

3 • *How Human Hunters Hunt*

3.1 Introduction

Hunting of wild animals, for meat and other body parts (e.g., pelts, horns, antlers) has been part of the human story for millennia. In this book, we focus only on the hunting of wild animals by humans for food. In this chapter we describe how humans hunt with a focus on technology and on the cultural and anthropological aspects of hunting; the topic of optimal hunting is addressed in Chapter 4. In broad terms, hunting can be subsistence, commercial, or recreational (Fig. 3.1, Ojasti 1996). We do not address recreational hunting, which refers to activities in which the main objective is the personal enjoyment of the hunter, rather than food or profit (e.g. trophy lion hunting, Whitman *et al.* 2004). Recreational hunting may have roots in traditional subsistence hunting or commercial hunting activities (McCorquodale 1997). We also do not address the removal of predators that can be dangerous to people or domestic animals, or the removal of pests that destroy crops or kill livestock, except when these animals are being used as wild meat.

Only in subsistence hunting is the sole purpose to provide food for the hunters and their families and hence it plays a vital role in their sustenance and even survival (Peres 2000). By contrast, commercial hunting takes place when natural products are exploited to be sold for profit. The consequences of unsustainable commercial harvesting of marine and terrestrial wild animals are now clearly felt throughout the globe (Di Minin *et al.* 2019). The impacts of uncontrolled commercial hunting on wildlife in the tropics and subtropics are also significant; these topics are discussed more in depth in Chapters 2 and 6 of this book.

In some countries, subsistence hunting is defined by law as just hunting for personal consumption, and it is often considered illegal to sell any surplus. Conversely, the sale of some of the animals hunted but not eaten by the hunters or their families, sometimes the most valuable species, can be an important source of income (Alexander *et al.* 2015; Coad *et al.* 2010; Schulte-Herbrüggen *et al.* 2013). However, Van Vliet

