

The hunting modes of human predation and potential nonconsumptive effects on animal populations

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ABSTRACT

When seeking prey, predators adaptively deploy strategies coarsely divided into sit-and-wait, sit-and-pursue, or active hunting modes. Though the hunting modes of many predators have been extensively studied, the implications of the hunting modes of human (*Homo sapiens*) predation are not yet fully understood. We conducted an extensive literature review to document human hunting modes and explore the ways in which these modes may shape animal populations via nonconsumptive effects (NCEs) of human predation. Among 167 studies published between 1972 and 2020, we found that humans used 27 hunting tools among 19 different hunting techniques when pursuing terrestrial prey. Most accounts described humans as using the active hunting mode (58%; $n = 140$ of 241), followed by the sit-and-wait hunting mode (41%; $n = 99$ of 241), and finally the sit-and-pursue hunting mode (2%; $n = 4$ of 241). While non-human predators tend to be evolutionarily adapted to the use of just one hunting mode, humans showed profound plasticity by deploying all three hunting modes in pursuit of prey species from 34 taxonomic orders spanning six orders of magnitude in body size (from 27 g to 4,400 kg). Considerable evidence has documented the vast number of ways in which humans directly impact the functioning of the natural world. Our research complements that work by demonstrating the indirect pathways by which humans may affect animal populations and the landscapes over which these interactions occur, via NCEs deriving from the hunting modes of human predation, with important implications for animal conservation.

Keywords: Conservation, Consumptive effects, Habitat domain, Human, Hunting Mode, Nonconsumptive effects, Predator-prey interactions

INTRODUCTION

Predation, though often defined more broadly, specifically describes an interspecies interaction in which all or a significant portion of the biomass of one species is consumed by the other (see Abrams 2000). The act of predation then, comprises not only the interactions of predators and their prey, as conventionally thought, but also host-parasitoid relationships and granivory, among others (Sih 1980; Frank 1994; Hulme and Benkman 2002). Within the context of the interactions of predators and prey, predation does not merely imply killing, but also prey consumption (Abrams 2000; Preisser et al. 2005). This detail is vital because it outlines the ways in which predator and prey fitness, demography, and population stability are linked and presents a foundation by which these factors can be mathematically predicted (Levin 1976; Peterson and Page 1988; Kareiva 1987; Arditi and Ginsburg 1989; Krebs et al. 2001). As prey are seeking to avoid being eaten, many navigate a series of costly tradeoffs to elude predators (Edmunds 1974; Relyea 2002; Werner and Peacor 2003). Adaptive traits in prey then often come in the form of defenses, whether they be behavioral or morphological, induced by previous encounters with predators (Harvell 1990; Barry 1994; Tollrian and Harvell 1999). Furthermore, as predators can trigger both consumptive and nonconsumptive effects (NCEs) in prey populations (Paine 1966; Sih et al. 1985; Abrams 1995; Schmitz and Suttle 2001; Say-Sallaz et al. 2019), the spatio-temporal configuration of predator-prey interactions have important implications for landscape composition via cascading mechanisms (Schmitz et al. 2004; Winnie and Creel 2017). Thus, predation is a formidable element capable of shaping the structure of predator-prey populations and the ecosystems over which interspecies interaction occur (Gould 1977; Dawkins and Krebs 1979; Taylor 1984; Luttbeg et al. 2020).

Seeking to maximize predation efficiency, predators have evolved the use of specific hunting modes (Schmitz 2005; Preisser et al. 2007). These modes describe the physical strategies that predators deploy in the pursuit of prey (Huey and Pianka 1981; Schoener 1971). Coarsely, there are three hunting modes that have evolved among predators including sit-and-wait, sit-and-pursue, and active (McLaughlin 1989; Schmitz 2007, 2008). Sit-and-wait, also referred to as ambush, predators remain still in habitat where the probability of encountering preferred prey is high, and strike when prey are within reach (e.g., Olive 1982). Sit-and-pursue predators also conceal themselves until prey are detected at which point they begin to pursue prey (i.e., stalk or chase; e.g., Thaker et al. 2011). Finally, the third hunting mode is the active form where a predator moves about the landscape in search of prey (e.g., Barton and Schmitz 2009). Predator species employing this hunting mode are often referred to as coursing hunters (MacNulty et al. 2007). Each hunting mode has adaptively evolved via some combination of predator life history characteristics, animal-habitat relationships, and previous predator-prey interactions (Carey and Wahl 2011; Belgrad and Griffen 2016). The spatio-temporal disbursement of predator cues varies according to each hunting mode with important implications for the nature and strength of the consumptive and NCEs of predation in the habitat domains within which these predator-prey interactions take place (Schmitz 2005; Preisser et al. 2007; Miller et al. 2014; Northfield et al. 2017; Schmitz et al. 2017). Given the veritable arms race that loosely describes predator-prey interactions (Dawkins and Krebs 1979; Sih 1984, 2005), the costs and benefits of these different hunting modes lie at the very heart of the evolution of social behavior for both predators and prey (Krebs and Davies 2009; Lima and Dill 1990).

Via the honing forces of evolution by natural selection, predators tend to deploy just one of these hunting modes (Schmitz 2008) though some have been found to be able to dynamically

switch among hunting modes in response to prevailing environmental conditions (Helman 1990; Scharf et al. 2006; Michael and Adams 2009; Donihue 2016). Extensive research has examined predator hunting modes across taxonomic orders (see Preisser et al. 2007). An important extension of this research is to consider the ways in which humans (*Homo sapiens*) contribute to the structuring of prey populations via hunting modes and the implications of such structuring on animal conservation. Such voracious predators, humans have actually been referred to as a *super* predator species (Darimont et al. 2015; Oriol-Cotterill et al. 2015a,b) in acknowledgement of their demonstrated ability to consume species at rates many times higher than any other non-human predator (Barnosky et al. 2012; Dirzo et al. 2014; McCauley et al. 2015). Importantly, the super predator descriptor is not entirely accurate given that this prevailing depiction captures human lethality not related to consumption (e.g., vehicle strikes, management culls, conflict killing; see Montgomery et al. 2020). Regardless of the fact that humans kill more often than they consume however, they remain a dominant predator on earth (Reznick et al. 1990; Palumbi 2001; Liberg et al. 2012; Milner-Gulland and Bennett 2003). Humans clearly hunt prey using a diversity of techniques (Fig. 1) though, it is not known exactly which hunting mode(s) humans employ. Pursuit of this research could reveal the complex pathways by which humans contribute to ecosystem structuring via the exertion of both consumptive and NCEs on prey populations.

