



## **Do brown bears *Ursus arctos* avoid barbed wires deployed to obtain hair samples? A videographic assessment**

Authors: Wold, Katherine, Wirsing, Aaron J., and Quinn, Thomas P.

Source: Wildlife Biology, 2020(1)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00664>

---

BioOne Complete ([complete.BioOne.org](https://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](https://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.



# Do brown bears *Ursus arctos* avoid barbed wires deployed to obtain hair samples? A videographic assessment

Katherine Wold, Aaron J. Wirsing and Thomas P. Quinn

K. Wold (<https://orcid.org/0000-0001-8787-8040>) and T. P. Quinn (<https://orcid.org/0000-0003-3163-579X>) ✉ ([tquinn@uw.edu](mailto:tquinn@uw.edu)), School of Aquatic and Fishery Sciences, Univ. of Washington, Seattle, WA 98195, USA. – A. J. Wirsing (<https://orcid.org/0000-0001-8326-5394>), School of Environmental and Forest Sciences, Univ. of Washington, Seattle, WA, USA.

Studies of the movements and abundance of predators can reveal their ecological roles and facilitate their conservation. These studies rely increasingly on noninvasive methods such as hair collection and camera traps. Insights from hair sampling, however, may be compromised if collection devices elicit avoidance behavior. To determine the extent to which brown bears *Ursus arctos* avoided barbed wire deployed to collect hair samples, we paired two wires on each of six small streams with motion-activated video recorders in the Wood River system, southwestern Alaska, where bears prey on sockeye salmon *Oncorhynchus nerka*. Of 350 videos showing a bear approaching the wire with an unambiguous result, the bear contacted the wire in 80.9% and avoided it 19.1% of the approaches. Females more often avoided the wire than did males (39% versus 20%), and bears more frequently avoided the wire at night (23.6%) than during daytime (10.8%) and crepuscular (19.1%) periods. Other comparisons (bears in groups versus single bears, and adults versus cubs) were not significantly different. The high proportion of approaches that led to contact with the wire indicates that this hair-sampling method is generally successful. Our findings also suggest, however, that interpretation of data obtained from such sampling should consider the possibility of biases with respect to sex and time of day.

Keywords: barbed wire, bears, DNA, non-invasive sampling, sampling bias

Studying movements and populations of carnivores is key to understanding their roles in ecosystems and setting effective conservation policy. For many large carnivores such as bears *Ursus* spp., collection of movement and abundance data via direct observation or physical capture (e.g. for the purposes of tagging or telemetry) can be invasive (Cattet et al. 2008), time-consuming, expensive and requires skill and training (Cutler and Swann 1999), though the utility of these approaches been demonstrated repeatedly (Fortin et al. 2013a). Alternatively, noninvasive methods like hair or fecal sampling and camera traps can also reveal individual carnivore behavior and population processes (Mace et al. 1994, Boulanger et al. 2004, Wasser et al. 2011, Fortin et al. 2013b). The reliability of these techniques, however, depends on their ability to capture (detect) animals without bias (Waits and Paetkau 2005, Ebert et al. 2010, Kelly et al. 2012, Patkó et al. 2016). Thus, field assessments of carnivore capture success and heterogeneity are vital for validating

non-invasive sampling approaches that might be in lieu of, or as a complement to, invasive methods.

Hair snares, both baited (Woods et al. 1999, Shardlow and Hyatt 2013) and unbaited (Boulanger et al. 2008), and camera traps are commonly deployed to study bears, complementing information obtained from telemetry (Anderson and Lindzey 2003, Sand et al. 2005). In some areas, bait is not necessary to draw in bears for hair sampling. For example, unbaited wires deployed near streams with abundant Pacific salmon *Oncorhynchus* spp. spawning in them may yield many hair samples suitable for analysis (Beier et al. 2005, Quinn et al. 2014, Wirsing et al. 2018). Areas with a natural attractant such as salmon are favorable for non-invasive hair collection because they do not affect the distribution and movements of bears. However, the collection of hair samples from bears (and other animals) with wires might be compromised if individuals avoid the wires to any significant extent, and biased if the avoidance differs among individuals. Lamb et al. (2016), for instance, reported that female brown bears *U. arctos* were less represented among hair samples from rub trees relative to baited wire snares. Sawaya et al. (2012) found that hair traps under-sampled male brown bears but were efficient for female brown bears and black bears *Ursus americanus* of both sexes, whereas samples from rubs had

