, D. LEWIS, B.N. MCLELLAN, M. PROCTOR, AND C. STROBECK. 1999. Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616–27.
- YAMAUCHI, K., S. KURAKAKE, T. MOROSAWA, M. KONDO, R. UNO, T. YUASA, H. TSURUGA, H.B. TAMATE, AND M. YONEDA. 2014. A pilot study of the hair-trapping method in Asiatic black bears (*Ursus thibetanus*): Determination of optimal survey period for estimating population size. Mammal Study 39:191–200.

Received: August 10, 2018 Accepted: July 15, 2019 Associate Editor: C. Costello