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ORIGINAL RESEARCH

A Framework for Assessing Impacts of Wild Meat Hunting Practices in the Tropics

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Abstract
Terrestrial wildlife is being hunted for consumption by humans in the tropics at an unprecedented rate, and the often unsustainable nature of this harvest has profound implications not only for biodiversity and ecosystem function, but also for human livelihoods. Whilst the nature and impacts of this practice have been studied in numerous contexts and localities, a comprehensive treatment of the social, economic, and environmental determinants of both hunter decision-making and hunting outcomes has been lacking. In this review we discuss influences of hunting methods and effort on the types of animals caught, the efficiency of harvest, and the implications of these factors for sustainability. We highlight gaps in current understanding, and identify the most important data requirements. Our approach provides a framework for the design of future studies into wild meat hunting and its impacts, promoting the efficient targeting of priority areas of research.

Keywords Wild meat · Bushmeat · Defaunation · Sustainable harvest · Snaring · Biodiversity · Human hunting · Africa, Amazonia, Southeast Asia

Introduction

The overhunting of wild animals for sale and subsequent human consumption is a major threat to biodiversity in the tropics (Milner-Gulland *et al.* 2003; Ripple *et al.* 2016; Benitez-Lopez *et al.* 2017), and has direct impacts on human nutrition and livelihoods (Nasi *et al.* 2011; Cawthorn and Hoffman 2015), as well as indirect impacts on ecosystem function (e.g., Vanthomme *et al.* 2010; Effiom *et al.* 2013). Estimates of wildlife offtake for 2010 in the Amazon and Congo basins approximate 1.3 million and 4.5 million tonnes, respectively (Nasi *et al.* 2011), and where they have been calculated, offtake indicators show a rising trend (Ingram *et al.* 2015). The threats posed by unsustainable harvesting on this scale may be most acute in southeast Asia, where hunting is driven not only by demand for meat but also by lucrative markets for a huge range of wildlife products, and where impacts are exacerbated by globally unmatched rates of deforestation (Harrison *et al.* 2016).

Conservation scientists study hunting to quantify its ecological impacts and contributions to livelihoods, estimate its sustainability, and predict how it might respond to changing economic, environmental, and social conditions. An extensive body of field-based research has demonstrated the ecological impacts of hunting, typically involving ‘hunter-follows’ to estimate the efficiency of different methods (e.g., Noss 1998; Kümpel *et al.* 2008; Coad *et al.* 2013), whilst survey data at a range of spatial scales have identified influences of economic status, market forces, and armed conflict on hunter behaviour (e.g., Brashares *et al.* 2004, 2011; Wilkie *et al.* 2005; Nackoney *et al.* 2014; McNamara *et al.* 2016). Models have been used to extrapolate these results, for example predicting impacts of economic changes on hunting sustainability and human livelihoods (Milner-Gulland and Leader-Williams 1992; Damania *et al.* 2005; Conrad and Lopes 2017).

Significant challenges remain, however. The factors that could influence hunting pressure – including, but not limited

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to, consumer demand, poverty, governance, civil unrest, and cultural change – are numerous and inter-related (Lindsey *et al.* 2013; Cawthorn and Hoffman 2015), and many of the links between drivers and outcomes are still to be elucidated. In particular, the mechanisms by which external drivers influence hunter behaviour, and hence hunting practices, remain under-studied. This is unsurprising given that illegal hunting is a sensitive topic, so can rarely be addressed by direct methods (Gavin *et al.* 2010).

Interventions aimed at reducing the prevalence of hunting can also (or merely alternatively) affect method choice (e.g., prompting a switch from more detectable methods such as gun hunting to less detectable ones such as snaring). It can also affect the locations of hunting areas (e.g., by deterring hunters from entering protected areas or shifting them to less patrolled areas). These changes might go unnoticed by existing monitoring protocols as their outcomes might be apparent across different spatial and temporal scales to the intervention itself (Wu 2009; Sodhi *et al.* 2011). The potential for unintended consequences such as these can be minimised by a better *a priori* understanding of hunting systems. Therefore, our objective in this paper is to guide researchers aiming to study human hunting systems by (a) providing a basic framework for considering the set of factors likely to influence hunting behaviour, (b) summarising current understanding of these factors and the linkages between them, and (c) identifying outstanding questions and knowledge-gaps that ought to be prioritised for future study. The literature is focussed primarily on the hunting of larger terrestrial animals in Africa, Amazonia, and southeast Asia.

The paper is split into two main sections, covering the methods (e.g., equipment types) and intensity (e.g., temporal and spatial distributions of effort) of hunting, respectively. We argue that this is a useful way to conceptually divide hunting practices; both are influenced by numerous external drivers (social, environmental, economic), but in distinct ways and with different implications. However, both aspects must be considered in order to evaluate the impacts of hunting behaviour on wildlife populations and the ways in which they might respond to change. They may also interact in important ways – for example, the relationship between offtake and time spent hunting is very different for gun- and snare-hunters. The contents of these sections are organised around a framework for conceptualising the links among environment, hunter behaviour, and hunting offtake (Fig. 1). We conclude with a summary that includes key challenges and recommendations.

Hunting Methods

We discuss the factors that influence a hunter's choice of hunting method, and the implications of that choice in terms of offtake. In many cases these decisions will be more or less imposed (rather than merely influenced) by social and economic conditions, but the implications for wildlife are the same.