We conducted a review of the peer-reviewed literature to quantify human hunting modes. While humans are capable predators across every biome where they occur on earth (Darimont et al. 2009), we focused our analysis on human hunting of animals in the terrestrial spatial domain. We made this distinction because of the large-scale machinery (e.g., trawling, longline, and trapping fishing vessels) that is common in aquatic ecosystems. Despite the fact that the application of such industrious technologies strains the description of hunting modes, our intent

was to examine human hunting rather than fishing. Among the resultant literature, we quantified the human hunting technique, the prey species pursued, and the location of the study. We then fit each hunting technique into one of the three hunting modes and discuss the spatial and contextual patterning that became evident. We discuss the implications of this research for the role of humans in trophic ecology, the potential NCEs on prey populations that can derive from human predation, and the management and conservation of animal populations in the geological epoch now widely referred to as the Anthropocene.

METHODS

Literature Review In March of 2020, we completed a review of peer-reviewed literature evaluating human predation of terrestrial animals. We executed our review in the Web of Science, Google Scholar, and JSTOR search engines via the application of the following terms; (human AND predator OR superpredator) AND (hunting OR poaching OR harvest OR trophy hunting OR consumptive OR subsistence). We note here that our central interest was to document the hunting modes used by humans when acting as predators. Thus, in line with the Abrams (2000) definition provided above, the purpose of human hunting must be to consume animal biomass. Thereby, we excluded from consideration instances in which humans kill animals, but consumption is not central. These include vehicle strikes, management culls, and human-animal conflict killings, to name a few. We did however, make one exception; trophy hunting. Trophy hunting refers to the killing of an animal for the purpose of harvesting specific morphological characteristics (Montgomery et al. 2020). Thus, consumption of the animal biomass is often a secondary motivation. However, while trophy hunting may not always be an act of human predation, it is certainly representative of an act of human hunting and therefore, worthy of our examination. We do acknowledge however, that other instances in which humans

kill animals may indeed trigger NCEs. While such a pursuit was beyond the scope of our investigation, we offer it as a future research thread that is certainly worthy of examination.

We assessed all literature resulting from this review and retained those studies with research objectives that were aligned with our analysis. We eliminated from consideration studies that did not include examples of hunting, mentioned hunting but the technique was not well-described, or studies that included hunting but did not specify the prey species. We then re-read all retained literature and recorded the: *i*) study objective, *ii*) location of the study system, *iii*) species of animal(s) hunted, and *iv*) description of the hunting technique(s). Depicting the location of the study spatially, we used a Chi-Squared test to assess the null hypothesis that the representation of human hunting modes would not vary by continent. Then, using the description of hunting technique and tools used, we then documented the specific hunting modes (e.g., sit-and-wait, sit-and-pursue, or active) deployed by humans in each of these studies. We note here that there were many instances in which a single study described multiple human hunting modes.

To evaluate patterns of association between the human hunting modes and the individual prey species selected, we recorded the body mass of each prey using the Phylogenetic Atlas of Mammal Macroecology (Faurby et al., 2018; 2019) and the CRC Handbook of Avian Body Masses (Dunning 2007). For reptiles and amphibians, we used average body mass estimates featured on websites for each specific species. We then compared the body mass of the prey species targeted by humans using box and whisker plots fit for each hunting mode.

RESULTS

A total of 675 studies were returned from our literature review. After removal of studies with inconsistent research objectives, we retained 167 studies (published between 1972 and 2020) for analysis. The location of this research exhibited a high degree of variability around the

world with the total number of study locations across continents exceeding the number of studies conducted, indicative of the fact that more than one study site could be described in a single publication ($n = 172$; Fig. 2). Approximately 28% ($n = 47$ of 169) of these studies were based in Europe, followed by North America (21%, $n = 35$), and Africa (21%, $n = 36$). Asia (15%, $n = 26$), South America (13%, $n = 22$), and Australia (1%, $n = 4$) had the least amount of research on human hunting in terrestrial ecosystems (Fig. 2). The Chi-Squared tests showed that the spatial configurations of research outputs documenting the active ($p < 0.001$) and sit-and-wait ($p < 0.001$) hunting modes were significantly different around the world while that of the sit-and-pursue hunting mode was not statistically different ($p = 0.08$).

Among this literature, we detected 800 instances of human hunting of a total of 393 animal species across 34 taxonomic orders. The body mass of these species ranged from 27 g to 4,400 kg, spanning six orders of magnitude. The average body mass of human prey was 61 kg with a standard deviation of 294 kg. Humans hunted animal species with very broad body mass ranges across every hunting mode though the central tendencies of prey selection did not statistically differ by hunting mode (Fig. 3).

We detected considerable variation in the different hunting tools employed by humans (Table 1). There were 27 different tools used by humans to hunt prey (Table 1). Among all accounts, the hunting tool used most commonly was firearms representing 36% of all tools ($n = 158$ of 438). Dogs were often used as a supplemental tool ($n = 70$ of 438) regularly accompanying human hunters. Traps ($n = 52$ of 438) and snares ($n = 34$ of 438) were also commonly used tools to hunt prey. Examples of less frequently documented hunting tools included clubs, blowpipes, axes, and knives (Table 1). We note that there were several tools that were applied across the three different hunting modes (Table 1).