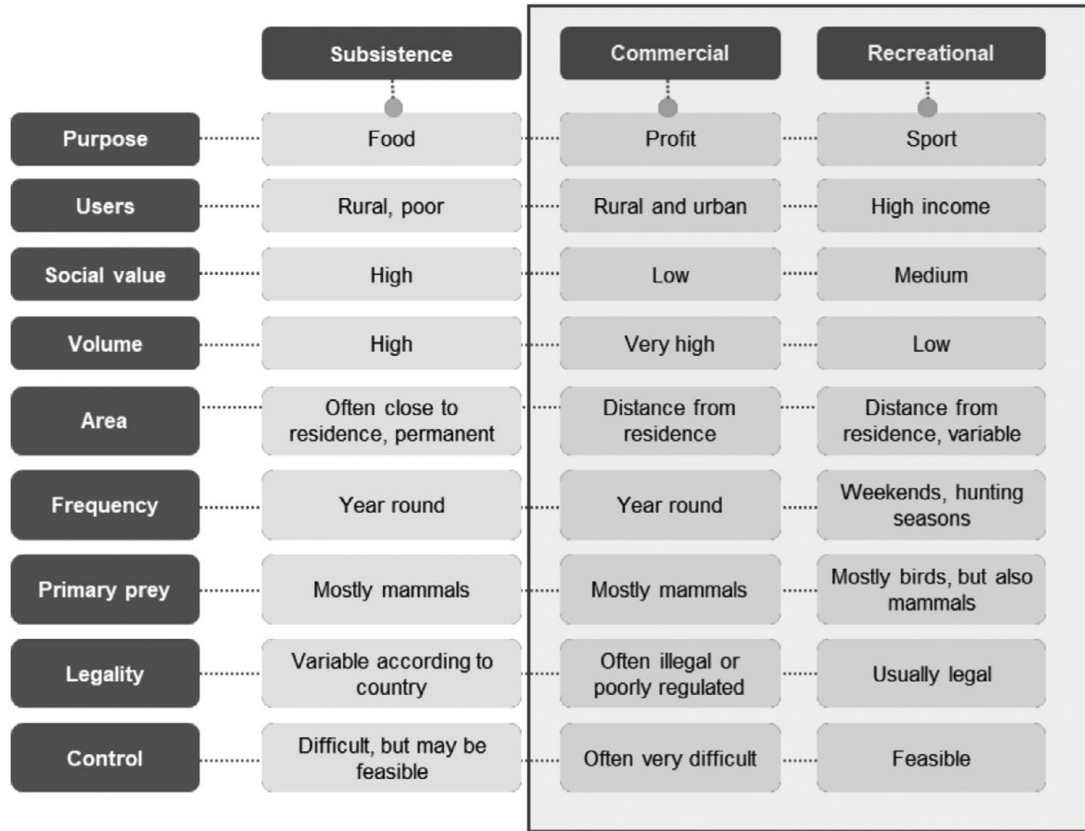


Figure 3.1 Comparison of main attributes of subsistence, commercial and recreational hunting (modified from Ojasti 1996).

et al. (2019) argue strongly that formal regulations in many tropical countries are ill adapted to the reality in which rural and Indigenous Peoples live and that reforms which clarify the rights to sell surplus of meat and align land tenure rights with wildlife use rights are imminently needed. Many rural families sell surplus wild meat (see e.g. El Bizri *et al.* 2020b), and this can provide a very important source of income; if the right regulations are in place, surplus sale of wild meat should be permitted in rural settings (see also Chapter 8). Frequency of wild meat consumption and sale of wild meat are positively associated with proximity to markets, especially in urban centres (e.g. Sierra *et al.* 1999).

3.2 Hunting Technology

Since at least the past 200,000 years, when modern humans evolved, subsistence hunting for protein acquisition has dominated (Stanford & Bunn 2001). In fact, humans have spent more time as hunter-gatherers than as agriculturalists, industrialists or post-industrialists. This not only emphasizes the importance of hunting animals for our survival over many millennia but also highlights its role in the emergence and evolution of individual and social behaviour in our species. Because human beings are ill-adapted predators, lacking fangs, claws or high speed, hunting technology has filled this gap. Tools for hunting allow humans to expand the range of prey captured, reduce pursuit times and extend diet breadth by the use of methods for killing at a distance (spears, nets etc.), passive forms of animal capture (traps) and the use of methods to lure prey (decoys). In particular, projectile weaponry (such as the bow and arrow, and spearthrower and dart) has been a key strategic innovation that has aided ecological niche broadening and has allowed the dispersal of humans throughout the world (Shea 2006; Shea & Sisk 2010).

Numerous depictions of animals in prehistoric cave art clearly manifest the importance of hunting for human beings. Prehistoric cave art provides the most direct insight that we have into the earliest storytelling (Mithen 1989). One of the most primitive is the image portraying several figures that appear to represent therianthropes (human beings who metamorphose into other animals by means of shapeshifting) hunting wild pigs and dwarf bovids, the latter probably anoa, in the Leang Bulu' Sipong 4 cave in the limestone karsts of Maros-Pangkep, South Sulawesi, Indonesia (Fig. 3.2). The animals are being hunted by figures with animal characteristics who carry long thin objects that the authors interpret as spears and/or ropes. The interpretation of the scene is that it is a communal hunt, likely a game drive



Figure 3.2 Drawings found in Leang Bulu'Sipong 4 cave, south of Sulawesi, showing a buffalo being hunted by part-human, part-animal creatures holding spears and possibly ropes (from Aubert *et al.* 2019; reprinted with permission from Nature Springer and M. Aubert).

where animals of any species are driven from cover and directed towards waiting hunters. This image, created at least 43,900 years ago and described in 2019 (Aubert *et al.* 2019), has already been replaced as the oldest-known painting by the discovery of a figurative painting of a Sulawesi warty pig, dated to be 45,500 years old (Brumm *et al.* 2021).

In the following sections we describe the available evidence for the different forms of weapons and techniques used in hunting animals in the past and highlight both the importance hunting has had in the sustenance of humans over millennia but also how hunting technology itself has impacted their physical, social and cognitive evolution.