Hunting Methods and their Determinants

Hunting methods – encompassing both the equipment used and the manner in which they are typically employed – can be

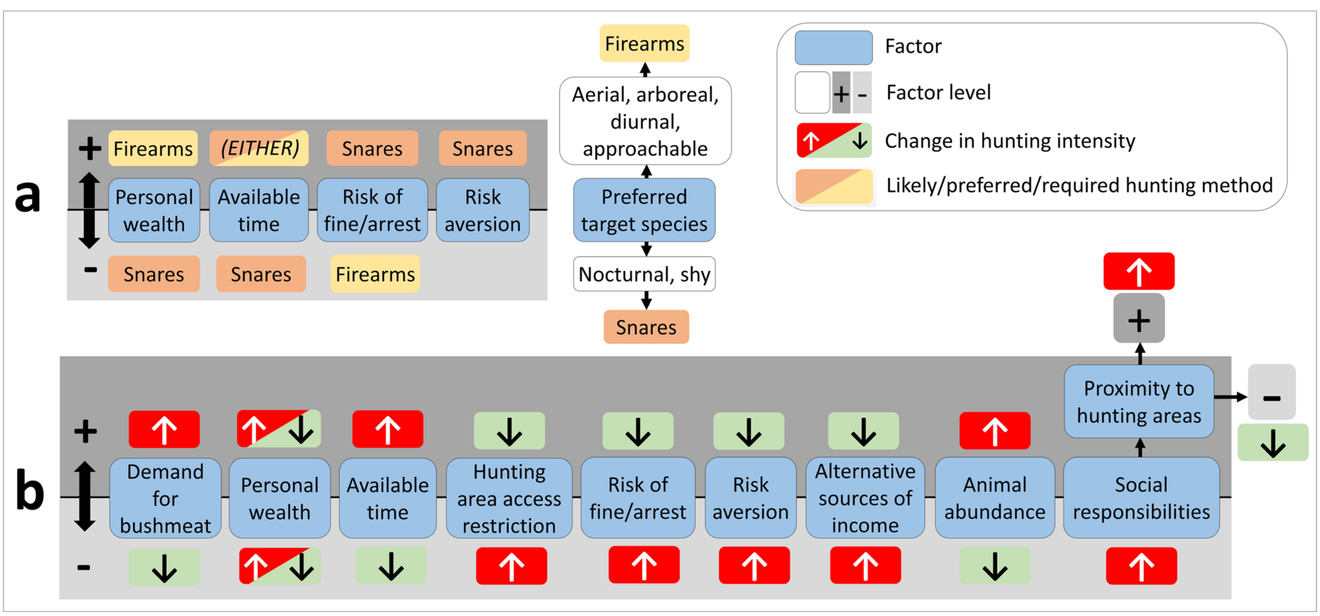

Fig. 1 Hunting activity necessarily follows from decisions made by individual hunters. An understanding of the factors that influence those decisions will help researchers to plan research and to develop effective intervention strategies. We split decisions into two types: those regarding methods used (**a**) and those regarding intensity (**b**)

usefully split into categories of 'active' (e.g., shooting) and 'passive' (e.g., snaring). We describe the most commonly used methods, and discuss the circumstances under which each might be favoured and the implications for the individual hunter.

A snare is a noose that tightens around a body part of an animal and holds it until the hunter returns. Snares are typically left unsupervised and checked periodically. Despite frequently being illegal (see below), snaring can be an attractive means of obtaining meat and/or income, largely due to the low economic barrier to entry, especially when compared with gun-hunting (Kümpel *et al.* 2010; McNamara *et al.* 2016). For example, in Quangnam Province, Vietnam, a kilogram of muntjac (*Muntiacus truongsonensis*) meat would cover the cost of 20 snares (MacMillan and Nguyen 2014). Indeed, the free availability of metal cable may be one of the key drivers determining the abundance of snaring (Walters *et al.* 2015); most of the 84,396 snares removed over eight years from the Savé Valley Conservancy in Kenya were thought to have been fashioned from wire taken from the perimeter fence (Lindsey *et al.* 2011). However, whilst a set snare can theoretically remain effective for several months, older snares have lower capture rates than newer ones (Coad 2007; Kümpel *et al.* 2009), probably due to wire corrosion and (where applicable) loss of tension in the branch used to tighten the noose (H. Ibbett, pers. obs.).

Firearms have played a major role in the intensification of the wild meat trade throughout the tropics, largely replacing more primitive projectile weapons such as bows, spears, and blowpipes (Alvard 1995; Stearman 2000; Fa and Brown 2009; Luskin *et al.* 2014). Exceptions include countries where firearm laws are strict, such as Indonesia and Vietnam (Luskin *et al.* 2014; Harrison *et al.* 2016), and communities living under firearm prohibitions in protected areas (PAs) (e.g., Manu National Park, Peru; Shepard *et al.* 2012). For example, in Equatorial Guinea the government began to remove firearms from the civilian population in 1974; in one village of 200–300 people on Bioko island, 25 shotguns were owned prior to 1974, falling to just one by 1986, before rising again to five by 1990 (Butynski and Koster 1994). Gun hunting remained rare in the country into the 2000s (Kümpel *et al.* 2009), partly as a result of a ban imposed on the Bubi ethnic group following a rebellion in 1998 (Vega *et al.* 2013), but shotgun hunting is common enough now to threaten primate populations in the non-Bubi parts of the island (Cronin *et al.* 2016).

There are two basic categories of hunting firearm – shotguns and rifles – which differ in the number of projectiles that are used for each shot. Shotguns are usually loaded with a large number of small projectiles (pellets) that spread when they leave the barrel, allowing moving targets to be hit; rifles fire a single projectile (bullet) which retains accuracy and power for greater distances than a shotgun (Heard 2008). Modern rifles and shotguns are loaded from the breech – the proximal end of the barrel – but some hunters use the older-style 'muzzle-loading' muskets, in which a charge of gunpowder is poured into the distal end (muzzle) of the barrel, followed by the projectile (Madhusudan and Karanth 2002; Martin *et al.* 2013). These guns are relatively primitive but still capable of killing the largest animal species, such as hippos and elephants (Brown and Marks 2007).