Hunting techniques varied from simple methods such as placing traps or coursing for prey on foot, to more complicated measures such as the use of fire and vehicles (Table 2). The hunting technique that was recorded most frequently was hunters coursing for prey ($n = 102$ of 329), followed by hunters using spotlights to stun prey ($n = 100$ of 332), hunters setting out traps ($n = 75$ of 329), and then hunters coursing with dogs ($n = 44$ of 329). In total, we recorded 19 different hunting techniques that we assigned to a hunting mode (Table 2).

The most commonly used hunting mode was the active mode documented in 58% ($n = 139$ of 241) of all human hunting descriptions. The sit-and-wait hunting mode was documented in 40% ($n = 99$ of 241) of the descriptions with the sit-and-pursue hunting mode only being described four times (2%; Fig. 2). Hunting techniques used in the active hunting mode included coursing with firearms, coursing with dogs, and capturing animals by hand, among others (Table 1). Sit-and-wait human hunting techniques included traps, snares, and firearms if used from a stand or blind, while sit-and-pursue hunting techniques included opportunistic hunting while performing other tasks such as farming or herding (Table 1).

DISCUSSION

Humans are exceptional consumers of the world's animal populations (Reznik et al. 1990; Palumbi et al. 2001). Capable of initiating defaunation at rates that are up to 14 times higher than other non-human predators (Darimont et al. 2015), it is challenging to estimate with precision the number of species that humans have now hunted to extinction (Barnosky et al. 2004; Ripple et al 2016; Otto 2018). Consequently, the consumptive effects of human predation are well understood. However, the NCEs of humans behaving as predators are not as clear. This lack of understanding can, at least partially, be explained by the fact that the costs of the behavioral decisions that animals make to avoid human predation are not commonly estimated

(Montgomery et al. 2020). Without an understanding of these costs, it is not feasible to estimate the NCEs of human predation. This reality however, does not diminish the potential importance of these NCEs on prey populations and ecosystem structure. For instance, NCEs can represent a large proportion of the total impact of predation and should be accounted for when designing conservation strategies for large mammals (Say-Sallaz et al. 2019). Furthermore, it is these costs that have been suggested to be integral to emergent practices seeking to manage over-abundant mammal populations (see Crooms et al. 2013). If humans do exert NCEs, then management actions can use different strategies of human hunting to regulate animal populations both directly and indirectly. While emergent research must quantify the costs of prey responses to human predation, examination of human hunting modes provides another way to predict these potential NCEs.

Hunting modes have implications for NCEs because of the cues that predators naturally deposit in the environment when pursuing prey (Schmitz 2005). The disbursement of these cues, which are perceptible to prey (i.e., visual, audible, or chemical), vary not only as a function of the predator species, but also according to the hunting mode used (Turner et al. 2000; Luttbeg and Trussell 2013). For instance, the active hunting mode should have broad disbursement of cues given that the predator species is, more or less, constantly moving about the environment in search of prey (Preisser et al. 2007). To a prospective prey species, these cues would be comparatively predictable and common. In contrast, sit-and-wait hunting is envisioned to have the most localized cues, followed closely thereafter by sit-and-pursue, given the tendency of these predators to wait until prey are encountered (Schmitz et al. 2017). The distribution and strength of these cues provide important information to prey species seeking to avoid being killed (Sih 1992). Thus, the cues of predation are integral to the anti-predator behavioral

responses of prey (Relyea 2003; Sih et al. 2010). These behavioral responses are suggested to be strongest in relation to sit-and-wait predators, where predation risk is imminent, intermediate in relation to sit-and-pursue predators, and weakest in relation to active predators (Preisser et al. 2007; Schmitz et al. 2017). Within this context, the combination of predator hunting mode and habitat domain width (determined by the space use of the subject animals) facilitate predictions of the nature and strength of NCEs with subsequent implications for ecosystem structure via the potential cascading effects of predation (Miller et al. 2014; Northfield et al. 2017). While this conceptual theory has been evaluated among a variety of ecological systems, humans have yet to be widely considered. As our research has shown, humans are a highly versatile predator deploying all three hunting modes. Thus, it seems warranted that the contributions of human predation ought to be considered in future studies of the NCEs of predation on prey populations.

Among a meta-analysis of non-human species, predators deploying the active hunting mode were most common ($n = 68$ species), followed by sit-and-pursue predators ($n = 23$ species), and finally sit-and-wait predators ($n = 6$ species; Preisser et al. 2007). We found that humans most commonly hunt terrestrial prey using the active mode (58%), followed by the sit-and-wait mode (40%) with only minimal evidence in which the sit-and-pursue mode (2%) was deployed. Thus, humans tended to either course for their prey or wait in a spot where their likelihood of encountering prey was high before striking. The most common example of humans acting as active predators included hunting on foot using firearms while common sit-and-wait techniques included firearm or bow hunting from a hide, trapping, and snaring (Tables 1 and 2). Interestingly, examples of humans using the sit-and-pursue mode were highly rare. These instances were restricted to occasions in which humans were performing other activities (e.g., tending to agricultural gardens) when prey species were detected and opportunistically pursued.

Although our review included a wide range of published studies on human hunting behaviour we acknowledge that the quantity of documented examples of hunting modes and tools could have been skewed towards topical subjects. For example, a sit-and-pursue hunting strategy involving hilltop surveillance and subsequent pursuit of the target animal is often employed by poachers in areas with variable terrain in southern Africa but was not reported in any of the publications retrieved for this study. Consequently, our results describing the relative frequency of hunting modes and tool use should be interpreted with caution. Despite this caveat, it is likely that the active and sit-and-wait hunting modes are indeed the most frequently used hunting modes employed by humans given their comparative dominance in the literature. However, it is not presently clear whether prospective prey species are able to detect variation in human cues across these different hunting modes.