3.2.1 Projectile Hunting: Changes for the Better

Like most aspects of early biological and cultural evolution (e.g. Groucutt *et al.* 2015), the origin and development of projectile technology remain poorly understood. The earliest evidence for launched weapons used in both hunting and warfare for any hominid comes from several wooden spears found in Schöningen, Germany. These spears, dated ~400,000 BP,

that is before the emergence of modern humans (Thieme 1997), were either hand-held, short-ranged thrusting weapons (Shea 2006; Thieme 1997) or throwing weapons for distances up to 20 metres (Milks *et al.* 2019). Relatively large, heavy spears sometimes tipped with stone armatures were typical of Neanderthal hunting, where Neanderthal upper limb and upper body morphology has been suggested to be an adaptation to the energetic and mechanical requirements of using thrusting spears (Churchill 2014). Thrusting and short-distance throwing spears preconditioned hunting strategies, and hunting with spears has often been equated with large hunter group size (Wadley 2010). The subsequent appearance of distance weapons is a critical development in human hunting technology. As a result, the arsenal of spears used by AMH was considerably larger, compared to Neanderthals who only used thrusting spears (Churchill 2014) or short-distance throwing lances (Milks *et al.* 2019). What were previously thought to be the oldest-known spears, those found in Clacton-on-Sea, UK (Oakley *et al.* 1977), and Lehringen, Germany (Movius 1950), dated to the Middle Pleistocene, have been debated because associated faunal remains do not necessarily demonstrate hunting (Klein 1987). For example, the Lehringen spear was found between the ribs of an elephant skeleton, but some authors have suggested that these sites are spring-, stream- or lakeside localities where it is difficult to separate bones that may represent natural deaths from human kills (Klein 1987). By contrast, the association of the Schöningen spears with stone tools and butchered remains of more than ten horses confirms them as hunting weapons, suggesting that systematic hunting that employed projectile technology was already present in pre-modern hominids.

The oldest backed stone blades have been found at Twin Rivers, Zambia, in deposits of approximately 300,000 BP (Barham 2002). Backed stone blades have one thick, blunt side suitable for hafting, with the attachment of the blades to wooden spears or arrows (Fig. 3.3). The design and preparation of backed tools, the preparation of hafts and the final hafting require problem-solving and planning that is usually associated with modern humans (Ambrose 2001). Indeed, new fossil finds, identified as *Homo sapiens*, from Jebel Irhoud, Morocco, place backed tool preparation at the same time as the emergence of AMH in Africa. These fossils, dated $315,000 \pm 34,000$ BP, show a mosaic of key modern human morphological features of early or recent AMH and more primitive cranial morphology (Hublin *et al.* 2017). The new technology together with new behaviour, including syntactic language, possibly allowed modern humans to expand their range into previously unoccupied Congo Basin tropical