---

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <<http://creativecommons.org/licenses/by/4.0/>>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

high detection rates for brown bears of both sexes but low rates for black bears of both sexes. Male bears may avoid areas frequented by humans to a greater extent than females with cubs (Rode et al. 2006, Steyaert et al. 2016), thus the scent of humans around sampling sites might affect male sampling efficiency. Adult bears might also be more cautious around areas of human activity than sub-adults (Nellemann et al. 2007), and might also have experienced the wires in previous years, and so might more often avoid them. Bears might more often contact wires at night than during the day, when wires are presumably easier to see. Bears can forage on salmon successfully at night, but sub-adults and females with cubs may avoid nocturnal foraging because of the threat posed by socially dominant and potentially infanticidal adult males (Klinka and Reimchen 2002). By implication, subordinate individuals and females with young may be hyper-vigilant at night and less likely to make contact with wires. Finally, social interactions among groups of bears might make them more likely to contact wires than individual bears, but avoidance of the wire by one bear might make others less likely to contact it as well. Thus, there are many possible sources of bias in the collection rates of hair samples from wire snares.

The goal of this study was to examine the extent and patterns of wire avoidance by brown bears. To do so, we paired motion-activated video recorders with unbaited barbed wires, deployed along streams during the salmon spawning season in south-western Alaska. We determined the overall proportion of approaches by bears to the wires that resulted in apparent avoidance, and then tested the null hypotheses that avoidance was independent of the bear's sex, age class, group size and time of day.

## Methods

The data were collected as part of a long-term study of brown bear predation on sockeye salmon *Oncorhynchus nerka* at a series of streams in the Wood River system in Bristol Bay, Alaska (Quinn et al. 2001, 2017, Carlson et al. 2009). A preliminary study using still images paired with unbaited barbed wires deployed on six streams indicated some avoidance by bears (there were some images of a bear but no corresponding hair sample). However, the images revealed too little about bear behavior to test any predictions regarding factors that might influence avoidance (Quinn et al. 2014). In the summer of 2016, we set motion-activated cameras to record videos of bear behavior during the sockeye salmon spawning season (mid-June through late August) on six small streams flowing into Lake Aleknagik. The streams differ somewhat in width, depth and the density and timing of spawning by sockeye salmon but all are narrow and shallow enough to be suitable for wire deployment (Quinn et al. 2017, Wirsing et al. 2018).

Each stream had two barbed wires, at least several hundred meters apart, stretched between trees at a height of about 50–55 cm above the streambed (Wirsing et al. 2018). The cameras (Bushnell Trophy Cam HD) were attached to trees on the bank approximately 2 m above the ground using nylon straps. They were set to record 30 s videos and used infrared motion sensors to capture videos during periods of low light. The SD cards were collected and exchanged every other day.

The videos showed 885 encounters with brown bears (counting multiple bears as separate encounters). No black bears were detected but the cameras were often activated by birds (chiefly glaucous-winged gulls *Larus glaucescens*) but also moose *Alces alces*, in addition to the humans who came to check the wires every other day on five of the streams, and daily (for other sampling) on Hansen Creek. The appearance of humans was typically between 11:00 and 16:00 h. The streams are too small to support recreational fishing, and no humans other than our crew were detected on the videos. For each of the videos with brown bears, we recorded each bear's response to the barbed wire, as well as the stream, wire number, date, time of day, approximate age of the bear (adult, yearling cub or spring cub), the bear's sex (when possible) and group size. Time of day was later categorized as day, night, dawn and dusk, the latter being defined as 1 h before and after sunrise and sunset, respectively, using daily values for this latitude and longitude. At this latitude (59°3'N) and time of year, the days were long; for example, in July the average times of sunrise and sunset were 05:50 h and 23:25 h, and in August they were 06:55 h and 21:00 h.

