Human–Wildlife Interactions 11(2):192–207, Fall 2017

Humans as prey: coping with large carnivore attacks using a predator–prey interaction perspective

Vincenzo Penteriani[1], Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University - Campus Mieres, 33600 Mieres, Spain, and Department of Conservation Biology, Estación Biológica de Doñana, C.S.I.C., c/Américo Vespucio s/n, 41092 Seville, Spain *penteriani@ebd.csic.es*

Giulia Bombieri[1], Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University - Campus Mieres, 33600 Mieres, Spain

José María Fedriani, Centre for Applied Ecology "Prof. Baeta Neves," Institute Superior of Agronomy, University of Lisbon, Tapada da Ajuda, 1349-017 Lisboa, Portugal

José Vicente López-Bao, Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University - Campus Mieres, 33600 Mieres, Spain, and Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, 73091 Riddarhyttan, Sweden

Pedro José Garrote, Centre for Applied Ecology "Prof. Baeta Neves," Institute Superior of Agronomy, University of Lisbon, Tapada da Ajuda, 1349-017 Lisboa, Portugal

Luca Francesco Russo, Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University - Campus Mieres, 33600 Mieres, Spain

María del Mar Delgado, Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University - Campus Mieres, 33600 Mieres, Spain

Abstract: The number of attacks on humans by large carnivores in North America is increasing. A better understanding of the factors triggering such attacks is critical to mitigating the risk of future encounters in landscapes where humans and large carnivores coexist. Since 1955, of the 632 attacks on humans by large carnivores, 106 (17%) involved predation. We draw on concepts and empirical evidence from the Predator–Prey Interaction Theory to provide insights into how to reduce predatory attacks and, thus, improve human–large carnivore coexistence. Because large carnivore-caused mortality risks for humans are comparable to those shown by other mammal species in response to predation risk, framing predatory attacks under a theory underpinning predator–prey interactions may represent a powerful tool for minimizing large carnivore attacks. Most large carnivores have marked crepuscular and nocturnal activity; by minimizing outdoor activities in high-risk areas from sunset to sunrise, humans could reduce the number of predatory attacks. The most effective way in which prey avoid predation, but still utilize risky areas, is by adopting temporal changes in activity patterns. The human age groups most often targeted by large carnivores are essentially the same as when predators in general search for prey, namely the youngest individuals. Thus, increased parental vigilance and education for children may be a key factor to reduce predatory attacks. Lastly, because group size can affect predator–prey encounter rates and outcomes in different ways, large groups of people can decrease predation rates. Many humans may no longer consider predation by large carnivores to be a logical or plausible consequence of our predator-naïve behavior because humans now only occasionally represent prey for such species. However, the solution to the conflicts represented by large carnivore attacks on humans requires the implementation of correct strategies to face these rare events.

Key words: bear, *Canis latrans*, *Canis lupus*, cougar, coyote, grey wolf, human–wildlife conflicts, large carnivores, predation, predator–prey interactions, *Puma concolor*, *Ursus americanus*, *Ursus arctos horribilis*, *Ursus maritimus*

Large predator attacks on humans are increasing (Conover 2002, Ferretti et al. 2015, Fukuda et al. 2015, Penteriani et al. 2016). The increased incidences have been attributed to ever-increasing encroachment of humans into areas inhabited by large carnivores (Penteriani et al. 2016). Since 1955, >600 attacks by 6 large carnivores (i.e., grizzlies [*Ursus arctos horribilis*], black bears [*Ursus americanus*], polar bears [*Ursus maritimus*], cougars [*Puma concolor*], grey wolves [*Canis lupus*], and coyotes [*Canis latrans*]) have been reported in North America

[1]These authors contributed equally to this work.

(Penteriani et al. 2016). Almost half of the well-documented attacks were triggered by what is considered by some to be inappropriate human behaviors (Penteriani et al. 2016). After decades of a lack of coexistence between humans and large carnivores in many regions of developed countries, where large carnivores were intensively hunted in the past and are now recovering (Chapron et al. 2014), people may lack the necessary knowledge about how to avoid aggressive encounters with large carnivores and what to do when these occur.

Evolutionary theory suggests that humans have been biologically selected for their capacity to survive environmental threats (Silove 1998). Archaic neurobehavioral survival mechanisms (i.e., those behaviors that allowed humans to survive in predator-rich environments at the beginnings of the history of humanity) may have been particularly effective in protecting hominins in early ecosystems where they would regularly encounter and compete with large carnivores and other predators for food and shelter (Silove 1998). However, human evolution in the continually more technological environments of developed countries may have gradually precipitated the loss of many survival mechanisms (or diminished them at least).

The increased incidences of large carnivore attacks on humans in recent decades (Ferretti et al. 2015, Fukuda et al. 2015, Penteriani et al. 2016), coupled with increased encroachment of humans into areas inhabited by large carnivores, suggests it is reasonable to expect a further increase in attacks in the near future. Thus, it is imperative to understand the main factors contributing to these attacks, as well as risky scenarios, to develop best management practices that can be implemented to reduce the number of large carnivore attacks on humans.

Humans are not the only victims in large carnivore attacks. When attacks occur, the large carnivores responsible are generally removed from the population. Lethal removal of the individual responsible for the attack is an effective intervention in preventing future attacks by a given individual. However, because of the attack, negative attitudes toward these species may be reinforced (Conover 2008). If large carnivore lethal removal campaigns are instituted after an attack occurs, these actions can have long-term conservation consequences for the species.

Large carnivore population decline due to human lethal control may reconfigure the biological diversity in the affected systems (Ordiz et al. 2013). The interactive effects of large carnivores in ecosystems may drive trophic cascades (e.g., Werner and Peacor 2003, Mech 2012, Ordiz et al. 2013). Thus, we are now faced with a classic “Propositio de lupo et capra et fasciculo cauli,” or “running with the hare and hunting with the hounds” problem: to find an equitable solution for 2 apparently competing sides at the same time—human safety and human–large carnivore coexistence.

Here, we focus on a specific type of attack by 6 species of North American large carnivore (Figure 1), the so-called predatory attacks (i.e., incidents where humans were attacked and/or killed with the presumed purpose of being consumed; Penteriani et al. 2016). Specifically, we draw on concepts and empirical evidence from Predator–Prey Interaction Theory to gain insights into how to reduce predatory attacks (Berryman 1992, Abrams 2000). As the effects of large carnivore-caused mortality risk in humans are comparable to those shown by other mammal species in response to predation risk, we propose that framing predatory attacks under such a theory may represent a powerful tool for minimizing large carnivore attacks. Understanding the mechanisms behind these attacks on humans is therefore crucial to people’s safety, and education appears to be an effective win-win strategy to reduce this conflict (Redpath et al. 2013).