Humans undoubtedly leave behind cues detectable by animals when they move through a landscape (Smith et al. 2017; Clinchy et al. 2016; Montgomery et al. 2020). We believe that an important line of future inquiry should experimentally assess whether animals respond differently to cues from humans deploying the sit-and-wait, sit-and-pursue, and active hunting modes. Once again, there is good reason to believe that there should be variation. Traps and snares, for example, can be made from a variety of sources including sisal rope, metal wire, metal cages, and a number of synthetic materials (e.g., nylon; Muñoz-Igualada et al. 2008; Becker et al. 2013; Mudumba et al. 2020). Each of these materials has chemical properties that should be perceptible to animals as cues. Additionally however, there would also be cues associated with the human manipulation of these traps and snares. The ability to capture animals in traps (even including camera traps), for instance, declines with human scent contamination (Spencer 2007; Muñoz et al. 2014). To use another example, the disbursement of cues of a

274 human hunter using a bow and arrow in a tree stand (i.e., sit-and-wait) could be reasonably
275 hypothesized to be different than a human hunter using the same tool to stalk prey (i.e., active
276 hunting mode). Research quantifying such variation is needed to document the strength of the
277 NCEs that humans may have on animal populations.

278 While the NCEs of human hunting may be beneficial to meet management goals of
279 overabundant animal populations (i.e., Cromsigt et al. 2013), they could be positively
280 detrimental to the conservation of rare species. Illegal harvest is one of the primary contributors
281 to biodiversity loss globally (Milner-Gulland and Bennett 2003; Ripple et al. 2016). However,
282 the research on this topic has, almost exclusively, reported on the consumptive, rather than
283 nonconsumptive, effects of that harvest. Consequently, there is a need to understand whether
284 NCEs can derive from illegal human harvest. Such research has likely not been widely assessed
285 because it is highly complex to elucidate these effects. Many forms of human-animal interaction
286 are benign, in the sense that they don't result in the death of the animal. It is not presently known
287 however, whether animals can decipher between the cues of humans that are benign versus those
288 that are hunters. A possibility here is that animals may become habituated to benign human
289 presence, making them more vulnerable to hunters (see Montgomery et al. 2020). If such a
290 habituation were to take place, then it is likely that the NCEs of harvest (legal or illegal) would
291 be minimized. However, such a hypothesis would lie in contrast to the risk-disturbance
292 hypothesis which predicts that human disturbance and human predation pressures should be
293 perceived similarly by animals, particularly for those species that reside in systems where they
294 are subjected to human harvest (Gill and Sutherland 2000; Frid and Dill 2002). Additional
295 research, which formally tests the risk-disturbance hypothesis, will need to be conducted to

quantify the potential NCEs of human hunting with important implications both for the management and conservation of animal populations.

The vast majority of predators on earth have evolved the use of one hunting mode (Preisser et al. 2007). They either sit-and-wait, sit-and-pursue, or actively stalk their prey. Some predators have demonstrated an ability to switch between two hunting modes given biotic or abiotic changes to the environments in which they reside (Scharf et al. 2006; Michael and Adams 2009). No predator is able to use all three hunting modes, nor deploy such a range of hunting techniques, as humans. We have shown that humans are an exceptionally versatile predator capable of deploying one, two, or three hunting modes and using scores of different tools in the process. These results suggest that animals are likely exposed to highly confusing landscapes of human cues. For instance, cues of active human predators may be broadly disbursed about the landscape, while cues of sit-and-wait human predators would be more localized. Also among these landscapes however, would be the cues of non-lethal humans (i.e., walkers, hikers, and birders). As we have highlighted, additional research is needed to assess the extent to which animals are capable of differentiating among the cues associated with these different phenotypes of humans and to determine whether anti-human predator behavioral decisions carry costs that can scale to have NCEs on prey populations. Nevertheless, in synthesizing the results of our analysis, what our review makes clear is that humans are a very different kind of predator with important implications for animal conservation.

REFERENCES

- Abrams, P.A., 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *The American Naturalist*, 146(1), pp.112-134.
- Abrams, P.A., 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics*, 31(1), pp.79-105.