Each bear's response to the wire was categorized based on interpretation of the videos to first determine whether it approached within ca 1 m of the wire or moved in a manner that could not be classified as an approach (i.e. visible but moved at the periphery of view and did not approach the wire). Approaches to the wire were categorized as physical contact (typically evident from movement of the wire and the bear) or apparent avoidance of the wire (abrupt retreat or sharp turn). Proportions of avoidances were compared between sexes, age categories, group sizes and times of day. For the purposes of this study, only data from bears that approached and then contacted or avoided the wire were used; other, ambiguous videos were not included in the analysis. When examining the behavior of bears in groups, each bear's approach, followed by contact or avoidance, was calculated as a separate event (i.e. one bear might contact the wire while others might not). Statistical significance was determined using Pearson's  $\chi^2$  tests to establish whether the proportion of avoidances differed with respect to the chosen variable (e.g. female versus male, solo versus group, etc.).

## Results

Among the 885 bears seen in videos, 367 were classified as approaching the wire. In the other videos, the bears were either moving in a direction that did not cause them to approach the wire ( $n=39$ ), or the images were not clear enough to determine whether or not it approached the wire ( $n=479$ ). Of the 367 videos showing approaches, in 17 it was ambiguous whether the bear contacted the wire or not. Of the 350 unambiguous approaches, 19.1% showed apparent avoidance and 80.9% resulted in contact with the wire (for examples, Fig. 1, 2; videos in Supplementary material Appendix 1 Fig. A1, A2). Our subsequent analyses compared subsets of the data to determine patterns of avoidance related to attributes of the bears or time of day. The contact rate among wires ranged from 60.7% to 100%, so at no wire did avoidance predominate.



Figure 1. Still image from a video (Supplementary material Video A1) showing a brown bear that apparently inspected and then walked away from a wire deployed to obtain hair samples on Hansen Creek, Alaska.

It was not always possible to determine sex due to the lighting, camera angle and bear position, but of the 350 approaches, 28 female and 90 male bears were identified. Females avoided the wire more often than did males (39.3% of interactions versus 20.0%; Table 1;  $\chi^2 = 4.29$ , 1 df,  $p = 0.038$ ). There were 274 videos containing adult bears (including those in which sex could not be determined) and 65 videos containing yearling and spring cubs. Adult bears avoided the wire in 21.2% of the approaches, whereas cubs avoided the wire in 12.3% of them (Table 1;  $\chi^2 = 2.63$ , 1 df,  $p = 0.10$ ). The videos showed 298 individual bears, and 52 in groups from 2 to 4 bears. Individual bears avoided the wire 20.5% of the time, whereas bears in groups avoided the wire in 11.5% of interactions (Table 1;  $\chi^2 = 2.28$ , 1 df,  $p = 0.13$ ). The bears were least often detected in the day (Fig. 3). Of the 350 approaches analyzed, 23.7% were during daylight, 17.1% at dusk, 44.9% at night and 14.3% at dawn, indicating a very low approach rate in the day. Bears avoided the wire in 10.8% of the approaches in the day, 19.1% during crepuscular periods combined (16.0% at dawn and 21.7% at dusk) and 23.6% at night (Table 1;  $\chi^2 = 7.32$ , 2 df,  $p = 0.026$ ).