Methods

Literature search

Records of large carnivore attacks (i.e., attacks resulting in physical injury or death) on humans by the grizzly, black bear, polar bear, cougar, grey wolf, and coyote were collected for North America (the United States and Canada) and represent a subset of the entire database (632 attacks) used in Penteriani et al. (2016). These records were collected from unpublished reports, graduate dissertations and theses, webpages (last accessed in February 2016, but currently available at the specific addresses listed by species below), books, and scientific articles. In addition, we reviewed news reports from online newspapers. To find

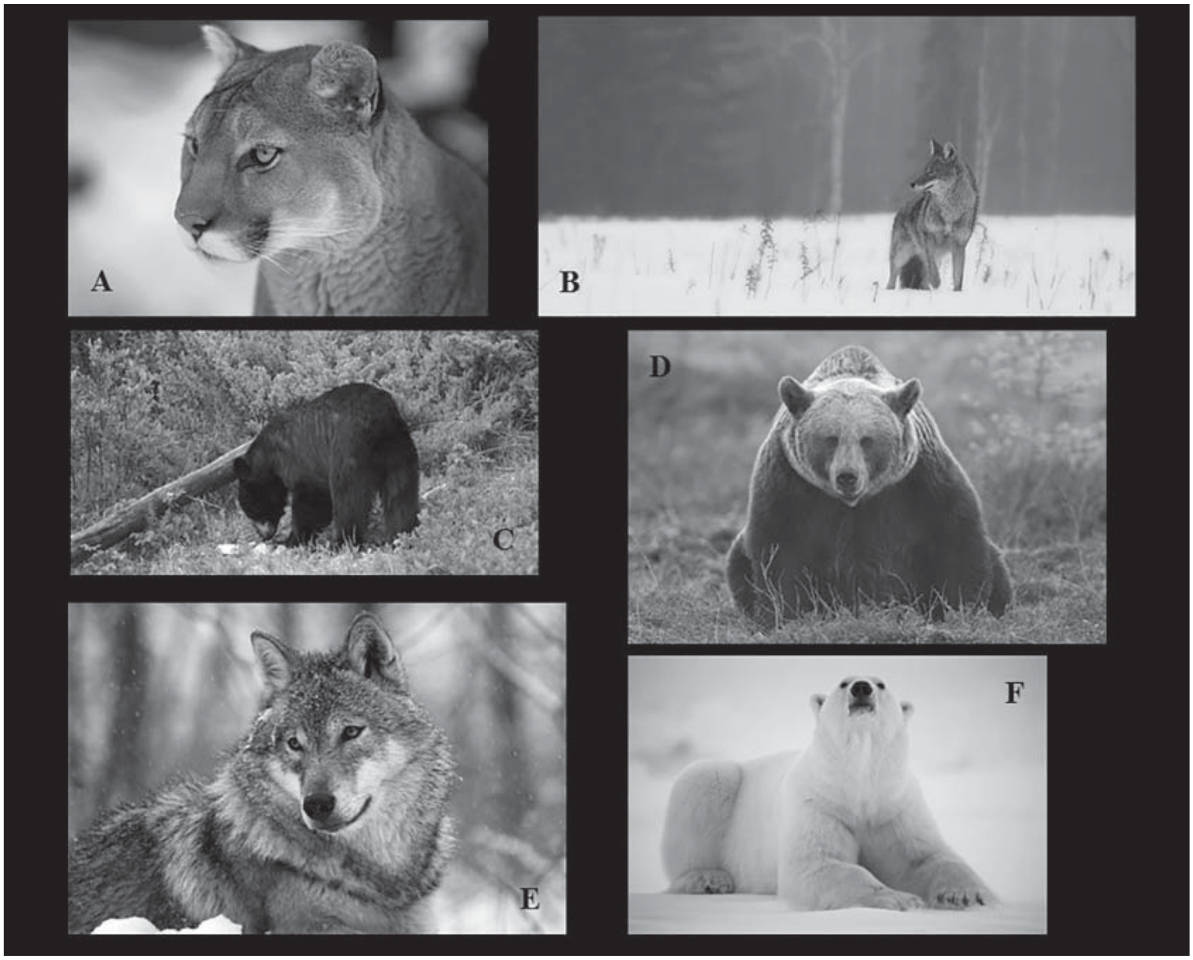

Figure 1. The 6 species of North American large carnivore considered in this study. Cougars (A) and coyotes (B) were responsible for most of the recorded predatory attacks since 1958, followed by black (C) and brown bears (D). The lowest rates of predatory attacks were recorded for grey wolves (E) and polar bears (F). *(Photos courtesy of: (A) L. Bystrom, <http://www.123rf.com>, Image ID 50597908; (B) L. Bystrom, <http://www.123rf.com>, Image ID 53790957; (C) V. Penteriani; (D) V. Penteriani; (E) Belizar, <http://www.123rf.com>, Image ID 12013462); and (F) W. Kaszkin, <http://www.123rf.com>, Image ID 8045876.)*

specific webpages on large carnivore attacks and online newspapers for each species, we searched on Google using the combination of the terms *species name* + *attack* and *species name* + *attack* + *human*. We limited our search to predatory events occurring during the last six decades, as information on attacks were scarce before the 1950s. Given the multiple sources of information used to collect recorded attacks and the sensational nature and media impacts of attacks that end with injury or death of the victim, the general patterns we evaluated are representative because we followed the same procedure for each species and, thus at a minimum, an equally biased sample of attacks for the 6 large carnivores. Because of the use of diverse sources of information, several attacks were reported in multiple sources during the search. Thus, we used information such as date, locality and sex/age of the victims to prevent duplicate records in the dataset. When possible, we recorded the following information for each attack: 1) species; 2) year; 3) month; 4) country; 5) time of the attack, which was classified into 3 categories: twilight, day, night; 6) composition of party attacked; and 7) outcome of the attack (i.e., attack resulting in human injury or death). Because each attack was generally reported by different sources of information, we were able to verify the quality of these reports by comparing them and only using the information that coincided between the different sources.

Species-specific sources on large carnivore attacks

Grizzlies and black bears. Information for both bear species was compiled from: 1) Herrero (2002); 2) List of fatal bear attacks in North America

(Wikipedia, <http://en.wikipedia.org/wiki/List_of_fatal_bear_attacks_in_North_America>, accessed January 6, 2016); 3) Fatal bear attack statistics for the USA and Canada (Black Bear Heaven, <http://www.blackbearheaven.com/bear-attack-statistics.htm>, accessed January 6, 2016); and 4) online newspapers. Additionally, we obtained information for the black bear from Herrero et al. (2011) and California black bear public safety incidents (California Department of Fish and Wildlife, <https://www.wildlife.ca.gov/News/Bear/Bear-Incidents>, accessed January 6, 2016).

Cougar. Data on attacks by this species were collected from: 1) Beier (1991); 2) Colorado Division of Wildlife (2011); 3) List of mountain lion attacks (Cougar Info, <http://www.cougarinfo.org/attacks.htm>, accessed January 6, 2016); 4) Mountain lion attacks from 1991 to 2000 (Cougar Info, <http://www.cougarinfo.org/attacks2.htm>, accessed January 6, 2016), Mountain lion attacks from 2001 to 2010 (Cougar Info, <http://www.cougarinfo.org/attacks3.htm>, accessed January 6, 2016), Mountain lion attacks from 2011 to now (Cougar Info, <http://www.cougarinfo.org/attacks4.htm>, accessed January 6, 2016); and 5) online newspapers.