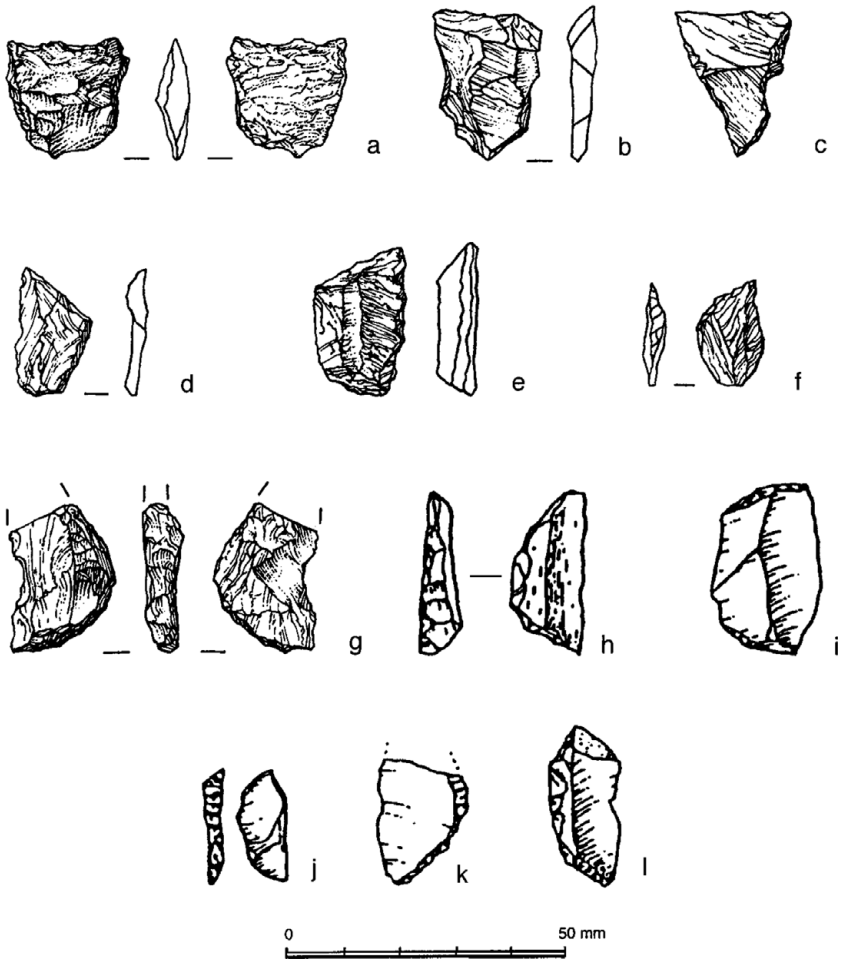


Figure 3.3 Backed tools from Twin Rivers (from Barham 2002 reprinted with permission from Elsevier).

forests (Barham 2001). Backed stone blades have been confirmed in East Africa at ~130,000 BP (Mehlman 1990) and in southern Africa between ~70,000 and ~60,000 BP (Wadley & Mohapi 2008). The latter paper describes Howiesons Poort Industry tools from Sibudu in South Africa, which are particularly interesting as they comprise diverse stone projectiles linked to different types of hunting tools. Tools made from dolerite were relatively large, too large for arrow heads, but suitable for darts and spearheads. Quartz tools were of a size of arrowheads, whilst hornfels tools

varied in size and appear to have been reused during their lifetime for different purposes by reshaping. Trace analyses suggest that most tools were parts of hunting weapons, in particular bows and arrows (Lombard & Phillipson 2010; Wadley & Mohapi 2008).

Although lithic projectile weaponry has been confirmed across Africa before ~50,000 BP, it appears not to have been widespread or in regular use in this continent, in Europe or the Levant (Shea 2006). However, by 45,000–40,000 BP, lithic projectiles were in use in most parts of the world occupied by humans (Knecht 1997), after dispersing out of Africa and arriving at the periphery of the Old World, Australia, Siberia and northwest Europe by 50,000–40,000 BP (Groucutt *et al.* 2015). This widespread use of distance weapons for large animal hunting and warfare is regarded as an epiphenomenon of the ‘Upper Palaeolithic’ behavioural revolution as it involves planning, social organization and the application of suitable technology. Such use of projectile weapons allowed the more accurate killing of large, potentially dangerous prey at a safe distance compared to hand-delivered thrusting methods. The contention is that these technological changes diminished the need for muscular strength, thus affording the more gracile anatomically modern humans a competitive advantage over Neanderthals (Churchill & Rhodes 2006). Moreover, the development of mechanically delivered projectile weapons, spearthrower-darts or bows and arrows, further improved hunting efficiency in modern humans. The earliest evidence of mechanically delivered projectile weapons was found at Grotta del Cavallo in southern Italy, discovered alongside signs of hunting of young horses (Sano *et al.* 2019). These projectiles, dated to between 40,000 and 45,000 BP, correspond to the early migration period of modern humans into Eurasia (Groucutt *et al.* 2015; O’Connell *et al.* 2018). The Grotta del Cavallo projectiles pre-date the previously known spearthrowers and arrows from France and Germany by more than 20,000 years (Cattelain 1997; Sano *et al.* 2019).