## Discussion

The findings of this study supported the assumption that unbaited barbed wires deployed across salmon spawning streams can effectively obtain hair samples from brown bears. Most (80.9%) of the recorded approaches resulted in contact with the wire. By implication, wires deployed in this fashion support DNA-based analysis of bear distribution and abundance (Mowat and Strobeck 2000), and stable isotope assessment of bear diets (Ben-David et al. 2004, Adams et al. 2017). Yet, we also found patterns of wire avoidance that might result in some bias in samples collected in this manner.

Female bears avoided the wires more often than did males. This finding was unexpected because females often seem to be more tolerant of human-disturbed areas than males, and may even use human activity as a shield against male infanticide (Rode et al. 2006, Steyaert et al. 2016). Most females identified in videos were accompanied by cubs, which could make them warier of potential dangers while foraging in streams. For example, elk *Cervus canadensis* in Yellowstone National Park spent more time being vigilant



Figure 2. Still image from a video (Supplementary material Video A2) showing a brown bear that contacted a wire deployed to obtain hair samples while it was catching a sockeye salmon in Eagle Creek, Alaska.

Table 1. Numbers of videos ( $n=350$ ) showing an approach to the wire by brown bears *Ursus arctos*, separated by sex, age, group size, time of day and the % of approaches in which the bear avoided the wire. Sample sizes vary because in some cases the bear could be categorized in one way (e.g. adult versus cub) but not another (e.g. sex).

Category	Approaches	% contact
Female	28	60.7%
Male	90	80.0%
Adult	274	78.8%
Cub	65	87.7%
Individual	298	79.0%
Group	52	91.1%
Day	83	89.2%
Crepuscular	110	80.9%
Night	157	76.4%

while with their offspring (Wolff and Horn 2003). Female bears may not necessarily be more wire shy, but rather just more protective of their young around human structures. For example, female black bears with cubs avoided human structures more than did females without cubs (Evans et al. 2019). Interestingly, in 2016 almost twice as many female bears were identified by DNA samples compared to males (Wirsing et al. 2018). Thus, our findings here suggest that the bear population foraging and moving along the streams may be even more female-biased than was indicated by the DNA samples alone.

There was no significant difference in avoidance by adults compared to cubs, owing in part to the low power to detect a difference that resulted from the unbalanced sample size. Qualitatively, however, cubs tended to contact the wire more often than did adults, so this possible source of bias should be considered further. Cubs are less likely to have previous experience with wires than adults, giving them less opportunity to develop the wariness of human structures seen in mature bears (Ordiz et al. 2011). It is likely that many adults captured on camera had prior experience with the wires (wires on our focal streams have been present since 2012). However, most approaches resulted in contacts, and many bears have been detected in multiple years (Wirsing et al. 2018, and further unpublished data), so avoidance did not characterize the population. Individual bears avoided the wire slightly more often than bears in groups, but the samples were not balanced and the difference was not statistically significant. Most of the groups of bears were mothers with cubs, so interpretation of the proportion of contacts by cubs confounds interpretation of bears in groups. As with the effect of bear age, the possibility of a difference in probability of contact, and hence having a hair sample collected, as a function of group size nevertheless warrants further scrutiny.

We detected significant diel patterns in both bear activity and likelihood of contacting the wire for a given approach. Of all 350 detections, only 14.9% were between 08:00 and 21:00 h (Fig. 3), consistent with previous work at these locations (Quinn et al. 2014). Elsewhere, in areas with negligible human activity, brown bears foraged during the day, but in areas with frequent or increasing human activity, bears foraged more often in the crepuscular period (Olson et al. 1998). Martin et al. (2010) also found that female brown bears commonly avoided creeks during daylight in areas with heavy human presence. However, in forested areas of