Grey wolf. Data on these attacks were collected from: 1) Linnell et al. (2002); 2) McNay (2002); 3) List of wolf attacks in North America (Wikipedia, <http://en.wikipedia.org/wiki/List_of_wolf_attacks_in_North_America>, accessed January 6, 2016); 4) List of wolf attacks (Wikipedia, <http://en.wikipedia.org/wiki/List_of_wolf_attacks>, accessed January 6, 2016); 5) Wolf attacks on humans (Wolf Attacks on Humans, <http://www.aws.vcn.com/wolf_attacks_on_humans.html>, accessed January 6, 2016); and 6) online newspapers.

Coyote. Data on attacks by this species were collected from: 1) Timm et al. (2004); 2) Carbyn (1989); 3) Hsu and Hallagan (1996); 4) Nolte et al. (2007); 5) Coyote attacks on humans (Wikipedia, <http://en.wikipedia.org/wiki/Coyote_attacks_on_humans>, accessed January 6, 2016); 6) Coyote attacks on children (Varmint Al's, <http://www.varmintal.com/attac.htm>, accessed January 6, 2016); 7) Coyote attacks on people in the U.S. and Canada (T. Chester, <http://tchester.org/sgm/lists/coyote_attacks.html>, accessed January 6, 2016); and 8) online newspapers.

Polar bear. Information for this bear species was recorded from: 1) List of fatal bear attacks in North America (Wikipedia, <http://en.wikipedia.org/wiki/List_of_fatal_bear_attacks_in_North_America>, accessed January 6, 2016); and 2) online newspapers.

Selection of predatory attack incidents

To conduct our analysis, we selected true predatory attacks using a multistep process that first reviewed all the events that were described as predatory. In general, predatory attacks are recognizable because: 1) human victims are treated as food (i.e., the victim, still alive, is dragged by the large carnivore far from the attack point to a more concealed location such as bushes or within a forest patch); 2) the body is hidden and covered with leaves and soil (a behavior recorded for both live and dead victims); 3) the victim is partially consumed after their death; and/or 4) a large carnivore has been found near the body. However, within this larger sample, we did not consider incidents were there was no evidence that the body had been consumed immediately after the kill. Finding a body that is partially eaten days after the disappearance of a person could have been a scavenging event following a natural or accidental death not directly linked with a large carnivore. We then reviewed police reports of investigations and/or descriptions of the dynamic and context of each attack. These reports were crucial to determining if an attack could be considered a true predation attack.

Based on our review, we identified 106 cases (16.8% of the 632 attacks recorded by Penteriani et al. 2016) in which the victim was attacked and dragged, killed (or killed and dragged), and partially consumed after being killed. Cases of attacks reported as predatory but with no associated official reports or those lacking detailed descriptions were excluded from our analyses.

Data analysis

Considering the total dataset on predatory attacks reported since 1958, we first assessed the general patterns of this specific type of attack on humans (i.e., number of cases in the study's timeframe, killing rates, and predatory events per species). We then reviewed the reported diel patterns of predatory attacks, party size, and age structure of victims. Lastly, we evaluated the potential direction of changes in prey traits that might reduce prey vulnerability.

Results and discussion

General patterns

During the last 6 decades, humans were killed in 40% of the recorded predatory attacks (n = 106; Appendix A). Most attacks occurred during the day (64%), but many of them also occurred at twilight (30%) and at night (6%). Children between 1 and 10 years old, the youngest (and smallest-sized) individuals involved in outdoor leisure activities, represented the 54% (n = 56) of human victims in predatory attacks. In most (56%; n = 45) of the 80 predatory events in which the information on group size was available, the attack happened to a person who was alone (Appendix A).

Two of the 3 smallest species of large carnivores were responsible for 70% of the predatory attacks. Cougars (n = 53 predatory attacks; 50%) and coyotes (n = 21; 20%) played the leading roles, followed by black bears (n = 17), grizzlies (n = 8), grey wolves (n = 6), and polar bears (n = 1).

Theory application

Predator–prey interactions have shaped the lives of many animals on Earth as they represent a dominant force influencing the behavior and ecology of all animals (Pettorelli et al. 2015, Zanette and Sih 2015). Because humans can be potential prey, and predators do not regularly select their prey randomly, we propose that the theoretical framework of predator–prey interactions could guide us in reducing the number of predatory encounters between large carnivores and people, in turn improving coexistence.

The reaction of large carnivores to the increasing number of people engaged in outdoor activities shows a response (Figure 2) that is a function of the availability of naïve and "maladjusted" people behaving inappropriately (e.g., people leaving their children unattended or running at night in areas inhabited by large carnivores; Penteriani et al. 2016). This suggests that the number of predatory attacks may be growing in frequency due to the increase of inappropriate behaviors by people who currently live in ecosystems where large carnivores have been extirpated, are absent, or are in low numbers (e.g., urban habitats). In this regard, theory predicts that the absence of predator risk results in the relaxation of risk avoidance behavior (Tambling et al. 2015). In other words, currently, most people involved in outdoor activities are not used to sharing the landscape with large carnivores.

Diel patterns of predatory attacks: consequences for human activity

Predator avoidance and prey selection are concepts central to the theories underpinning our current understanding of predator–prey interactions (Pettorelli et al. 2015). To avoid being predated upon, prey can respond to predation risk in a myriad of ways (Lima and Dill 1990, Creel and Christianson 2008). For example, when predators and prey share the same landscape, prey often modify their habitat selection patterns (Fedriani et al. 2000, Sergio et al. 2007) and/or reduce their activity at the most risky times of the day (i.e., when predators are more active; Brown et al. 2001, Penteriani et al. 2013).

Prey diel patterns are thought to be the result of adaptations to diverse local selective pressures (Owen-Smith and Goodall 2014), including predation risk (Monterroso et al. 2013). Predation risk often declines when and where prey reduce their activity at the peak of predator activity or when and where they are most easily located and captured by potential predators (Caro 2005). When prey species share the landscape with large carnivores, they tend to be mostly diurnal, exhibiting increased nocturnal activity only when predation pressure is low (Tambling et al. 2015). These well-established mechanisms of predator avoidance could be applied to the case of humans as potential prey since most large carnivore species have marked crepuscular and nocturnal activity, especially in human-occupied habitats (Oriol-Cotterill et al. 2015).

Although most predatory attacks during the past 60 years occurred during the day (Appendix A), several of them also occurred at twilight and at night, when the presence of a large carnivore is more difficult to detect. By minimizing our outdoor activities from sunset to sunrise in high-risk areas, humans could potentially reduce the number of predatory attacks.