3.2.2 Nets, Traps, Snares and Other Methods

In contrast to lithic artefacts and, in some cases, larger wooden fragments, materials such as fibres do not preserve well in the archaeological record. Evidence for hunting with nets, traps and snares is therefore rare; such information is, however, of importance for our understanding of human evolution. The operation of these techniques constitutes a significant milestone in the development of memory and cognition in planning across space and time (Wynn & Coolidge 2003). Nonetheless, indirect

evidence from the Sibudu site in South Africa points to the use of snares during the Howiesons Poort Industry ~65,000–60,000 BP, possibly even ~70,000 BP (Wadley 2010). The high frequency and the relatively high taxonomic diversity of comparatively small mammals found at the site are consistent with modern snare hunting (Chapter 6) and not with hunting with projectile weaponry (bows and arrows or spears). This follows from our understanding of optimal foraging strategies (Chapter 4), which indicates that hunters prefer larger prey, especially when faunal assemblages are not depleted by overhunting, since during the Pleistocene human population density was likely to have been low. In Sibudu, the high frequency of small carnivores (including felids, viverrids, mongooses, mustelids and canids) does not suggest net hunting as these species are difficult to capture with this method but are easily caught with snares or traps. Trapping of carnivores often requires bait, often living. Using one prey animal to catch another presupposes a certain commitment to catch the carnivore. Generally, catching carnivores is more about protection against physical harm by such animals than for food since their meat is rarely preferred (see Section 3.4). The high number of carnivore remains in Sibudu suggest that they may have been caught for symbolic, medicinal or magic reasons, e.g. for their fur, teeth and claws. The high frequency of bushpig remains in Sibudu also suggests snare hunting because the species is nocturnal and dangerous to hunt. Although net hunting for bushpigs could have occurred, as demonstrated by Pygmy net hunters (Dounias 2016), these animals are strong enough to tear nets or break through the line of beaters rather than be cornered (Skinner & Chimimba 2005). The abundant remains of blue duiker, a common forest antelope, may point also to snaring since this relatively small animal is widely caught nowadays with snares throughout West and Central Africa (Fa *et al.* 2005) but is more difficult to hunt with bow and arrow or spears. However, duikers can be attracted in to the open by hunters imitating the call of a distressed animal (Brosset 1966; van Vliet *et al.* 2009). Finally, there is evidence that faunal assemblages in Sibudu became less diverse during the more recent Pleistocene, with fewer small mammals, bushpig or blue duiker remains being found. Wadley (2010) explains this change to be the result of larger hunter group sizes appearing as a result of population growth, thus allowing the hunting of large prey with spears. It is possible that, as observed in modern hunter-gatherers, as human group sizes increased large animals may have been primarily targeted by men, with the added benefit for the more skilled hunters to attain social prestige and kudos (see Section 3.4). Although in some

contexts women are known to participate in active hunts with men (e.g. Aka Pygmy net hunting, Noss & Hewlett 2001), until recently when snaring has become commonplace due to the use of more affordable and accessible cable (Noss 1998b), trapping animals may have been largely pursued by women. This division of labour between the sexes has been postulated in Fa *et al.* (2013) to explain the difference in hunting techniques used by Neanderthals and AMH in Pleistocene Iberia. Snare hunting therefore introduces an alternative to large prey hunting which increases food security when men are unable to bring prey home. For the Hadza in East Africa, the chances of obtaining large prey was only 3% or 45 days of failure between successes, whereas snaring was successful with only one to three days of failure in-between and an overall success rate 40 times higher than that for large prey (Hawkes *et al.* 1991, 2001).