- 321 Arditi, R. and Ginzburg, L.R., 1989. Coupling in predator-prey dynamics: ratio-
322 dependence. *Journal of Theoretical Biology*, 139(3), pp.311-326.
- 323 Barry, M.J., 1994. The costs of crest induction for *Daphnia carinata*. *Oecologia*, 97(2), pp.278-
324 288.
- 325 Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L. and Shabel, A.B., 2004. Assessing the
326 causes of late Pleistocene extinctions on the continents. *Science*, 306(5693), pp.70-75.
- 327 Barnosky, A.D., Hadly, E.A., Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M., Getz,
328 W.M., Harte, J., Hastings, A., Marquet, P.A. and Martinez, N.D., 2012. Approaching a
329 state shift in Earth's biosphere. *Nature*, 486(7401), p.52.
- 330 Barton, B.T. and Schmitz, O.J., 2009. Experimental warming transforms multiple predator
331 effects in a grassland food web. *Ecology Letters*, 12(12), pp.1317-1325.
- 332 Becker, M., McRobb, R., Watson, F., Droge, E., Kanyembo, B., Murdoch, J. and Kakumbi, C.,
333 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants
334 and large carnivores. *Biological Conservation*, 158, pp.26-36.
- 335 Belgrad, B.A. and Griffen, B.D., 2016. Predator-prey interactions mediated by prey personality
336 and predator hunting mode. *Proceedings of the Royal Society B: Biological*
337 *Sciences*, 283(1828), p.20160408.
- 338 Carey, M.P. and Wahl, D.H., 2011. Foraging modes of predators and behaviors of prey
339 determine the outcome of multiple predator interactions. *Transactions of the American*
340 *Fisheries Society*, 140(4), pp.1015-1022.
- 341 Clinchy, M., Zanette, L.Y., Roberts, D., Suraci, J.P., Buesching, C.D., Newman, C. and
342 Macdonald, D.W., 2016. Fear of the human "super predator" far exceeds the fear of large
343 carnivores in a model mesocarnivore. *Behavioral Ecology*, 27(6), pp.1826-1832.
- 344 Cromsigt, J.P., Kuijper, D.P., Adam, M., Beschta, R.L., Churski, M., Eycott, A., Kerley, G.I.,
345 Myrsterud, A., Schmidt, K. and West, K., 2013. Hunting for fear: innovating management
346 of human-wildlife conflicts. *Journal of Applied Ecology*, 50(3), pp.544-549.
- 347 Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E. and Wilmers,
348 C.C., 2009. Human predators outpace other agents of trait change in the wild.
349 *Proceedings of the National Academy of Sciences*, pp.pnas-0809235106.
- 350 Darimont, C.T., Fox, C.H., Bryan, H.M. and Reimchen, T.E., 2015. The unique ecology of
351 human predators. *Science*, 349(6250), pp.858-860.
- 352 Dawkins, R. and Krebs, J.R., 1979. Arms races between and within species. *Proc. R. Soc. Lond.*
353 *B*, 205(1161), pp.489-511.
- 354 Deutsch, D., 2011. *The beginning of infinity: Explanations that transform the world*. Penguin
355 UK.
- 356 Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J. and Collen, B., 2014. Defaunation
357 in the Anthropocene. *Science*, 345(6195), pp.401-406.

- Donihue, C.M., 2016. Aegean wall lizards switch foraging modes, diet, and morphology in a human-built environment. *Ecology and Evolution*, 6(20), pp.7433-7442.
- Dunning, J.B., 2007. CRC handbook of avian body masses. CRC Press.
- Edmunds, M., 1974. Defence in animals: a survey of anti-predator defences. Longman Publishing Group.
- Faurby, S., Davis, M., Pedersen, R. Ø., Schowanek, S. D., Antonelli, A., & Svenning, J. C. 2018. PHYLACINE 1.2: The phylogenetic atlas of mammal macroecology. *Ecology*, 99(11), 2626. <https://doi.org/10.1002/ecy.2443>
- Faurby, S., Davis, M., Pedersen, R. Ø., Schowanek, S. D., Antonelli, A., & Svenning, J. C. 2019. Data from: PHYLACINE 1.2: The phylogenetic atlas of mammal macroecology. Dryad, Dataset, <https://doi.org/10.5061/dryad.bp26v20>
- Frank, S.A., 1994. Coevolutionary genetics of hosts and parasites with quantitative inheritance. *Evolutionary Ecology*, 8(1), pp.74-94.
- Frid, A. and Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6(1).
- Gill, J.A., Sutherland, W.J., 2000. The role of behavioural decision making in predicting the consequences of human disturbance. In: Gosling, L.M. & Sutherland, W.J. (Eds.), *Behaviour and Conservation*. Cambridge University Press, Cambridge.
- Gould, S.J., 1977. Ever since Darwin: Reflection in natural history. Norton Press, New York, NY.
- Helfman, G.S., 1990. Mode selection and mode switching in foraging animals. In *Advances in the Study of Behavior* (Vol. 19, pp. 249-298). Academic Press.
- Huey, R.B. and Pianka, E.R., 1981. Ecological consequences of foraging mode. *Ecology*, 62(4), pp.991-999.
- Kareiva, P., 1987. Habitat fragmentation and the stability of predator-prey interactions. *Nature*, 326(6111), pp.388-390.
- Krebs, J.R. and Davies, N.B. eds., 2009. *Behavioural ecology: an evolutionary approach*. John Wiley & Sons.
- Krebs, C.J., Boonstra, R., Boutin, S. and Sinclair, A.R., 2001. What Drives the 10-year Cycle of Snowshoe Hares?. *BioScience*, 51(1), pp.25-35.
- Levin, S.A., 1976. Population dynamic models in heterogeneous environments. *Annual Review of Ecology and Systematics*, pp.287-310.
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. and Sand, H., 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proc. R. Soc. B*, 279(1730), pp.910-915.
- Luttbeg, B., Hammond, J.I., Brodin, T. and Sih, A., 2020. Predator hunting modes and predator-prey space games. *Ethology*, 126(4), pp.476-485.