When humans become potential prey for large carnivores, they are also subject to the

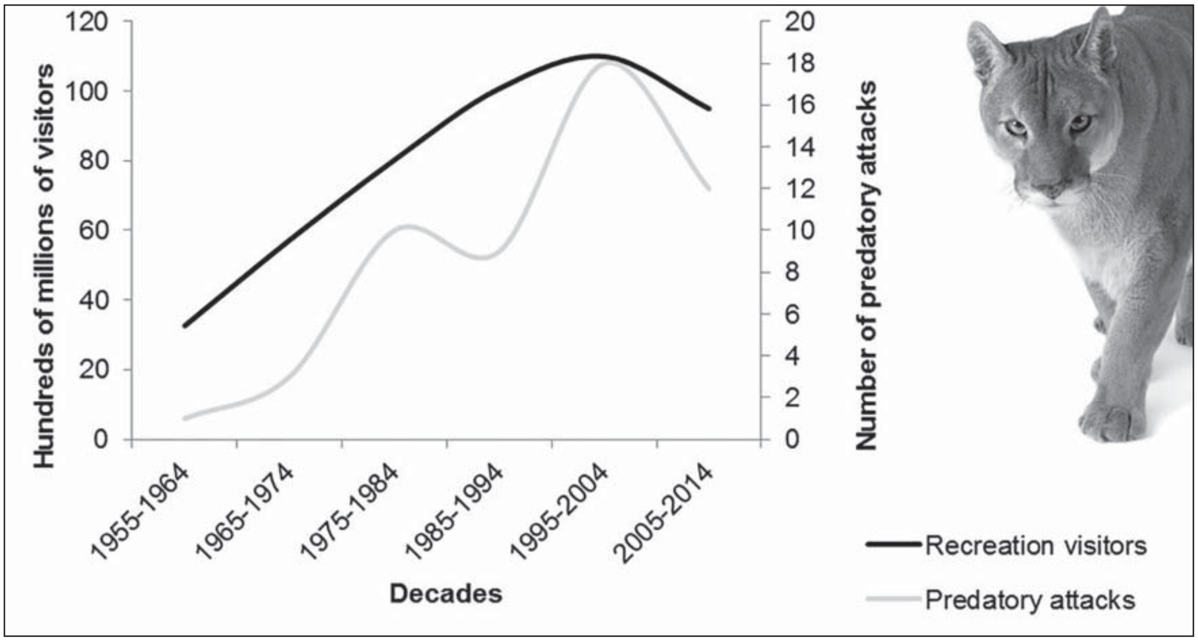

Figure 2. Number of visitors to North American protected areas and predatory attacks. The increasing trend of both the number of visitors to North American protected areas (data collected from National Park Service Visitor Use Statistics - IRMA data system, National Park Service, U.S. Department of the Interior, Natural Resource Stewardship and Science: <https://irma.nps.gov/Stats/Reports/National>, accessed January 6, 2016; more details in Penteriani et al. 2016) and predatory attacks by 6 species of North American large carnivore (grizzly, black bear, polar bear, cougar, grey wolf, and coyote) within protected areas. Coyote predatory attacks in urban habitats have been removed from this graph as they are independent of the number of visitors in protected areas *(cougar photo courtesy of Eric Isselee, <http://www.123rf.com>, Image ID 2598000).*

same landscape of fear that has been described for other prey species (i.e., the features of predation risk and associated antipredator behavioral responses that can be overlain on any heterogeneous landscape; Laundré et al. 2001). Putting our results into context, humans might schedule outdoor activities by copying what natural processes shaping predator–prey interactions have thus far shown us. The most effective way in which prey avoid predation, but still utilize risky areas, is by adopting temporal changes in activity patterns such as concentrating activities at times when carnivores are the least active (Oriol-Cotterill et al. 2015). Temporal adjustments will decrease the chance of risky situations without resigning our enjoyment of outdoor activities. Similarly, it is recommended to avoid habitat patches in which the detection of a large carnivore is only possible at short distances (e.g., dense forests and thick bushes).

Vigilance and group size

Vigilance represents another effective and frequent strategy adopted by prey under predation risk; that is, the behavioral response to the risk of predation is measurable as an increase in time allocated to vigilance (Hunter and Skinner 1998, Hochman and Kotler 2006, Pays et al. 2012). This aspect of the predator–prey relationship appears to be overlooked when people are enjoying outdoor activities (Penteriani et al. 2016). When predators are faced with a choice of prey, classical optimal foraging models predict that predators maximize their rate of energy intake by selecting the most profitable food item available (FitzGibbon 1990). This is a crucial piece of the story because the human age groups most often targeted by large carnivores during predatory attacks are essentially the same as when predators in general search for prey, namely the youngest individuals (Figure 3; Appendix A). Thus, parental vigilance and education for children is crucial, which means that preventive strategies, like the campaigns on pool safety, may be a key factor to reduce predatory attacks (e.g., Nixon et al. 1986, Blum and Shield 2000, Stevenson et al. 2003, Terzidis et al. 2007).

The pattern showed by the composition of the group the victim was in during the time of the attack over the last few decades may represent

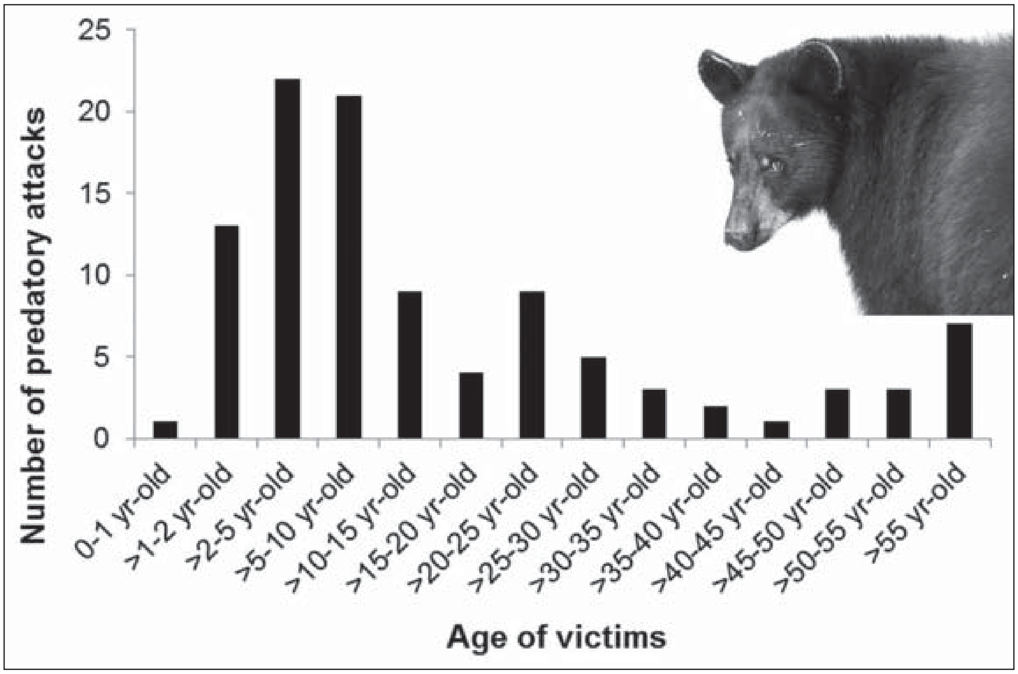

Figure 3. Predatory attacks and victim age. Predatory attacks by age of victim in 106 cases of attacks on humans as prey in North America from 1958 to 2014. As expected in predator–prey interactions, large carnivores tend to prey upon humans in the youngest age groups *(black bear photo courtesy of Belizar, <http://www.123rf.com>, Image ID 33366834).*