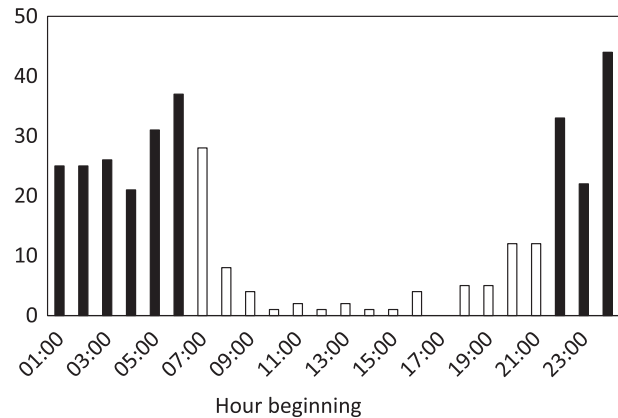


Figure 3. Histogram displaying the number of videos captured of 350 brown bears throughout the 24-h day as they approached barbed wire hair snares. Black bars represent night time and white bars represent daytime based on the day length during the sampling period.

Sweden, female brown bears rested in the day and foraged at night and in crepuscular periods (Moe et al. 2007), so to some extent this may be the natural pattern, though it can be magnified by human activity. The streams that we sampled are too small for any recreational fishing and there are no human residences along the streams, but the lake itself has considerable boating activity and there are some houses along the shoreline. The wires were all well upstream of the lake, so our own visitation to check the wires and cameras, and for other sampling, was essentially the only human presence on the streams. Our activity was limited to mid-day (generally about 11:00–16:00 h), so it is not possible to know what the patterns would have been had we not visited the streams at all.

Regardless of the causes of the diel activity patterns of the bears, time of day strongly affected the probability of wire avoidance. Despite the lower light levels, bears avoided the wire in 23.6% of interactions at night, compared to 10.8% of interactions during the day and 19.1% in crepuscular periods (Table 1). Interpretation of this result is complicated by possible interactions with the sex and maturity stage of the bear, and our sample size did not permit rigorous consideration of all these factors. Regardless of the explanation, the results indicate that factors linked to diel activity might also be associated with variation in wire avoidance, and by extension hair sampling probability.

Wire and camera placement seemed to affect the quality of observations and apparent rate of avoidance. At some sites the camera was pointed directly at the wire, which was helpful in determining if the bear contacted the wire, but likely missed bears that stopped farther downstream, out of camera view. Moreover, while habitat variables were too complex and numerous to permit rigorous analysis, wire placement seemed to affect the probability of wire contact. Where wires were placed above shallow areas of the creek with low gradient edges, we observed bears stepping up on the bank and walking around the wire, whereas in more confined areas the bears less often ascended the bank and more often contacted the wire. However, contacts exceeded avoidances at all wires so site-specific attributes did not undermine the overall effectiveness of the methodology.

In summary, our results showed that brown bears infrequently avoided unbaited wires deployed across shallow salmon-bearing streams for hair collection. Not surprisingly, therefore, the wires we have deployed as part of our ongoing study of bear–salmon interactions in south-western Alaska have yielded many hundreds of samples suitable for genetic population estimation (Wirsing et al. 2018) and stable isotope analysis (unpublished data). Salmon and bear populations are tightly linked, so greater knowledge of bear abundance, movements, and diets helps to understand the ways in which bears affect salmon population dynamics (Quinn et al. 2017) and evolution (Carlson et al. 2009), and nutrient flow in this ecosystem (Quinn et al. 2009), and other ecosystems (Hilderbrand et al. 1999, Helfield and Naiman 2006, Matsubayashi et al. 2015, Reimchen 2017, Deacy et al. 2019). Yet, our data also revealed that the wires did not sample bears uniformly with respect to sex and time of day, and possibly some interaction between group size and age. Consequently, interpretation of data from such samples should be appropriately cautious, particularly regarding conclusions that might be affected by the kinds of bias detected here such as sex ratio. Future studies with larger and more balanced sample sizes with respect to sex, age, time of day, group size, terrain around the wire, and other variables might support more extensive modeling to fully explore these patterns.

*Acknowledgements* – We especially thank Blakeley Adkins, Michael Tillotson, Catherine Austin and Anne Hilborn for help deploying the wires and cameras, and Chris Boatright and Jackie Carter for their coordination of the Aleknagik field camp. Alex Lincoln and Martini Arostegui assisted in manuscript preparation.