- MacNulty, D.R., Mech, L.D. and Smith, D.W., 2007. A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *Journal of Mammalogy*, 88(3), pp.595-605.
- McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H. and Warner, R.R., 2015. Marine defaunation: animal loss in the global ocean. *Science*, 347(6219), p.1255641.
- McLaughlin, R.L., 1989. Search modes of birds and lizards: evidence for alternative movement patterns. *The American Naturalist*, 133(5), pp.654-670.
- Michel, M.J. and Adams, M.M., 2009. Differential effects of structural complexity on predator foraging behavior. *Behavioral Ecology*, 20(2), pp.313-317.
- Miller, J.R., Ament, J.M. and Schmitz, O.J., 2014. Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *Journal of Animal Ecology*, 83(1), pp.214-222.
- Milner-Gulland, E.J. and Bennett, E.L., 2003. Wild meat: the bigger picture. *Trends in Ecology and Evolution*, 18(7), pp.351-357.
- Montgomery, R.A., 2020. Poaching is not one big thing. *Trends in Ecology and Evolution* <https://doi.org/10.1016/j.tree.2020.02.013>
- Montgomery, R.A., D.W. Macdonald, and M.W. Hayward., 2020. The inducible defenses of large mammals to human lethality. *Functional Ecology* 34:2426–2441.
- Mudumba, T., D. Heit, S. Jingo, and R.A. Montgomery. 2020. The landscape configuration and lethality of snare poaching. *African Journal of Ecology* DOI: 10.1111/aje.12781
- Muñoz-Igualada, J., Shivik, J.A., Domínguez, F.G., Lara, J. and González, L.M., 2008. Evaluation of cage-traps and cable restraint devices to capture red foxes in Spain. *The Journal of Wildlife Management*, 72(3), pp.830-836.
- Muñoz, D., Kapfer, J. and Olfenbittel, C., 2014. Do available products to mask human scent influence camera trap survey results?. *Wildlife Biology*, 20(4), pp.246-252.
- Northfield, T.D., Barton, B.T. and Schmitz, O.J., 2017. A spatial theory for emergent multiple predator–prey interactions in food webs. *Ecology and Evolution*, 7(17), pp.6935-6948.
- Olive, C.W., 1982. Behavioral response of a sit-and-wait predator to spatial variation in foraging gain. *Ecology*, 63(4), pp.912-920.
- Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C. and Macdonald, D.W., 2015a. Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, 124(10), pp.1263-1273.
- Oriol-Cotterill, A., Macdonald, D.W., Valeix, M., Ekwanga, S. and Frank, L.G., 2015b. Spatiotemporal patterns of lion space use in a human-dominated landscape. *Animal Behaviour*, 101, pp.27-39.
- Otto, S.P., 2018. Adaptation, speciation and extinction in the Anthropocene. *Proceedings of the Royal Society B*, 285(1891), p.20182047.

- 432 Paine, R.T., 1966. Food web complexity and species diversity. *The American Naturalist*,
433 100(910), pp.65-75.
- 434 Palumbi, S.R., 2001. Humans as the world's greatest evolutionary force. *Science*, 293(5536),
435 pp.1786-1790.
- 436 Peterson, R.O. and Page, R.E., 1988. The rise and fall of Isle Royale wolves, 1975–1986. *Journal*
437 *of Mammalogy*, 69(1), pp.89-99.
- 438 Preisser, E.L., Bolnick, D.I. and Benard, M.F., 2005. Scared to death? The effects of intimidation
439 and consumption in predator–prey interactions. *Ecology*, 86(2), pp.501-509.
- 440 Preisser, E.L., Orrock, J.L. and Schmitz, O.J., 2007. Predator hunting mode and habitat domain
441 alter nonconsumptive effects in predator–prey interactions. *Ecology*, 88(11), pp.2744-
442 2751.
- 443 Relyea, R.A., 2002. Costs of phenotypic plasticity. *The American Naturalist*, 159(3), pp.272-
444 282.
- 445 Relyea, R.A., 2003. How prey respond to combined predators: a review and an empirical
446 test. *Ecology*, 84(7), pp.1827-1839.
- 447 Reznick, D.A., Bryga, H. and Endler, J.A., 1990. Experimentally induced life-history evolution
448 in a natural population. *Nature*, 346(6282), p.357.
- 449 Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey,
450 P.A., Macdonald, D.W., Machovina, B. and Newsome, T.M., 2016. Bushmeat hunting
451 and extinction risk to the world's mammals. *Royal Society Open Science*, 3(10),
452 p.160498.
- 453 Say-Sallaz, E., Chamaillé-Jammes, S., Fritz, H. and Valeix, M., 2019. Non-consumptive effects
454 of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip
455 of the iceberg. *Biological Conservation*, 235, pp. 36-52.
- 456 Scharf, I., Nulman, E., Ovadia, O. and Bouskila, A., 2006. Efficiency evaluation of two
457 competing foraging modes under different conditions. *The American Naturalist*, 168(3),
458 pp.350-357.
- 459 Schoener, T.W., 1971. Theory of feeding strategies. *Annual Review of Ecology and*
460 *Systematics*, 2(1), pp.369-404.
- 461 Schmitz, O., 2005. Behavior of predators and prey and links with population-level processes.
462 Pages 256–278 in P. Barbosa and I. Castellanos, editors. *Ecology of predator–prey*
463 *interactions*. Oxford University Press, Oxford, UK.
- 464 Schmitz, O.J., 2007. Predator diversity and trophic interactions. *Ecology*, 88(10), pp.2415-2426.
- 465 Schmitz, O.J., 2008. Effects of predator hunting mode on grassland ecosystem function. *Science*,
466 319(5865), pp.952-954.
- 467 Schmitz, O.J. and Suttle, K.B., 2001. Effects of top predator species on direct and indirect
468 interactions in a food web. *Ecology*, 82(7), pp.2072-2081.

- Schmitz, O.J., Krivan, V. and Ovadia, O., 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, 7(2), pp.153-163.
- Schmitz, O.J., Miller, J.R., Trainor, A.M. and Abrahms, B., 2017. Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space. *Ecology*, 98(9), pp.2281-2292.
- Sih, A., 1980. Optimal foraging: partial consumption of prey. *The American Naturalist*, 116(2), pp.281-290.
- Sih, A., 1984. The behavioral response race between predator and prey. *The American Naturalist*, 123(1), pp.143-150.
- Sih, A., 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *The American Naturalist*, 139(5), pp.1052-1069.
- Sih, A., 2005. Predator-prey space use as an emergent outcome of a behavioral response race. *Ecology of predator-prey interactions*, 11, pp.240-255.
- Sih, A., Crowley, P., McPeck, M., Petranka, J. and Strohmeier, K., 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, 16(1), pp.269-311.
- Sih, A., Bolnick, D.I., Luttbeg, B., Orrock, J.L., Peacor, S.D., Pintor, L.M., Preisser, E., Rehage, J.S. and Vonesh, J.R., 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos*, 119(4), pp.610-621.
- Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y. and Wilmers, C.C., 2017. Fear of the human ‘super predator’ reduces feeding time in large carnivores. *Proceedings of the Royal Society B: Biological Sciences*, 284(1857), p.20170433.
- Spencer, J., 2007. *Guide to trapping*. Stackpole Books.
- Taylor RJ. 1984. Predation. London: Chapman & Hall.
- Thaker, M., Vanak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M. and Slotow, R., 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, 92(2), pp.398-407.
- Tollrian, R. and Harvell, C.D. eds., 1999. The ecology and evolution of inducible defenses. Princeton University Press.
- Turner, A.M., Bernot, R.J. and Boes, C.M., 2000. Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails. *Oikos*, 88(1), pp.148-158.
- Werner, E.E. and Peacor, S.D., 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84(5), pp.1083-1100.
- Winnie Jr, J. and Creel, S., 2017. The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs*, 12, pp.88-94.