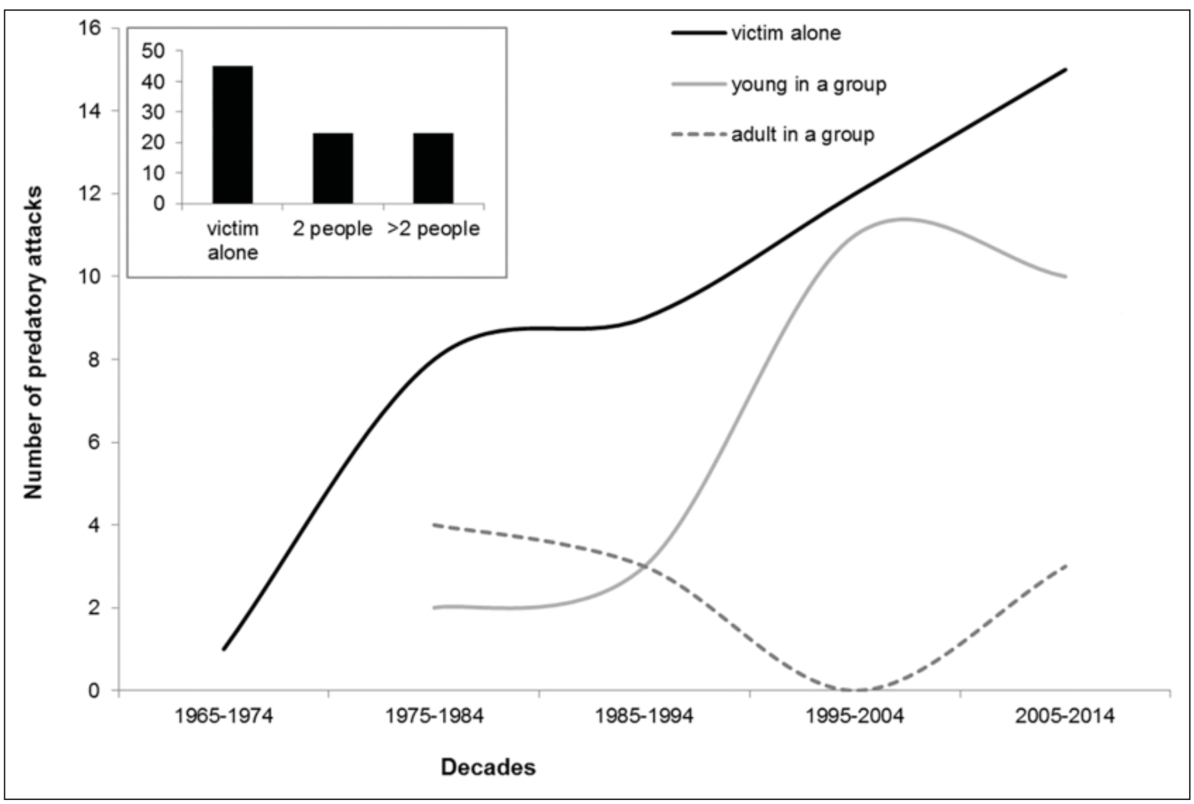

Figure 4. Targets of large carnivore predatory attacks. Over the last 5 decades, the proportion of lone individuals and young people have increased as the target of large carnivore predatory attacks, similarly to what occurs in predator–prey systems driven by size-selective predation. The small inset shows the percentage of predatory attacks in 3 levels of human party size.

important information to better understand and reduce predatory attacks (Figure 4). Predator–prey relationships indicate that group size can affect predator–prey encounter rates and outcomes in different ways (Oriol-Cotterill et al. 2015). Several studies support the suggestion that predators can increase their hunting success by selecting to hunt smaller prey groups (FitzGibbon 1990). The likelihood of detecting an approaching predator is greater for larger groups (the "many eyes effect;" Pulliam 1973) and the principle of dilution reduces each individual's chance of being caught. Thus, predators preferentially focus on isolated individuals or, again, the youngest ones within a group (FitzGibbon 1990). The same pattern has been observed for predatory attacks on humans (Figure 4): large carnivores increase their predation rates on lone individuals and children, which frequently happens when they are searching for more usual prey.

Unidirectional axis of prey vulnerability: how natural prey may reduce human predation risk

Abrams (2000) coined the phrase "unidirectional axis of prey vulnerability" to refer to the direction of changes in a prey's traits that reduce prey vulnerability (i.e., those features of a prey species that may reduce predation rate). This is appropriate, for example, if the focal trait is body size and the predator feeds most efficiently on prey within a limited size range (Mougi 2012; Figure 3).

Following Mougi's (2012) model on predator–prey dynamics, a theoretical model supports these previous considerations. Let's consider that a is the capture rate (i.e., the per capita rate at which a predator captures its prey), which is a function of the predator focal preference v (the size of the prey) and the prey defensive trait/behavior u—that is, $a(u - v)$, which is appropriate for size-specific predation. Specifically, a is a bell-shaped function $a = a_0 e^{-\theta(u-v)2}$, where a_0 is the maximum capture rate and θ is the shape parameter of the function. If the value of the prey's trait/behavior u is greater or smaller than that of the predator's preference v, the prey can effectively escape predation, so a is very small. In contrast, if the value of the predator's focal preference v is close to that of the prey's u, then the capture rate a is high (Mougi 2012). This specifically applies to the scenario that we previously highlighted: large predators prevalently focus their predatory attacks on the youngest individuals (Figures 3 and 4) and those who are unaccompanied (Figure 4). In other words, if the most targeted ages and party sizes increase when people are sharing the landscape with large carnivores, the efficiency of the latter will decrease because the abundance of their preferred prey will decrease. This effect can be practically obtained by preferentially favoring large party sizes (the less attacked groups of people, see Figure 4), composed of adult individuals (Figure 3). Additionally, when children are present, they should stay within the party and be under constant supervision; as previously remarked, wandering children are the most vulnerable to become prey.

Predator–prey interactions as an arms race

Dawkins and Krebs (1979) were among the first to present the current view of predator–prey coevolution as an arms race. Most interactions in nature are asymmetrical, and there is some evidence that predator–prey interactions are frequently characterized by greater responses of prey to predators than vice versa (Vermeij 1987). The response of prey to an improvement in a predator's ability to capture is more likely to be a decrease in its inherent vulnerability (Abrams 1990). In this victim–exploiter scenario, in which 1 species benefits at the expense of another species, the victim is expected to continuously evolve so as to decrease the strength of its interactions with predators. In addition, victims of antagonistic interactions are often thought to have a stronger incentive to win than their exploiters (Vermeij 1987), and the prey is able to escape if it matches the predator's strategy (Gavrilets 1987). Humans need to dive into a sort of arms race with large carnivores by modifying their behaviors on the basis of the knowledge of the factors that can increase the occurrence of a predatory attack.

Thus, it is reasonable to expect that people living in close contact with large carnivores have a high likelihood of having learned how to reduce risky situations with large carnivores and maintain such knowledge over time. Conversely, people sporadically moving from urban to natural areas may have learned everything on how to survive in a dangerous neighborhood or how to avoid being struck by a vehicle, but nothing on how to behave when visiting large carnivore areas. For this reason, we consider that specific information and prevention efforts should be especially directed toward urban populations. In addition, it is in cities and larger towns where most people are concentrated and, as a result, urban areas probably represent the major source of potential victims for large carnivore predatory attacks. Furthermore, large carnivore numbers are increasing in multi-use landscapes and suburban areas, where people may lack appropriate information on how to coexist with them.