*Permissions* – The sampling was permitted by the University of Washington's Institutional Animal Care and Use Committee, and the Alaska Department of Fish and Game.

## References

- Adams, M. S. et al. 2017. Intrapopulation diversity in isotopic niche over landscapes: spatial patterns inform conservation of bear–salmon systems. – *Ecosphere* 8: e01843.
- Anderson, C. R. and Lindzey, F. G. 2003. Estimating cougar predation rates from GPS location clusters. – *J. Wildl. Manage.* 67: 307–316.
- Beier, L. R. et al. 2005. From the field: a single-catch snare to collect brown bear hair for genetic mark–recapture studies. – *Wildl. Soc. Bull.* 33: 766–773.
- Ben-David, M. et al. 2004. Consumption of salmon by Alaskan brown bears: a tradeoff between nutritional requirements and the risk of infanticide? – *Oecologia* 138: 465–474.
- Boulanger, J. et al. 2004. Monitoring of grizzly bear population trends and demography using DNA mark–recapture methods in the Owikeno Lake area of British Columbia. – *Can. J. Zool.* 82: 1267–1277.
- Boulanger, J. et al. 2008. Multiple data sources improve DNA-based mark–recapture population estimates of grizzly bears. – *Ecol. Appl.* 18: 577–589.
- Carlson, S. M. et al. 2009. Does variation in selection imposed by bears drive divergence among populations in the size and shape of sockeye salmon? – *Evolution* 63: 1244–1261.
- Cattet, M. et al. 2008. An evaluation of long-term capture effects in ursids: implications for wildlife welfare and research. – *J. Mammal.* 89: 973–990.
- Cutler, T. L. and Swann, D. E. 1999. Using remote photography in wildlife ecology: a review. – *Wildl. Soc. Bull.* 27: 571–581.
- Deacy, W. W. et al. 2019. Variation in spawning phenology within salmon populations influences landscape-level patterns of brown bear activity. – *Ecosphere* 10: e02575.
- Ebert, C. et al. 2010. Individual heterogeneity as a pitfall in population estimates based on non-invasive genetic sampling: a review and recommendations. – *Wildl. Biol.* 16: 225–240.
- Evans, M. J. et al. 2019. Hourly movement decisions indicate how a large carnivore inhabits developed landscapes. – *Oecologia* 190: 11–23.
- Fortin, J. K. et al. 2013a. Temporal niche switching by grizzly bears but not American black bears in Yellowstone National Park. – *J. Mammal.* 94: 833–844.
- Fortin, J. K. et al. 2013b. Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. – *J. Wildl. Manage.* 77: 270–281.
- Helfield, J. M. and Naiman, R. J. 2006. Keystone interactions: salmon and bear in riparian forests of Alaska. – *Ecosystems* 9: 167–180.
- Hilderbrand, G. V. et al. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. – *Oecologia* 121: 546–550.
- Kelly, M. J. et al. 2012. Noninvasive sampling for carnivores. – In: Boitani, L. and Powell, R. A. (eds), *Carnivore ecology and conservation: a handbook of techniques*, Oxford Univ. Press, pp. 47–69.
- Klinka, D. R. and Reimchen, T. E. 2002. Nocturnal and diurnal foraging behavior of brown bears (*Ursus arctos*) on a salmon stream in coastal British Columbia. – *Can. J. Zool.* 80: 1317–1322.
- Lamb, C. T. et al. 2016. Factors influencing detection of grizzly bears at genetic sampling sites. – *Ursus* 27: 31–44.
- Mace, R. D. et al. 1994. Estimating grizzly bear population size using camera sightings. – *Wildl. Soc. Bull.* 22: 74–83.
- Martin, J. et al. 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). – *Can. J. Zool.* 88: 875–883.
- Matsubayashi, J. et al. 2015. Major decline in marine and terrestrial animal consumption by brown bears (*Ursus arctos*). – *Sci. Rep.* 5: 9203.
- Moe, T. F. et al. 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). – *Can. J. Zool.* 85: 518–525.
- Mowat, G. and Strobeck, C. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling and mark–recapture analysis. – *J. Wildl. Manage.* 64: 183–193.
- Nellemann, C. et al. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. – *Biol. Conserv.* 138: 157–165.
- Olson, T. L. et al. 1998. Brown bear diurnal activity and human use: a comparison of two salmon streams. – *Ursus* 10: 547–555.
- Ordiz, A. et al. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. – *Oecologia* 166: 59–67.
- Patkó, L. et al. 2016. Even a hair casts its shadow: review and testing of noninvasive hair collecting methods of carnivore species. – *North-West J. Zool.* 12: 130–140.
- Quinn, T. P. et al. 2001. Influence of breeding habitat on bear predation, and age at maturity and sexual dimorphism of sockeye salmon populations. – *Can. J. Zool.* 79: 1782–1793.
- Quinn, T. P. et al. 2009. Transportation of Pacific salmon carcasses from streams to riparian forests by bears. – *Can. J. Zool.* 87: 195–203.
- Quinn, T. P. et al. 2014. Complementary use of motion-activated cameras and unbaited wire snares for DNA sampling reveals diel and seasonal activity patterns of brown bears (*Ursus arctos*)