508 **TABLES**

509 **Table 1.** The hunting tools used by humans in pursuit of prey species deriving from a literature
 510 review of research published between 1972 and 2020. The count of the application of those
 511 hunting tools and the proportions of those tools used in each human hunting mode.

Hunting Tool	Count	Hunting Mode		
		Active	Sit-and-wait	Sit-and-pursue
Firearms	158	0.28	0.07	0.01
Dogs	71	0.16	0.00	0.00
Traps	53	0.00	0.12	0.00
Snares	34	0.00	0.08	0.00
Bows	21	0.03	0.01	0.01
Spears	20	0.05	0.00	0.00
Machetes	14	0.03	0.00	0.01
Hands	9	0.02	0.00	0.00
Clubs	7	0.01	0.00	0.01
Nets	7	0.02	0.00	0.00
Blowpipes	6	0.01	0.00	0.00
Crossbow	4	0.01	0.00	0.00
Pit-falls	4	0.00	0.01	0.00
Axes	3	0.01	0.00	0.002
Sticks	3	0.01	0.00	0.00
Explosives	2	0.00	0.01	0.00
Javelins	2	0.002	0.00	0.002
Knives	2	0.01	0.00	0.00
Slingshots	2	0.01	0.00	0.00
Electric shocks	1	0.002	0.00	0.00
Feet	1	0.002	0.00	0.00
Fire	1	0.002	0.00	0.00
Harpoons	1	0.002	0.00	0.00
Horse	1	0.002	0.00	0.00
Lasso	1	0.002	0.00	0.00
Net corrals	1	0.002	0.00	0.00
Stones	1	0.002	0.00	0.00

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Table 2. The application of hunting techniques, with corresponding hunting modes, used by humans to pursue prey species from a literature review of peer-reviewed research published between 1972 and 2020.

Hunting Technique	Hunting Mode	Count	Proportion
Hunters coursing for prey	Active	101	0.31
Hunters using spotlights to stun prey	Active	99	0.30
Hunters setting out traps	Sit-and-wait	74	0.23
Hunters coursing for prey with dogs	Active	44	0.13
Hunters conducting prey drives with dogs	Active	17	0.05
Hunters conducting prey drives	Active	15	0.05
Hunters coursing for prey with vehicles	Active	14	0.04
Hunters waiting in stand, blinds, towers, or hides	Sit-and-wait	12	0.04
Hunters waiting by bait piles	Sit-and-wait	11	0.03
Hunters waiting by sites frequented by prey	Sit-and-wait	9	0.03
Hunters coursing with the use of calls	Active	7	0.02
Hunters sitting and waiting for prey	Sit-and-wait	4	0.01
Hunters performing other activities and then opportunistically hunting prey	Sit-and-pursue	4	0.01
Hunters waiting and using call lures	Sit-and-wait	3	0.01
Hunters herding prey into net corrals	Active	1	0.003
Hunters digging out animal burrows	Active	1	0.003
Hunters using horses and lassos	Active	1	0.003
Hunters driving prey using fire	Active	1	0.003
Hunters setting up firing lines	Sit-and-wait	1	0.003

FIGURE LEGENDS

Fig 1. Examples of some of the common hunting techniques deployed by humans in pursuit of terrestrial prey. Each of these techniques can be associated with a specific hunting mode (i.e., sit-and-wait, sit-and-pursue, or active). The application of these hunting modes should be expected to be associated with the deposit of different cues of human predation. The tradeoffs that these cues might exert in prey could create nonconsumptive effects of human predation.

Fig. 2. The spatial configuration of studies examining human hunting modes that derived from a literature review of research published between 1972 and 2020. Across these studies, all three hunting modes (i.e., sit-and-wait, sit-and-pursue, and active) were used by humans among all of these continents.