Management implications

The study of predator–prey interactions offers wildlife managers and others some useful patterns, indicating that there are many circumstances under which a predator's optimal capture ability decreases when its prey becomes better at evading capture. For humans, simple changes in behavior remains the most efficient way to reduce the risk of large carnivore predatory attacks. Because humans may only represent occasional prey for large carnivores, many people may no longer consider predation by large carnivores to be a logical or plausible consequence of our predator-naïve behavior. For this reason, the solution to the conflict represented by large carnivore attacks on humans may be compared to an arms race, where humans evolve correct strategies to face these rare events. But, whatever these strategies, we must necessarily base our behavior on information, education, and prevention.

Acknowledgments

Three anonymous referees and T. Messmer provided very helpful suggestions that improved the manuscript.

Literature cited

Abrams, P. A. 1990. The evolution of antipredator traits in prey in response to evolutionary change in predators. Oikos 59:147–156.

Abrams, P. A. 2000. The evolution of predator-prey interactions: theory and evidence. Annual Review of Ecology, Evolution, and Systematics 31:79–105.

Beier, P. 1991. Cougar attacks on humans in the United States and Canada. Wildlife Society Bulletin 19:403–412.

Berryman, A. A. 1992. The origins and evolution of predator–prey theory. Ecology 73:1530–1535.

Blum, C., and J. Shield. 2000. Toddler drowning in domestic swimming pools. Injury Prevention 6:288–290.

Brown, J. S., B. P. Kotler, and A. Bouskila. 2001. Ecology of fear: foraging games between predators and prey with pulsed resources. Annales Zoologici Fennici 38:71–87.

Carbyn, L. N. 1989. Coyote attacks on children in western North America. Wildlife Society Bulletin 172:444–446.

Caro, T. M. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, Illinois, USA.

Chapron, G., P. Kaczensky, J. D. C. Linnell, M. von Arx, D. Huber, H. Andrén, J. V. López-Bao, M. Adamec, F. Álvares, O. Anders, L. Balčiauskas, V. Balys, P. Bedő, F. Bego, J. C. Blanco, U. Breitenmoser, H. Brøseth, L. Bufka, R. Bunikyte, P. Ciucci, A. Dutsov, T. Engleder, C. Fuxjäger, C. Groff, K. Holmala, B. Hoxha, Y. Iliopoulos, O. Ionescu, J. Jeremić, K. Jerina, G. Kluth, F. Knauer, I. Kojola, I. Kos, M. Krofel, J. Kubala, S. Kunovac, J. Kusak, M. Kutal, O. Liberg, A. Majić, P. Männil, R. Manz, E. Marboutin, F. Marucco, D. Melovski, K. Mersini, Y. Mertzanis, R. W. Mysłajek, S. Nowak, J. Odden, J. Ozolins, G. Palomero, M. Paunović, J. Persson, H. Potočnik, P.-Y. Quenette, G. Rauer, I. Reinhardt, R. Rigg, A. Ryser, V. Salvatori, T. Skrbinšek, A. Stojanov, J. E. Swenson, L. Szemethy, A. Trajçe, E. Tsingarska-Sedefcheva, M. Váňa, R. Veeroja, P. Wabakken, M. Wölfl, S. Wölfl, F. Zimmermann, D. Zlatanova, and L. Boitani. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517–1519.

Colorado Division of Wildlife. 2011. Reported lion attacks on humans, 1990 to present. Report n° 80216-1000, Denver, Colorado, USA.

Conover, M. R. 2002. Resolving human–wildlife conflicts: the science of wildlife damage management. Lewis Publishers, Boca Raton, Florida, USA.

Conover, M. R. 2008. Why are so many people attacked by predators? Human–Wildlife Conflicts 2:139–140.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23:194–201.

Dawkins, R., and J. R. Krebs. 1979. Arms races between and within species. Proceedings of the Royal Society of London B 202:489–511.

Fedriani J. M., T. H. Fuller, R. M. Sauvajot, and E. C. York. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

Ferretti, F., S. Jorgensen, T. K. Chapple, G. De Leo, and F. Micheli. 2015. Reconciling predator conservation with public safety. Frontiers in the Ecology and the Environment 13:412–417.

FitzGibbon, C. D. 1990. Why do hunting cheetahs prefer male gazelles? Animal Behaviour 40:837–845.

Fukuda, Y., C. Manolis, K. Saalfeld, and A. Zuur. 2015. Dead or alive? Factors affecting the survival of victims during attacks by saltwater crocodiles (*Crocodylus porosus*) in Australia. PLOS ONE 10(5): e0126778.

Gavrilets, S. 1997. Coevolutionary chase in exploiter-victim systems with polygenic characters. Journal of Theoretical Biology 186:527–534.

Herrero, S. 2002. Bear attacks: their causes and avoidance. Lyons Press, Guilford, Connecticut, USA.

Herrero, S., A. Higgins, J. E. Cardoza, L. I. Hajduk, and T.S. Smith. 2011. Fatal attacks by American black bear on people: 1900–2009. Journal of Wildlife Management 75:596–603.

Hochman, V., and B. P. Kotler. 2006. Patch use, apprehension, and vigilance behavior of Nubian ibex under perceived risk of predation. Behavioral Ecology 18:368–374.

Hsu, S.S., and L.F. Hallagan. 1996. Case report of a coyote attack in Yellowstone National Park. Wilderness and Environmental Medicine 2:170–172.

Hunter, L. T. B., and J. D. Skinner. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour 135:195–211.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk and bison: re-establishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1401–1409.

Lima, S. L., and L. M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and synthesis. Canadian Journal of Zoology 68:619–640.

Linnell, J. D. C., R. Andersen, Z. Andersone, L. Balciauskas, J. C. Blanco, L. Boitani, S. Brainerd, U. Breitenmoser, I. Kojola, O. Liberg, J. Løe, H. Okarma, H. C. Pedersen, C. Promberger, H. Sand. E. J. Solberg, H. Valdmann, and P. Wabakken. 2002. The fear of wolves: a review of wolf attacks on humans. NINA Oppdragsmelding 731, Norway.

McNay, M. E. 2002. A case history of wolf–human encounters in Alaska and Canada. Alaska Department of Fish and Game, Wildlife Technical Bulletin 13.

Mech, D. L. 2012. Is science in danger of sanctifying the wolf? Biological Conservation 150:143–149.

Monterroso, P., P. C. Alves, and P. Ferreras. 2013. Catch me if you can: diel activity patterns of mammalian prey and predators. Ethology 119:1044–1056.

Mougi, A. 2012. Predator–prey coevolution driven by size selective predation can cause anti-synchronized and cryptic population dynamics. Theoretical Population Biology 81:113–118.

Nixon, J., J. Pearn, I. Wilkey, and A. Corcoran. 1986. Fifteen years of child drowning—a 1967–1981 analysis of all fatal cases from the Brisbane drowning study and an 11 year study of consecutive near-drowning cases. Accident Analysis & Prevention 18:199–203.