Standard firearms are relatively expensive – sufficient to exclude some hunters altogether (Nasi *et al.* 2011; Sirén and Wilkie 2014) – but locally made alternatives are not uncommon in the tropics (Barboza *et al.* 2011; Paudel 2012; Gardner and Davies 2014). In 2005, a locally produced shotgun could be purchased in Cameroon for between 6% and 21% of the price of an imported weapon (Nchanji 2005). A firearm may be a one-off purchase, meaning that its use is relatively unaffected by economic change, but ammunition for modern weapons is often expensive; for Baka hunters in Yasuoka's (2006) study in Cameroon, a single rifle cartridge cost six times more than the meat from a duiker carcass. As a result, many hunters in the tropics reload their own cartridges with locally produced gunpowder (Brown and Marks 2007; Vieira et al. 2015), or revert to muzzle-loaders when ammunition prices increase (Sirén and Wilkie 2014), though using 'loose' powder (as opposed to cartridges) increases the likelihood of misfiring in humid environments, and these weapons are likely to be more dangerous for the user and less efficient as hunting tools (Carpaneto and Fusari 2000; Brown and Marks 2007).

Snaring requires a relatively low degree of basic skill (Kümpel 2006; Wilcox and Nambu 2007; Hayashi 2008), though there does appear to be an influence of experience on snare-hunting success (Kümpel 2006; Coad 2007). In Kümpel's (2006) study in Equatorial Guinea, one individual trapper was exceptionally prolific, with a rate of capture per trap more than five times higher than the average for the other hunters at the site, a difference not attributable to higher effort.

Gun hunting has the disadvantage of noise; gunshots may scare away wildlife (Alvard 1993; Hodgkinson 2009) and alert ranger patrols to the presence of the hunter in PAs; (Madhusudan and Karanth 2002; Gandiwa 2011). No study has yet attempted to quantify the relative detection probabilities for gun- and snare-hunters (it would require detailed spatial data on the hunters detected by patrols, as well as their actual distributions), nor whether the two types of hunter perceive this risk differently, but it is a potentially important factor for hunting motivations in PAs. Evidence for hunters switching between methods in response to changes in perceived detection risk is currently only anecdotal; Rogan *et al.* (2017) speculated that the desire to avoid detection may explain the recently reported practice of hunting large animals on horseback or motorbikes without firearms in Tanzania and Botswana (see also Kiffner *et al.* 2014; Eustace 2017), and hypothesised that an increase in law enforcement activities would further promote secretive methods of hunting. Knapp (2012) suggested that the threat of detection by patrols had caused a shift towards night-time hunting in the western Serengeti, though such behaviour might equally reflect a need for increased efficiency in the face of declining wildlife abundance. Conversely, whilst gun-hunters are presumably more conspicuous than snare-hunters, they are also perceived to be more dangerous by ranger patrols (Ford 2005; Henson *et al.* 2016; Moreto 2016), who may consequently avoid confrontations for fear of injury or death (Holmern *et al.* 2007).

Hunting methods also differ in their versatility. Damp conditions can hinder a gun-hunter; muzzle-loaders will not fire when the powder is wet, and even powder within shotgun cartridges can become damp and unusable (Hames 1979; Noss 1995). Snares are more resilient, though metal cable will eventually rust. Guns – particularly muzzle-loaders and locally made shotguns – also pose a risk to the user; weak metalwork and/or over-loading with powder can cause a potentially fatal explosion in the breech (Carpaneto and Fusari 2000; Brown and Marks 2007).

Physical effort invested in snaring may be considerable, and limit snare-hunting to those who have few demands on their time. Where wildlife is depleted, snaring involves travelling long distances at frequent intervals, with attendant costs in terms of energy, economic opportunity, and social capital. All other things being equal, a complete snare hunt entails at least twice the travel of a gun hunt (or else an extended stay in the hunting area, imposing opportunity costs), since the snares must be left for a period of time. Coad (2007) argued that time spent in the forest took snare-hunters away from family responsibilities, including the requirement to "protect their family (wives) from other men"; moving into the forest to stay in temporary hunting camps was seen as "slightly mad."

Capture Efficiency

The durability and simplicity of metal cable has allowed snaring to be conducted on industrial scales (Gray *et al.* 2018); in Fa and Garcia Yuste's (2001) study site, an average of 25.9 hunters per month accounted for 107,945,772 snare–nights over a 16-month period. Snares are found across the tropics, though they are far less commonly mentioned in wild meat literature from the Neotropics than from the Old World. The passive nature of snaring also means that it can easily be integrated into daily routines; indeed snares are often set in the margins of crop fields, granting the hunter at least a non-zero chance of capturing an animal when he or she is engaged in other activities such as farm work (Sato 1983), or even gun-hunting (Kümpel 2006; Rist *et al.* 2008). In one sense, snaring is extremely efficient, given that the snare is operational even while the hunter is absent, but quantifying efficiency is problematic.