It is possible that pit trap hunting may have occurred as early as 40,000 BP. In a study in the Japanese Archipelago as many as 376 traps were excavated from 51 Pleistocene sites (Sato 2012). These were pits of about 1–2 metres in diameter, which may have been used for medium-sized prey such as wild boar and deer. Similarly, pit traps of over 20 metres in diameter have been discovered in Mexico containing a large assemblage of mammoth bones (Instituto Nacional de Antropología e Historia (Mexico) 2019). With an age of ~15,000 years they stem from the period of the peopling of the Americas and attest the versatility of humans hunting animals for food.

The oldest known confirmed evidence of the use of poison for hunting purposes dates to about 24,000 BP from the Border Cave in South Africa (d'Errico *et al.* 2012a). Although the identification and interpretation of archaeological micro-residuals of arrow poison is notoriously difficult (Bradfield *et al.* 2015), biochemical traces have been identified as arrow poison (d'Errico *et al.* 2012b). The technical and symbolic items also found at the site suggest that the Border Cave inhabitants used the same material culture 44,000 BP as today's San people, predating by 24,000 years the current consensus for the emergence of San hunter-gatherer cultural adaptations. The findings include bone points that are identical to San poisoned arrow points. Arrow points dated 37,000–35,000 BP, which could have been used with poison, have also been found at the White Paintings Rock Shelter in Botswana (Robbins *et al.* 2012). Today, San use beetle larvae and plant extracts to prepare poison for their arrow heads (Lee *et al.* 1976).

Another technological revolution appeared with the use of nets for hunting small and medium-sized prey. The first evidence for net hunting

comes from the Pavlov and Dolní Věstonice sites in the Czech Republic (Pringle 1997; Soffer 2000, 2004) where clay fragments have been found bearing impressions of nets woven from wild plants and dated ~27,000 to ~25,00 BP. Evidence of the use of these nets is the large number of hare, fox and other small mammal bones found in the same site. The suggestion is that net-hunting is likely to have played an important role for food acquisition, introducing communal hunting practices that allowed children and women to participate (Soffer 2000). In the case of Aka Pygmy forest foragers of the Central African Republic women net-hunt more frequently than men (Noss & Hewlett 2001). In this particular context, women participated in net hunts when game was relatively abundant, they received relatively high caloric returns from hunting, they had access to the means/technology just as men, and importantly, Aka men did not prohibit them from participating. Thus, systems that are flexible between the sexes and ages and that adapt to prey abundance are likely to have been advantageous. When large prey was less abundant, the possibility of obtaining large numbers of small and medium-sized prey might have contributed to the development of larger, more settled populations as indicated from numerous archaeological finds for the Gravettian hunter-gatherers from Spain to southern Russia (Soffer 2000). This new technology may have also contributed to the diminishing selection pressure for muscularity, vital for large mammal hunting without mechanically delivered projectiles (see Soffer, cited in Pringle 1997).

3.3 Modern Hunting Techniques

Table 3.1 gives an overview of hunting methods from a total of 125 study populations where adequate information has been published. Available data reflects a strong bias towards Africa ($n = 90$) compared to South/Central America ($n = 21$) and Asia ($n = 13$). In Africa, much research interest has been directed towards hunter-gatherer societies, in particular the different Pygmy communities ($n = 33$). Information on the proportions of different hunting methods encountered is often not directly comparable with each other because they refer to different baseline units such as hunters (e.g. 10% of hunters used guns only) or the number of animals killed with each method. Moreover, some studies distinguish between technology used to kill animals, such as firearms and traps, from techniques such as hunting with dogs and horses, whilst some studies combine both, especially hunting with dogs (dogs may be used to chase and corner animals but also to kill their prey). For example,

Table 3.1 Overview of hunting methods from a total of 125 study populations. When the mix of hunting methods differed or when different combinations of hunting methods were observed either over time or between study communities, studies are listed with separate entries for time or location