Nolte, D. L., W. M. Arjo, and D. H. Stalman, editors. 2007. Proceedings of the 12th Wildlife Damage Management Conference. Wildlife Damage Management Working Group of The Wildlife Society, Corpus Christi, Texas, USA.

Ordiz, A., R. Bischof, and J. E. Swenson. 2013. Saving large carnivores, but losing the apex predator? Biological Conservation 168:128–133.

Oriol-Cotterill, A., M. Valeix, L. G. Frank, C. Riginos, and D. W. Macdonald. 2015. Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. Oikos 124:1263–1273.

Owen-Smith, N., and V. Goodall. 2014. Coping with savanna seasonality: comparative daily activity patterns of African ungulates as revealed by GPS telemetry. Journal of Zoology 293:181–191.

Pays, O., P. Blanchard, M. Valeix, S. Chamaillé-Jammes, P. Duncan, S. Périquet, M. Lombard, G. Ncube, T. Tarakini, E. Makuwe, and H. Fritz.

2012. Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. Oecologia 169:419–430.

Penteriani, V., M. M. Delgado, F. Pinchera, J. Naves, A. Fernández-Gil, I. Kojola, S. Härkönen, H. Norberg, J. Frank, J. M. Fedriani, V. Sahlén, O.-G. Støen, J. E. Swenson, P. Wabakken, M. Pellegrini, S. Herrero, and J. V. López-Bao. 2016. Human behaviour can trigger large carnivore attacks in developed countries. Scientific Reports 6:20552.

Penteriani, V., A. Kuparinen, M. M. Delgado, F. Palomares, J. V. López-Bao, J. M. Fedriani, J. Calzada, S. Moreno, R. Villafuerte, L. Campioni, and R. Lourenço. 2013. Responses of a top and a meso predator and their prey to moon phases. Oecologia 173:753–766.

Pettorelli, N., A. Hilborn, C. Duncan, and S. M. Durant. 2015. Individual variability: the missing component to our understanding of predator–prey interactions. Advances in Ecological Research 52:19–44.

Pulliam, H. R. 1973. On the advantages of flocking. Journal of Theoretical Biology 38:419–422.

Redpath, S. M., J. Young, A. Evely, W. M. Adams, W. J. Sutherland, A. Whitehouse, A. Amar, R. A. Lambert, J. D. Linnell, A. Watt, and R. J. Gutiérrez. 2013. Understanding and managing conservation conflicts. Trends in Ecology and Evolution 28:100–109.

Sergio, F., L. Marchesi, P. Pedrini, and V. Penteriani. 2007. Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? Animal Behaviour 74:1607–1616.

Silove, D. 1998. Is posttraumatic stress disorder an overlearned survival response? An evolutionary-learning Hypothesis. Psychiatry 61:181–190.

Stevenson, M. R., M. Rimajova, D. Edgecombe, and K. Vickery. 2003. Childhood drowning: barriers surrounding private swimming pools. Pedriatics 111:E115–119.

Tambling, C. J., L. Minnie, J. Meyer, E. W. Freeman, R. M. Santymire, J. Adendorff, and G. I. H. Kerley. 2015. Temporal shifts in activity of prey following large predator reintroductions. Behavioral Ecology and Sociobiology 69:1153–1161.

Terzidis, A., A. Koutroumpa, I. Skalkidis, I. Matzavakis, M. Malliori, C. E. Frangakis, C. DiScala, and E. Th. Petridou. 2007. Water safety: age-specific changes in knowledge and attitudes following a school-based intervention. Injury Prevention 13:120–124.

Timm, R. M., R. O. Baker, J. R. Bennett, and C. C. Coolahan. 2004. Coyote attacks: an increasing suburban problem. Transactions of the North American Wildlife and Natural Resources Conference 69:67–88.

Vermeij, G. J. 1987. Escalation and evolution. Harvard University Press, Cambridge, Massachusetts, USA.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100.

Zanette, L., and A. Sih. 2015. Gordon Research Conference on Predator–Prey Interactions: From genes, to ecosystems to human mental health. Bulletin of the Ecological Society of America 96:165–173.

Associate Editor: Terry A. Messmer

Appendix 1. Original database on predatory attacks (period 1958–2014), a subset of the whole database used by Penteriani et al. (2016).

Species	Year	Month	Country	Time of day[a]	Age of victim	Party composition[b]	Party composition1[c]	Party composition2[d]	End of attack[e]
Grizzly	1976	9	Alaska		25	5	1	1	3
Grizzly	1976	9	Montana	1	22	7	3	3	3
Grizzly	1980	7	Montana		19	6	2	3	3
Grizzly	1983	6	Montana	3	23	6	2	3	3
Grizzly	1984	7	Wyoming	3	25	5	1	1	3
Grizzly	2010	7	Montana		48	5	1	1	3
Grizzly	2011	8	Wyoming		59	5	1	1	3
Grizzly	2012	10	Alaska		54	5	1	1	3
Black bear	1958	8	Alberta	2	7	0	2		3
Black bear	1976	9	British Columbia	2	10	1	1	1	2
Black bear	1977	8	Alaska	2		5	1	1	2
Black bear	1978	5	Ontario	2	15	3	3	2	3
Black bear	1980	8	Alberta		44	5	1	1	3
Black bear	1980	8	Alberta	1	24	6	2	3	3
Black bear	1991	5	Alberta		12				3
Black bear	1991	10	Ontario		32	6	2	3	3
Black bear	1991	10	Ontario		48	6	2	3	3
Black bear	2000	5	Tennessee		50	5	1	1	3
Black bear	2002	8	New York		0,5	1	1	1	3
Black bear	2007	6	Utah		11	3	3	2	3
Black bear	2007	7	British Columbia		31	5	1	1	3
Black bear	2008	5	Quebec		70	5	1	1	3
Black bear	2011	6	British Columbia		72	5	1	1	3
Black bear	2013	6	Alaska		64	6	2	3	3
Black bear	2014	5	Alberta	2	36	7	3	3	3
Cougar	1970	6	Colorado	2	2	1	1	1	2
Cougar	1971	1	British Columbia		12	0	2		3

Appendix 1 continued on next page...

Appendix 1 continued.