Efficiency can be described in basic terms as harvest divided by effort, but the latter is difficult to quantify in a uniform manner. Effort has been characterised in a variety of ways in the literature, though usually as some form of time or distance measure; for snare-hunters, the number of snares is also frequently used (see Rist *et al.* 2008 for a thorough treatment). This lack of consistency could hamper attempts to draw general conclusions about hunting sustainability, since direct comparisons are difficult. However, whilst a degree of standardisation might be useful, it is probably not meaningful to try to directly compare efficiencies between passive and active forms of hunting, even if efforts could be compared. 'Time' is an obvious but problematic metric because the inputs are continuous for gun-hunters and sporadic for snare-hunters, yet totalling the separate inputs of the latter would be inappropriate given that the length of time a snare is left in the forest has an important bearing on offtake. For example, a common measure of effort is 'snare-nights,' the product of the number of snares and the number of nights for which they are left set. However, there are two means by which snare-checking interval (which is not the same as the total time during which the snare is active, because not all unchecked snares will be inactive) influences the likelihood that a set snare will yield an edible carcass. Firstly, a snare occupied by a caught animal is a missed opportunity to capture another (Rist *et al.* 2008), and a snare may be sprung without capturing anything (Sato 1983), rendering it useless until the hunter returns. Secondly, captured animals left in snares are vulnerable to rotting and to scavenging by predators (Hawkes *et al.* 1991; Noss 1998; Wilkie and Carpenter 1999; Kümpel 2006). A simple model of a snare-hunter operating 20 snares reveals up to a three-fold difference in useable harvest size for snares checked daily, rather than once, over a thirty-day snaring period, taking already-closed snares and rotting rates into account (Box 1). The measure 'snare-nights' is therefore uninformative without the checking interval. Note that in this example, the relationship between harvest and effort is non-linear; however, a hypothetical hunter who sets 20 additional snares in a separate area – instead of doubling the checking interval in the first area – might achieve a linear relationship, and therefore greater efficiency (assuming no dispersal of wildlife between areas).

Distance measures likewise lack comparability, since distance travelled might broadly correspond to animal encounter rate for gun-hunters, but for snare-hunters there may not be a linear relationship between distance travelled and number of snares set, and it is the latter that influences capture success.

Selectivity

Snares are often described as indiscriminate or non-selective (e.g., Lindsey *et al.* 2011; MacMillan and Nguyen 2014;

Becker *et al.* 2013), and unintended bycatch must be included in any ecological assessment of snare-hunting impacts. However, several factors may allow hunters to dictate the size, and even species, of animal caught. Snares are predominantly set on the ground but may also (much more rarely) be set in trees to catch birds and arboreal mammals (Bulmer 1968; Noss 1995; Golden 2009). Deliberate spatial placement – both fine-scale (e.g., outside burrows, along animal tracks, near fruit trees or water holes, arboreal vs terrestrial) and larger-scale (e.g., habitat type) – can change the likelihood of capturing particular taxa, and the properties of the snare itself are also influential, including height above the ground, loop diameter, wire thickness, snare design (leg or neck), and pressure required to trigger the snare (Colell *et al.* 1994; Noss 1998; Fa and Garcia Yuste 2001; Kümpel 2006; Rist *et al.* 2008; Pangau-Adam *et al.* 2012). Coad (2007) asked snare-hunters in Gabon which species each individual snare was designed to capture, and compared the actual catch with that expected if catch proportions were driven by relative species abundances. Animal trails were attributed to one of six species, which was the species subsequently caught on 51% of occasions ($N = 1028$), indicating that hunters were able to use snare placement to influence the species they caught. Rist *et al.* (2008) also found that capture probabilities of four of the five most commonly trapped species in their Equatorial Guinea site were significantly associated with trap type. Duikers, for example, were exclusively caught in leg traps, whilst small carnivores were captured equally in leg and neck traps. Varying the thickness of wire strands used to make the noose is a further means of species selectivity. Snare-hunters in southeastern Cameroon used double strands for targeting medium-sized duikers (*Cephalophus* spp.), and single strands for the smaller blue duiker (*Philantomba monticola*); the larger animals could reportedly break through the single-strand nooses (Yasuoka *et al.* 2015). In snares set on animal paths in Gabon, Coad (2007) found a significant relationship between the identity of the animal assumed by hunters to have made the path and the number of strands used for the noose.

Whilst snare-hunters do have some control over the species they target, they are nonetheless primarily limited to terrestrial taxa; snares may be placed in trees (e.g., Golden 2009), but this may involve considerable extra effort, as well as the risk of injury. Guns allow more practical hunting of arboreal mammals as well as birds, and the gun-hunter also has a greater degree of influence over individual targets, such that selectivity could theoretically be limited only by their identification skills, though different firearms have different effective ranges and capabilities. Low-powered, small-calibre weapons limit the hunter to small-bodied animals; rifles (as opposed to shotguns) restrict hunters to stationary targets (Table A2, online Supporting Information). The largest animals, such as buffalo, elephant, or rhino, typically require large-calibre rifles (though see Stiles 2011 for accounts of elephants hunted with relatively small-calibre assault rifles). Hunting these potentially dangerous animals has attendant risks for the hunter (Martin *et al.* 2013; Eustace 2017), though beyond anecdotal accounts it is not known how hunters weight the relative costs and benefits of hunting these species. The risks are not confined to gun-hunters, however; snare-hunters in the western Serengeti reported conflict with lions who were attracted to dying herbivores in snares (Knapp 2012).

The extent to which a gun-hunter can target individual species may be mediated by animal behaviour as well as by hunter skill, and this factor can interact with the choice of method to determine selectivity (Holmern *et al.* 2006; Mysterud 2011). For example, species differ in the ease with which they may be approached (Altmann 1958; Blumstein *et al.* 2003; Fernández-Juricic *et al.* 2004); the distance at which an animal typically flees a human observer – the 'flight initiation distance' – will determine how often it will be within range of a projectile weapon, and may change in response to disturbance, including hunting pressure (Marealle *et al.* 2010; Tarakini *et al.* 2014; Kiffner *et al.* 2014; Muposhi *et al.* 2016). Yasuoka *et al.* (2015) hypothesised that blue duiker were more vulnerable to gun-hunters than Peter's duiker (*C. callipygus*) because they were less wary of humans, responded to hunters' bleating calls, and tended to 'freeze' when caught in a flashlight beam. This freezing behaviour is widely reported for a range of species, and in some cases the retina reflects the light in a conspicuous manner (Willcox and Nambu 2007; Newton *et al.* 2008; van Vliet and Nasi 2008; Gandiwa 2011). As well as facilitating targeting of certain species, modern flashlights have widened opportunities for active hunting for at least two other reasons. Firstly, they allow hunting to take place during otherwise 'vacant' hours (Dounias 2016), and during times when detection by ranger patrols is less likely (Nyahongo *et al.* 2005; Holmern *et al.* 2007). Secondly, they allow pursuit-hunters to target nocturnal species that otherwise could only be caught in snares (Coad 2007). This means that hunting with torches at night is potentially much easier than daytime hunting, allowing less skilled hunters to be successful, and further raising the efficiency of more skilled hunters (Wilkie and Carpenter 1999; Hodgkinson 2009; Barboza *et al.* 2011). It is not clear whether hunters currently lacking flashlights (or those for whom batteries are particularly expensive; Parry *et al.* 2009) would increase hunting effort if they had access to them, or whether they would simply shift the timing of hunting in order to concentrate on other economic activities during daylight hours. However, a switch to nocturnal hunting is unlikely to be cost-free; moving in the forest at night exposes humans to elevated risk of wildlife attack, especially where elephants are present (Sitati and Ipara 2012; Acharya *et al.* 2016), and working at night limits the scope for daytime activities.