Country, population, study period	Firearms	Modern snares	Explosives	Dogs	Traps	Bow & arrow	Spear	Club, stick	Knives / machetes / axes	Crossbow	Catapult/slingshot	Blowpipes	Fire	Trad.snares	Net	Hand	Others	Reference
Africa																		
Benin, 2017	x																	Ahmadi <i>et al.</i> (2018)
Botswana, review	x			x	x													Barnett (2000b)
Botswana, San, 1987/8				x		x	x	x										Ikeya (1994)
Botswana, San, 1990–2001		x		x	x	x	x	x								x		(Liebenberg (2006)
Botswana, 2014/5	x	x		x				x							x		x	Rogan <i>et al.</i> (2017)
Cameroon, mostly Badjoué, some Baka Pygmies, 2002/3/9/16	x	x															x	Ávila <i>et al.</i> (2019)
Cameroon, 2013	x	x		x			x									x		Bobo <i>et al.</i> (2015)
Cameroon, 1996	x	x																Delvingt (1997)
Cameroon, Fang (Bantu), 1984–91	x	x			x									x				Dounias (2016)

(cont.)

Table 3.1 (cont.)

Country, population, study period	Firearms	Modern snares	Explosives	Dogs	Traps	Bow & arrow	Spear	Club, stick	Knives / machetes / axes	Crossbow	Catapult/slingshot	Blowpipes	Fire	Trad.snares	Net	Hand	Others	Reference
Cameroon, Baka Pygmies, 2012/3	x	x			x		x		x				x				x	Duda <i>et al.</i> (2017)
Cameroon, Baka Pygmies, 2013		x																Fa <i>et al.</i> (2016)
Cameroon, Baka Pygmies, 2002		x					x		x							x		Fa <i>et al.</i> (2016)
Cameroon, Pygmies & non-Pygmies, 1994–6	x	x								x								Fimbel <i>et al.</i> (1999)
Cameroon, 1997	x	x																Fotso and Ngnegueu (1998)
Cameroon, Baka Pygmies, 2001/2	x	x		x			x		x							x		Hayashi (2008)
Cameroon, 1988	x	x																Infield (1988)
Cameroon, 1994/5		x																Muchaal and Ngandjui (1999)

Cameroon, Fang (Bantu), 1904–9	x		x	x	x	x		x	x	Tessmann (1913a, 1913b)	
Cameroon, Banyangi, 1999–2002	x	x	x		x					Willcox and Nambu (2007)	
Cameroon, Mbo, 1999–2002	x	x			x					Willcox and Nambu (2007)	
Cameroon, Banyangi, 2007	x		x	x						Wright and Priston (2010)	
Cameroon, Baka Pygmies, 2002	x	x	x			x				Yasuoka (2006a)	
Cameroon, non-Pygmy visitors, 2002	x	x								Yasuoka (2006a)	
Cameroon, Baka Pygmies, 2002/3	x	x			x	x			x	Yasuoka (2006b)	
Cameroon, Baka Pygmies, 2005	x	x			x	x			x	Yasuoka (2009)	
Cameroon, Baka Pygmies, 2002–14		x								Yasuoka <i>et al.</i> (2015)	
Cameroon, Konabembe, site 1, 2012/13	x	x							x	Yasuoka <i>et al.</i> (2015)	
Cameroon, Konabembe, site 2, 2012/13	x	x							x	Yasuoka <i>et al.</i> (2015)	
Central African Republic, Bofi & Aka Pygmies, 1999–2003	x	x		x	x				x	x	Lupo and Schmitt (2005, 2017)
Central African Republic, 1994		x									Noss (1998a, 1998b)

(cont.)

Table 3.1 (cont.)