Species	Year	Month	Country	Time of day[a]	Age of victim	Party composition[b]	Party composition1[c]	Party composition2[d]	End of attack[e]
Cougar	1974	1	New Mexico		8	0	2		3
Cougar	1976	7	British Columbia		26	5	1	1	3
Cougar	1976	7	British Columbia		7				3
Cougar	1976	12	Colorado	1	14				2
Cougar	1986	3	California	2	5	3	3	2	2
Cougar	1986	8	British Columbia	1	6				2
Cougar	1988	5	British Columbia		9				3
Cougar	1989	9	Montana	1	5	1	1	1	3
Cougar	1989		Arizona	1	5				2
Cougar	1991	1	Colorado	2	18	5	1	1	3
Cougar	1991	3	California		3	7	3	3	3
Cougar	1992	3	California	2	9	3	3	2	2
Cougar	1992	5	British Columbia	2	7	3	3	2	3
Cougar	1992	7	Washington		29	5	1	1	2
Cougar	1993		California						2
Cougar	1994	4	California	1	40	5	1	1	3
Cougar	1994	5	British Columbia	2	7	0	2		2
Cougar	1994	7	Arizona	2	2	1	1	1	2
Cougar	1994	12	California	1	56	5	1	1	3
Cougar	1994	12	Colorado	1	25	5	1	1	2
Cougar	1996	6	Colorado	2		5	1	1	2
Cougar	1996	7	British Columbia	2	8	3	3	2	2
Cougar	1996	8	British Columbia	1	6	3	3	2	3
Cougar	1997	7	Colorado	2	4	3	3	2	2
Cougar	1997	7	Colorado	2	10	1	1	1	3
Cougar	1997	10	Colorado	2	20	5	1	1	2
Cougar	1997	11	Utah	2	64	5	1	1	2
Cougar	1998	4	Colorado	2	24	5	1	1	2
Cougar	1998	7	Montana	2	6	3	3	2	2
Cougar	1998	8	Montana	2	6	0	3	2	2
Cougar	1998	8	Washington		5				2
Cougar	1999	8	Washington	2	4	1	1	1	2
Cougar	1999	9	Idaho	2	11	0	2		2
Cougar	2000	4	Arizona	1	4	3	3	2	2

Appendix 1 continued on next page...

Appendix 1 continued.

Species	Year	Month	Country	Time of day[a]	Age of victim	Party composition[b]	Party composition1[c]	Party composition2[d]	End of attack[e]
Cougar	2001	1	Alberta	2	30	5	1	1	3
Cougar	2001	2	British Columbia	2	52	5	1	1	2
Cougar	2002	6	British Columbia	2	8	0	2		2
Cougar	2004	1	California	2	30	5	1	1	2
Cougar	2004	8	Alberta	2	5	1	1	1	2
Cougar	2005	7	British Columbia	2	4	3	3	2	2
Cougar	2006	4	Colorado	1	7	3	3	2	2
Cougar	2006	8	British Columbia	1	4	2	2	2	2
Cougar	2007	8	British Columbia	1	12	1	1	1	2
Cougar	2007	1	California	2	70	6	2	3	2
Cougar	2008	5	New Mexico	2	5	3	3	2	2
Cougar	2008	6	New Mexico	3	55	5	1	1	3
Cougar	2008	9	Washington	2	11	0	2		2
Cougar	2009	9	Washington	2	5	3	3	2	2
Cougar	2011	8	British Columbia	2	1,6	3	3	2	2
Cougar	2011	9	Idaho	1	10	1	1	1	2
Cougar	2012	8	British Columbia	1	7	3	3	2	2
Grey wolf	1982	1	Minnesota		19	5	1	1	2
Grey wolf	1996		Ontario		12	3	3	2	2
Grey wolf	1998		Ontario		1,7	3	3	2	2
Grey wolf	2000	4	Alaska		6	0	2		2
Grey wolf	2005	11	Saskatch-ewan		22	5	1	1	3
Grey wolf	2010	3	Alaska		32	5	1	1	3
Coyote	1980	7	California		1,1	2	2	2	2
Coyote	1981	8	California	2	3	1	1	1	3
Coyote	1985	4	Alberta		2	1	1	1	2
Coyote	1985	8	Alberta		4	1	1	1	2
Coyote	1988	7	British Columbia		1,6	0	2		2
Coyote	1988	8	British Columbia		3				2
Coyote	1996	6	California		3	3	3	2	2

Appendix 1 continued on next page...

Appendix 1 continued.

Species	Year	Month	Country	Time of day[a]	Age of victim	Party composition[b]	Party composition1[c]	Party composition2[d]	End of attack[e]
Coyote	1998	7	Massachusetts		3				2
Coyote	2001	7	British Columbia	2	1,3	2	2	2	2
Coyote	2001	12	California		3				2
Coyote	2004	6	California	2	7				2
Coyote	2004	6	California	2	3				2
Coyote	2005	4	Alberta	2	3	0	2		2
Coyote	2005	4	Alberta	2	2,5	2	2	2	2
Coyote	2006	4	Washington		1,6	1	1	1	2
Coyote	2007	4	New Jersey	2	1,8	0	2		2
Coyote	2008	5	California	2	2	1	1	1	2
Coyote	2008	5	California		2	1	1	1	2
Coyote	2008	12	California		7				2
Coyote	2013	7	California	2	2	2	2	2	2
Coyote	2013	10	Colorado	3	22	5	1	1	2
Polar bear	1990	12	Alaska		28				3

[a] 1 = twilight; 2 = day; 3 = night
[b] 0 = young victim + other young people; 1 = young victim alone; 2 = young victim + 1 person; 3 = young victim + 2 or more people; 4 = adult victim + young people; 5 = adult victim alone; 6 = adult victim + 1 person; 7 = adult victim + 2 or more people
[c] 1 = victim alone (1+5 of [b]); 2 = 2 people (0+2+4+6); 3 = 3 or more people (3+7)
[d] 1 = victim alone; 2 = young victim in a group of adults (1 or more adults); 3 = adult victim in a group (1 or more adults)
[e] 2 = injury; 3 = death

Vincenzo Penteriani is a permanent researcher at the Spanish Council of Scientific Research (CSIC). He is currently working on brown bears in the Cantabrian Mountains (northwestern Spain; www.cantabrianbrown-bear.org). His professional interests include brown bear ecology and behavior in human-modified landscapes and large carnivore attacks on humans.

Giulia Bombieri is a doctoral researcher at the Research Unit of Biodiversity (UMIB, University of Oviedo, Spain), working on large carnivore attacks on humans on a worldwide scale.

José María Fedriani is a principal investigator at the Center for Applied Ecology/InBio (University of Lisbon, Portugal) and focuses his research on unraveling the ecological and microevolutive consequences of plant–animal interactions in humanized landscapes. He has also investigated competitive interactions (including intraguild predation) among mammalian carnivores, both in North America and Europe.

José Vicente López-Bao is a researcher fellow at the Research Unit in Biodiversity (UO-CSIC-PA), Oviedo University, Spain. His research interests include large carnivore conservation and management in human-dominated landscapes.

Pedro José Garrote earned his B.S. and M.S. degrees at the University of Pablo de Olavide from Seville. He has just started his Ph.D. degree in biology at the University of Lisbon (Portugal). His scientific interests include plant-animal (seed dispersal) and human–wildlife interactions.

Luca Francesco Russo graduated with a bachelor's degree in natural sciences at the University Federico II of Naples and obtained a master's degree in zoology at the Complutense University of Madrid (2015, Spain) and a master's degree in wildlife conservation at the University of Parma (2017, Italy). He is interested in vertebrates and, in particular, in carnivore conservation and human–wildlife conflicts.

María del Mar Delgado received her M.S. degree in biology from the University of Seville (Spain) and her Ph.D. degree in ecology from Biological Station of Doñana (CSIC, Spain). Her primary goal is to carry out multidisciplinary, synthetic ecological and evolutionary research to gain an integrated understanding of the structure and dynamics of natural populations and communities by combining rigorous statistical analyses and modelling with long-term population monitoring data and field experiment conditions.