The selectivity of hunting methods has mixed implications for sustainability. Where hunting is selective, individual species are not necessarily depleted in proportion to their relative availability (Lu 2010; Constantino 2015). Deliberate 'switching' behaviour, whereby hunters focus attention away from rarer species and toward more abundant ones, can allow sustainable harvest even under heavy offtake pressure (Cowlishaw *et al.* 2005; Kümpel *et al.* 2009). Given the potential for selective targeting with snares, even hunting systems dominated by snaring may display this sort of dynamic response. However, some hunters may continue to target rare species, especially if they are particularly valuable (Wilkie *et al.* 2011; Young *et al.* 2016), and the presence of abundant, low-value species may effectively subsidise the more opportunistic harvesting of much rarer species that might have been able to recover had hunting become economically non-viable (Wilkie *et al.* 2011; Branch *et al.* 2013). The effects of hunting on populations may also be intra-specific (e.g., Holmern *et al.* 2006), with effects dependent upon the social organisation of the species (Milner *et al.* 2007; Mysterud 2011). For example, males may be more prone to encountering snares if they range further than females, or to being targets for gun-hunting if they are less cryptic in behaviour or colouration. It is also feasible that (inadvertent) selection for larger individuals could be achieved in some species by the number of wire strands used to make the noose. However, whilst hunters may target certain species or individuals, intentionally or not, there is no evidence in the literature concerning the relative impacts of intra-specific selectivity by hunting method, or the potential effects on population viability.

Hunting Intensity

The proportion of an individual's time spent hunting is dictated largely by their economic situation (Fig. 1). Hunting often serves as an economic buffer in times of hardship (Nasi *et al.* 2008; Cawthorn and Hoffman 2015), though it can also be a primary source of income (Milner-Gulland *et al.* 2003; Pangau-Adam *et al.* 2012; Alexander *et al.* 2015). The relative importance of wild meat – and hence the benefit accrued from hunting – can vary temporally; hunting is more likely to occur when crop harvests have been poor, during lulls in agricultural activity (Shively 1997; Brashares *et al.* 2011; Wilfred and MacColl 2015), and when wildlife abundance is particularly high, such as annual migrations of ungulates in East Africa (Holmern *et al.* 2007; Lindsey *et al.* 2011). In general, the complex relationships between a person's socioeconomic situation and their engagement in hunting are under-studied. The social status of a hunter may influence their willingness to hunt for profit (Coad 2007), and there appears to be much variation in this regard, with hunting associated with both prestige (e.g., Hawkes *et al.* 2001; Brown and Marks 2007) and poverty (e.g., Kümpel *et al.* 2010), or viewed with ambivalence (e.g., Hodgkinson 2009). The likelihood of a given individual 'dropping out' of hunting in order to pursue other economic activities may also be non-random, with younger or less efficient hunters doing so more readily, meaning that a drop in the number of adult males hunting in a community may not produce an equivalent reduction in offtake (Coad *et al.* 2013).

Unfortunately, robust, quantitative data on the trade-offs made by potential hunters who have alternative economic options are scarce. This is largely due to the sensitivity around hunting, necessitating indirect sampling methods such as choice experiments and the 'randomised response' and 'unmatched count' techniques, which are limited in the type of questions that can be asked, can be misunderstood by respondents, and inevitably produce 'noisy' data requiring large sample sizes (St. John *et al.* 2010; Nuno and St John 2015). There is also uncertainty over the extent to which stated preferences correlate with actual behaviour (Murphy *et al.* 2005; St. John *et al.* 2014). Finally, the results are typically nuanced and difficult to generalise. For example, two choice-experiment studies in Tanzania indicated that the donation of livestock would reduce incentives for hunting (Moro *et al.* 2013; Nielsen *et al.* 2014). However, in Moro *et al.*'s (2013) survey of villagers in an area where hunting is common, wealthier respondents valued hunting less than poorer ones, while among a sample of 325 active wild meat traders, the willingness to give up hunting was inversely related to household wealth (Nielsen *et al.* 2014).

In PAs, an obvious barrier to undertaking frequent hunting trips is the presence of ranger patrols, and the perceived threat of sanctions is likely to influence hunter behaviour to some degree (Keane *et al.* 2008; St. John *et al.* 2015). Illegal hunting activity is often concentrated near PA borders and/or points of easy access, for example in East Africa (Wato *et al.* 2006; Watson *et al.* 2013; Kimanzi *et al.* 2015), Cambodia (O'Kelly 2013), Paraguay (Hill *et al.* 1997), and Brazil (Kauano *et al.* 2017), suggesting that risk-avoidance has an influence on hunting movements within PAs. However, several authors have also reported spatial correlations between snare density and wildlife density (Nyahongo *et al.* 2005; Watson *et al.* 2013), including aggregations of snares at saltlicks, waterholes, lake edges, and rivers (Becker *et al.* 2013; Critchlow *et al.* 2015; Kimanzi *et al.* 2015). Indeed, the deterrent effect of patrolling is difficult to assess, and few studies are able to demonstrate a positive impact (Dobson *et al.* 2018, though see Moore *et al.* 2018). Hunting in PAs is common in many countries (Nyahongo *et al.* 2005; Duffy *et al.* 2016; Kauano *et al.* 2017; Rogan *et al.* 2017; Castilho *et al.* 2018), which suggests that the protection status of an area is not necessarily a good indicator of likely hunting pressure.