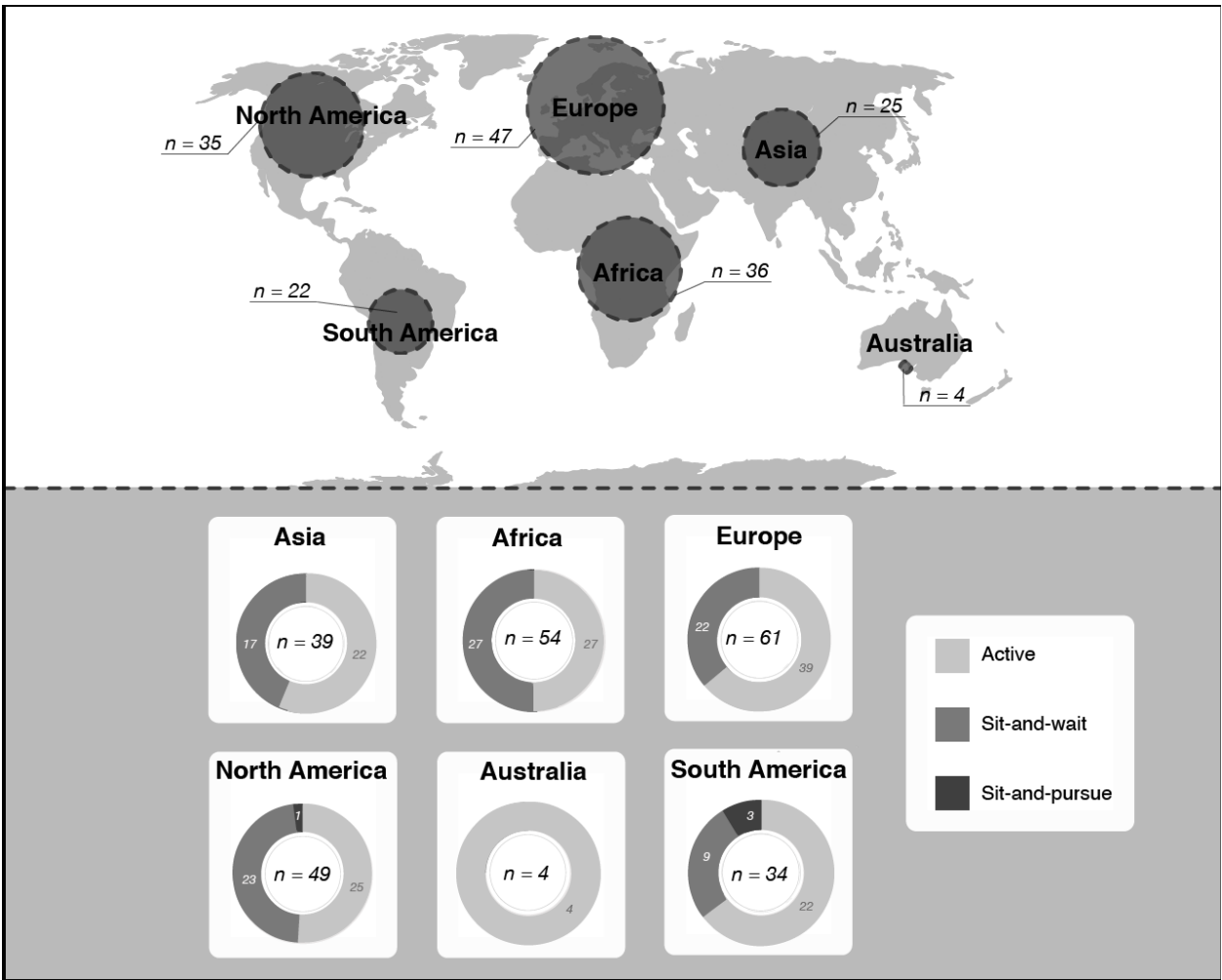
Fig. 3. The relationship between human hunting mode and the body mass of the prey species being hunted based on data from a literature review of studies published between 1972 and 2020. Box and whisker plots display the range of prey species body mass, in grams, of prey species targeted by human hunters using each of the hunting modes.

534 **FIGURES**535 **Fig. 1**

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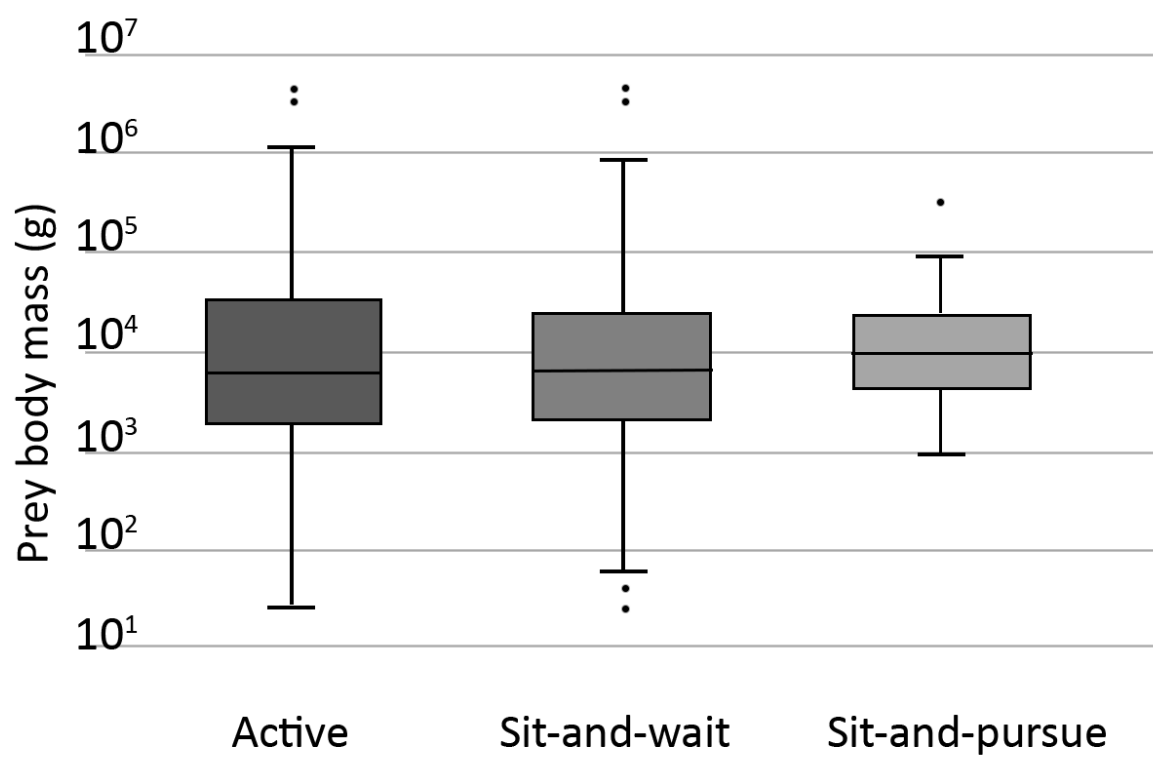
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Fig. 2



541 **Fig. 3**

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