- foraging on adult sockeye salmon (*Oncorhynchus nerka*). – Can. J. Zool. 92: 893–903.
- Quinn, T. P. et al. 2017. Diverse foraging opportunities drive the functional response of local and landscape-scale bear predation on Pacific salmon. – *Oecologia* 183: 415–429.
- Reimchen, T. E. 2017. Diverse ecological pathways of salmon nutrients through an intact marine–terrestrial interface. – *Can. Field-Nat.* 131: 350–368.
- Rode, K. D. et al. 2006. Sexual dimorphism, reproductive strategy and human activities determine resource use by brown bears. – *Ecology* 87: 2636–46.
- Sand, H. et al. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf – ungulate ecosystems. – *Wildl. Soc. Bull.* 33: 914–925.
- Sawaya, M. A. et al. 2012. Estimating grizzly and black bear population abundance and trend in Banff National Park using noninvasive genetic sampling. – *PLoS One* 7: e34777.
- Shardlow, T. F. and Hyatt, K. D. 2013. Quantifying associations of large vertebrates with salmon in riparian areas of British Columbia streams by means of camera-traps, bait stations and hair samples. – *Ecol. Indic.* 27: 97–107.
- Steyaert, S. M. J. G. et al. 2016. Human shields mediate sexual conflict in a top predator. – *Proc. R. Soc. B* 283: 20160906.
- Waits, L. P. and Paetkau, D. 2005. Noninvasive sampling tools for wildlife biologists: a review of applications and recommendations for accurate data collection. – *J. Wildl. Manage.* 69: 1419–1433.
- Wasser, S. et al. 2011. The influences of wolf predation, habitat loss and human activity on caribou and moose in the Alberta oil sands. – *Front. Ecol. Environ.* 9: 546–551.
- Wirsiing, A. J. et al. 2018. Alaskan brown bears (*Ursus arctos*) aggregate and display fidelity to foraging neighborhoods while preying on Pacific salmon along small streams. – *Ecol. Evol.* 8: 9048–9061.
- Wolff, J. O. and Horn, T. V. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. – *Can. J. Zool.* 81: 266–271.
- Woods, J. G. et al. 1999. Genetic tagging of free-ranging black and brown bears. – *Wildl. Soc. Bull.* 27: 616–627.

Supplementary material (available online as Appendix wlb-00664 at <[www.wildlifebiology.org/appendix/wlb-00664](http://www.wildlifebiology.org/appendix/wlb-00664)>). Video 1–4.