Legal considerations aside, hunters in different regions will experience varying degrees of freedom over where they may hunt, dictating the diversity and abundance of species available (and hence the harvest size; Coad 2007; Smith 2008; Table 1). Many studies describe village hunting territories that are more or less strictly respected, including in Central and West Africa (Muchaal and Ngandjui 1999; Fa and Garcia Yuste 2001; Hayashi 2008), the Neotropics (Peres and Nascimento 2006; Smith 2008), Arunachal Pradesh, India (Singh *et al.* 2014), Papua New Guinea (Mack and West 2005), and Papua, Indonesia (Pattiselanno 2008; Pangau-Adam *et al.* 2012), though these territories may be dynamic and delineated in part by wildlife distribution and socio-cultural factors as well as physical boundaries (Constantino 2015). Villagers from the Philippine province of Palawan reported that wild animals were viewed as an "open-access resource to which few restrictions applied"; this was an area where almost no commercial hunting took place but wild meat was nonetheless an important component of household economies (Shively 1997). However, the extent to which spatial rules are respected by hunters may depend upon the history of governance (Duffy *et al.* 2016); for example, successive colonial and national administrations in Gabon have rearranged traditional land use allocation systems, resulting in a looser and more ill-defined sense of land ownership and hunting rules (Coad 2007; Walters *et al.* 2015). In Ecuador, where subsistence hunting is legalised under some circumstances (and selling wild meat is always illegal), hunting rights are theoretically determined by ethnicity, but enforcement either of hunting behaviour or sale of wild meat is highly inconsistent, and hence does little to limit the trade (Espinosa *et al.* 2014; Cummins *et al.* 2015).

Benefits in terms of harvest must outweigh the costs of travel, which may be direct (time, physical effort, fuel) or indirect (increased exposure to law enforcement patrols; Hofer *et al.* 2000), but it is not clear whether there are absolute limits to the distances that hunters will travel from settlements to reach wildlife-rich areas (and such limits would presumably be context-specific). Road building to provide access to resources such as timber, oil, and minerals also exposes forests to greatly increased hunting pressure (Abernethy *et al.* 2013; Espinosa *et al.* 2014; Lessmann *et al.* 2016). Roads not only facilitate hunting, but also create links between rural populations of hunters and urban markets, potentially changing the economies of formerly subsistence-only communities by altering the cost-benefit balance in favour of commercial hunting (Espinosa *et al.* 2018). In a review of hunting in Central Africa, Abernethy *et al.* (2013) stated that village hunters typically travel less than 10 km from the village on daily trips, and an ongoing database pertaining to hunting of wild terrestrial species across the globe provides a mean per-village hunting territory of 301km^2 (SE ± 78 km^2, $n = 66$ villages) for this region, which approximates a circle of radius 9.8 km (calculated based on Ingram *et al.* 2015). However, where hunters set up temporary forest camps, hunting may occur at distances up to 50 km from permanent settlements, allowing hunters to access relatively non-depleted areas without incurring daily transport costs (Hayashi 2008; Prado *et al.* 2012; Abernethy *et al.* 2013; Van Vliet *et al.* 2014). The ability to leave permanent settlements for extended periods of time may therefore have a significant impact on an individual's opportunities for hunting and thus their potential response to altered economic circumstances.

Kümpel *et al.* (2009) found increasing snare density with distance from hunting camps in Equatorial Guinea (in direct contrast to the typical pattern of snare distribution in relation to settlements; Muchaal and Ngandjui 1999; Coad 2007), indicating a primary concern for per-snare harvest efficiency. However, at the same site, localised wildlife depletion did not cause hunters to move ever further afield, but instead to increase the average number of snares per hunter from 56 to 92 over a 13 year period (Kümpel 2006; Table 2), suggesting that although maximising yield was a major concern, the perceived travel cost was high, or at least that a threshold of acceptable travel distance existed. An alternative explanation is that the expected density of wildlife further into the forest was no higher, hence there would be relatively little to gain from the extra effort. Like snare-hunters in West Africa, pursuit hunters in the Neo-tropics have been reported to concentrate activities relatively close to settlements (within 10 km), and to achieve greater efficiency at more distant sites (Sirén *et al.* 2004; Smith 2008).

Knowledge Gaps and Future Directions

Despite the large volume of literature devoted to hunting practices, our review has highlighted several key knowledge gaps where future research could be usefully targeted (summarised in Box 2).

From a conservation perspective, perhaps the largest gap in current understanding concerns the behavioural responses of hunters to changing external conditions (e.g., the strategies adopted in response to large-scale economic, social, or ecological change), and the ways in which these changing external conditions interact with conservation interventions. Under altered economic circumstances, non-hunters may become hunters, and vice-versa, but there may also be more subtle switches between target species or hunting technologies and the role of hunting within the broader household economy. Despite case-specific insights, we lack the generalizable information on the decision-making process involved in these changes needed to move from description to prediction (contrast, for example, Moro *et al.* 2013 and Nielsen *et al.* 2014, discussed above). Models designed to predict hunting impacts have typically relied on the assumption of economic rationality in hunters or consumers (e.g., Damania *et al.* 2005; Rentsch and Damon 2013; Iwamura *et al.* 2014). This assumption may be a practical expedient, but there is increasing evidence that it fails to capture important aspects of reality (e.g., Rakotonarivo *et al.* 2017; Ponta *et al.* 2019). Knowledge of the discrepancy between economically optimal choices and actual behaviour would improve predictions of hunting offtakes under a given scenario. Experimental games and agent-based models (ABMs) are two promising tools for engaging with 'real' behaviour. Games offer an opportunity to test the rationality of human actors in realistic scenarios (Redpath *et al.* 2018), whilst ABMs have the flexibility to explore the implications of differences in individual strategies (DeAngelis and Grimm 2014).

Of crucial concern for conservationists is the impact of ranger patrols and other means of law enforcement on hunter behaviour, but whilst deterrence is almost assumed by default, evidence for a consistent effect is lacking (Dobson *et al.* 2018, but see Moore *et al.* 2018 for a convincing demonstration of reduced hunting activity as patrol effort increases). There is anecdotal evidence of hunters switching to less detectable and/or risky modes of hunting when faced with the threat of arrest (Rogan *et al.* 2017), but hunters might also respond by displacing effort to new locations or targeting different species, and the extent and ultimate conservation impacts of this switching behaviour remain unknown. We do not yet know enough to make reliable predictions about the impacts of changes to any given law enforcement regime. Ranger-derived data will require careful analysis to avoid the impacts of confounding variables (Keane *et al.* 2011; Dobson *et al.* 2018), and should ideally be accompanied by data from independent sources (e.g., concurrent household income surveys) in order to validate results by triangulation.

Other relative unknowns include individual-level determinants of hunting success, which alter the relative profitability, and hence economic attractiveness, of hunting. Snaring and shooting require different sets of skills, and the results of many studies imply that skill is an important factor in hunting success (e.g., Coad 2007; Kümpel *et al.* 2009). Understanding individual variation could allow conservationists to better design and target interventions (cf. Jones *et al.* 2018). However, the extent of this influence is currently unclear, and it could be mediated via numerous individual abilities, including snare construction, marksmanship, tracking and stalking animals, and the ability to anticipate the spatial distribution of animals. Koster *et al.*'s (2019) analysis of an extensive dataset from 1821 hunters across 40 sites worldwide shows that individual skill tends to peak between the ages of 30 and 35, but since 'skill' here is inferred by proxy from productivity, these data cannot, unfortunately, be used to unpick the relationship between these two variables. Future work could adopt longitudinal approaches (cf. Gray *et al.* 2015) in order to determine the most important determinants of individual variation in hunting ability and track how it changes over time as individuals learn or forget skills.

Research undertaken in this area should ideally be readily applicable to practical management action, and published in non-academic media or open-access journals (Fuller *et al.* 2014; Hogg *et al.* 2017) in order to prevent a gap emerging between academic and applied practice (Hogg *et al.* 2017; Taylor *et al.* 2017; Britt *et al.* 2018). Prioritisation of the questions listed here should be conducted in collaboration with on-the-ground practitioners (Tables 1 and 2).

Summary

Where hunting is an economic activity, choices about the methods used and the proportion of an individual's time spent on the activity will be influenced by an array of external factors. Estimates of hunting sustainability must be made in the knowledge that hunter decisions are context-dependent and liable to change. Researchers aiming to predict how sustainability might change over time should first identify the relevant drivers of, and constraints on, hunter choice in their study system in order to demarcate the options available to the individual. This process requires an understanding of the characteristics of different modes of hunting.

Some very general patterns are evident: Snaring is almost universal because of its accessibility; snares also allow a hunter to maintain at least a non-zero chance of capturing animals whilst they are primarily engaged in other economic activities; hunting with firearms requires a greater investment in terms of time and money, and probably a higher threshold of skill. The choice of hunting method, which dictates prey selectivity and hunter efficiency (though not in a straightforward manner), depends upon available capital, other demands on time, and degree of physical competence; hunting effort may be dictated not only by economic concerns but by social and cultural constraints; and the selection of areas used for hunting, which determines the animal populations at risk, is the result of an interaction between the potential offtake, law enforcement pressure, and social determinants of accessibility. Researchers need an understanding of these determinants of hunting decision-making as well as their implications for offtake in order to predict future trajectories of hunting impact on wildlife. Much of this understanding can be found in the literature (e.g., Lindsey *et al.* 2013; Cawthorn and Hoffman 2015), but much remains under-studied (Box 2).

Limited funding for conservation means that the effectiveness of potential interventions should be quantified as far as possible in order to facilitate comparisons between alternative options, whilst appreciating that the spatial and temporal scopes of hunting practices and the actions undertaken to limit them may vary. For example, the benefit of ranger patrols that displace hunters cannot be assessed without taking into account impacts in areas to which hunters are displaced (requiring a broad spatial focus), whilst benefits of economic policies such as infrastructure investment, education, or microfinance could take many years to fully accrue (requiring broad

Table 1 Hunting territory characteristics across the Tropics

Region	Country [reference]	Hunting territory size (km^2)	Includes satellite camps?	Number of hunters	Area per hunter (km^2)	Gun hunting activity in area	Snare hunting activity in area	Other activity	Notes
Central/West Africa	Gabon [1]	44.5	No	16	2.8	85% of trips			
Central/West Africa	Cameroon [2]	372 & 1497	No	80 & 156	4.7 & 9.6	31.4% of hunters; 47% of biomass	81.3% of hunters; 50% of biomass		
Central/West Africa	Central African Republic [3]	1000 & 110	Yes	60 & 21	16.7 & 5.2	33% of biomass	67% of biomass		Activity estimates for larger area only
Central/West Africa	Gabon [4]	102	No	–	0.26 (per person, not per hunter)				
Central/West Africa	Various [4]	Mean 196	–	–	0.96 (per person, not per hunter)				Data collated by Coad (2007)
South America	Peru [5]	303	No	61 adult males	5.0 (per adult male)	0% (in theory*)	0%	Almost 100% bow-and-arrow	Manu National Park; firearms prohibited
South America	Brazil [6]	78.5 (idealised range)	No	–		94% of all animals killed			Indigenous tribe; mainly subsistence hunting; hunting territory is per village

References: [1] van Vliet and Nasi (2008); [2] Bobo *et al.* (2015); [3] Noss (1995); [4] Coad (2007); [5] Ohl-Schacherer *et al.* (2007); [6] Constantino (2015)

*Some shotguns are available in the park and are used for hunting, despite legal restrictions (Levi *et al.* 2009)

Table 2 Snare hunting characteristics across the Tropics.

Region	Country [reference]	Snares per hunter (SD)	Average distance of snares from settlement or camp /km (SD)	Average distance of hunting camps from settlements /km	Snare density in hunting territory /km2	Checking interval /days	Relocation interval	Max. number of snares set per hunter per day	Notes
Central/West Africa	Cameroon [1]	117	Up to 15 km from village	–	30	–	–	–	Data collated by Coad (2007)
Central/West Africa	Cameroon [2]	25	Up to 3 km from the camp	10–20 (wet season) 20–50 (dry season, occasional)	(10-30 m apart on trails)	3	–	Approx. 10	Not commercial hunters (Baka people)
Central/West Africa	Cameroon [3]	21	Up to 2 km from village or camp	7.7–23.3	"intervals of several to tens of meters"	"every several days"	–	–	Not commercial hunters (Baka people)
Central/West Africa	Cameroon [4]	120	–	–	–				Snare number is median from 58 snare-hunters
Central/West Africa	Cameroon [5]	108	–	–	156	3.1	–	–	
Central/West Africa	Central African Republic [6]	74 (13.3)	–	3–25	4.2 (Bayanga); 7.8 (overlap between Bayanga and Mossapoula)	2.6	1–3 months	20–30	Density estimate not including areas overlapping with the hunting territory of a neighbouring village.
Central/West Africa	Central African Republic [7]	–	–	25	9.21	–	–	–	Data collated by Coad (2007)
Central/West Africa	Democratic Republic of Congo [8]		–			3.7		10–15 (1 hunter)	Not commercial hunters (Boyela people)
Central/West Africa	Equatorial Guinea (Bioko) [9]	–	–	–	–	3	–	–	
Central/West Africa	Equatorial Guinea [10]	390	–	28.3	56	–	–	–	Snares per hunter calculated by dividing snares per hunter per hunting trip (1484.6) by average trip duration (3.81 days).
Central/West Africa	Equatorial Guinea [11]	56 (in 1990); 92 (in 2003)	–	16.8	8.43	–	–	–	
Central/West Africa	Equatorial Guinea [12]	92.6	–	9.84	–	–	–	–	
Central/West Africa	Equatorial Guinea [13]	61–104	Median: 9.5 in 2003; 3 in 2010	Up to 35 km from settlement	–	–	–	–	Snare number is the range of medians in 1998, 2003 and 2010.
Central/West Africa	Gabon [14]	75.1 (11.2)	Mean: 2.2 (0.19)	7.9	45 (180 m-2 within 1 km, declining to 30 m-2 at 6 km from village)	4.0	9–10 months		Snare number is mean number active at any given time
Central/West Africa	Gabon [15]	15	Up to 2 km from village (further	–	–	3	–	50	Only men >45 years old used snares

Table 2 (continued)

Region	Country [reference]	Snares per hunter (SD)	Average distance of snares from settlement or camp /km (SD)	Average distance of hunting camps from settlements /km	Snare density in hunting territory /km2	Checking interval /days	Relocation interval	Max. number of snares set per hunter per day	Notes
			for gun-hunting at night)						
Central/West Africa	Nigeria [16]	>150	–	–	Every 3-5 m in line	–	1	–	
East Africa	Zambia [17]	–	–	–	–	"Every day or so"	–	–	
Oceania	Indonesia [18]	–	–	–	–	2–3.5	–	–	
South-east Asia	Vietnam [19]	150	–	–	–	–	–	15–20	Per year

References: [1] Ngnegueu and Fotso (1996); [2] Yasuoka (2006); [3] Hayashi (2008); [4] Wright and Priston (2010); [5] Bobo *et al.* (2011); [6] Noss (1995); [7] Dethier (1996); [8] Sato (1983); [9] Colell *et al.* (1994); [10] Fa and Garcia Yuste (2001); [11] Kümpel (2006); [12] Rist *et al.* (2008); [13] Gill *et al.* (2012); [14] Coad (2007); [15] van Vliet and Nasi (2008); [16] Akani *et al.* (2015); [17] Brown and Marks (2007); [18] Pangau-Adam *et al.* (2012); [19] MacMillan and Nguyen (2014)

temporal focus; Ferraro and Pattanayak 2006). Studies of effectiveness must be designed in such a way as to encompass this variation.

Conservation management plans often focus heavily on law enforcement, but there is little direct evidence for the threat of fines or incarceration altering hunter behaviour (Leader-Williams *et al.* 1990; Moore *et al.* 2018). Another major issue in translating research findings into practical recommendations for conservation action is understanding the information gained in research studies about hunters' trade-offs, especially the degree to which stated preferences translate into real behaviour. Finally, a more nuanced understanding of the factors driving individual hunters' decision-making will reduce the potential for unintended consequences from conservation interventions (Larrosa *et al.* 2016). For all of these questions, the extent of generalisability needs to be established. Studies of any given aspect of wild meat hunting tend to be geographically clustered, such that uncritical extrapolation of the results could lead to systematic errors (Taylor *et al.* 2015). A greater emphasis on comparative studies, using consistent approaches where possible, across widely differing contexts should be a future priority.

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