Country, population, study period	Firearms	Modern snares	Explosives	Dogs	Traps	Bow & arrow	Spear	Club, stick	Knives / machetes / axes	Crossbow	Catapult/slingshot	Blowpipes	Fire	Trad.snares	Net	Hand	Others	Reference
Central African Republic, Baka Pygmies, 1994/5		x							x					x		x		Noss (2000)
Central African Republic, 2005	x	x																Remis and Kpanou (2011)
Côte d'Ivoire, 2012	x	x						x	x									Gonedélé Bi <i>et al.</i> (2017)
DRC, Mbuti Pygmies, 1984–8						x	x		x					x	x		x	Carpaneto and Germi (1989)
DRC, Mbuti Pygmies, 1985					x									x				Fa <i>et al.</i> (2016)
DRC, Mbuti Pygmies, 1985					x	x	x							x			x	Fa <i>et al.</i> (2016)
DRC, Mbuti Pygmies, 1988					x	x	x										x	Fa <i>et al.</i> (2016)
DRC, Mbuti Pygmies, 1985					x		x							x			x	Fa <i>et al.</i> (2016)
DRC, Mbuti Pygmies, 1988					x	x	x							x		x		Fa <i>et al.</i> (2016)
DRC, Mbuti Pygmies, 1987					x	x	x							x			x	Fa <i>et al.</i> (2016)
DRC, Mbuti Pygmies, 1985					x	x	x							x			x	Fa <i>et al.</i> (2016)
DRC, Mbuti Pygmies, 1988					x	x	x							x			x	Fa <i>et al.</i> (2016)

DRC, Mbuti Pygmies, 1985			x	x	x			x		x	Fa <i>et al.</i> (2016)
DRC, Mbuti Pygmies, 1985	x							x	x		Fa <i>et al.</i> (2016)
DRC, Mbuti Pygmies, 1985											Fa <i>et al.</i> (2016)
DRC, Mbuti Pygmies, 1985		x								x	Fa <i>et al.</i> (2016)
DRC, Mbuti Pygmies, 1974/5/80/1								x			Ichikawa (1983)
DRC, 2014	x	x									Spira <i>et al.</i> (2019)
DRC, Mbuti Pygmies, 1978/9											Terashima (1983)
DRC, Efe Pygmies &, 1982/1983										x	Wilkie (1987, 1989)
DRC, Efe Pygmies & Lese horticulturalists, 1982/3	x	x								x	Wilkie (1987, 1989)
DRC, Lese horticulturalists, 1982/3	x	x									Wilkie (1987, 1989)
Equatorial Guinea, 1986/90	x	x									Butynski and Koster (1994)
Equatorial Guinea, 1997–2010	x	x									Cronin <i>et al.</i> (2010)
Equatorial Guinea, 1998/99	x	x									x Fa and García Yuste (2001)
Equatorial Guinea, 2003	x										Gill <i>et al.</i> (2012)
Equatorial Guinea, 2010	x										Gill <i>et al.</i> (2012)
Equatorial Guinea, 2002–4	x	x									Kümpel (2006); Kümpel <i>et al.</i> (2009)
Gabon, 1992	x									x	x Carpaneto <i>et al.</i> (2007)
Gabon, 1988	x	x									Lahm (1994)

(cont.)

Table 3.1 (cont.)

Country, population, study period	Firearms	Modern snares	Explosives	Dogs	Traps	Bow & arrow	Spear	Club, stick	Knives / machetes / axes	Crossbow	Catapult/slingshot	Blowpipes	Fire	Trad.snares	Net	Hand	Others	Reference
Gabon, Pouvi, Bateke, 2004–10	x	x			x													Walters <i>et al.</i> (2015)
Liberia, review	x			x	x												x	Bene <i>et al.</i> (2013)
Madagascar, 2010	x	x		x	x						x							Gardner and Davies (2014)
Madagascar, 2004	x	x		x	x		x				x				x			Golden (2009)
Madagascar, review (bats)	x				x			x			x			x		x	x	Jenkins and Racey (2009)
Malawi, review	x	x				x												Barnett (2000a)
Nigeria, 2012	x			x	x				x									Friant <i>et al.</i> (2015)
Republic of Congo, Mbuti Pygmies, 1992/3						x	x								x			Carpaneto and Germi (1989)
Republic of Congo Aka Pygmies, 1991/2	x	x			x		x	x	x	x				x	x		x	Kitanishi (1995)
Republic of Congo,	x	x																Marrocoli <i>et al.</i> (2019)

Table 3.1 (cont.)

Country, population, study period	Firearms	Modern snares	Explosives	Dogs	Traps	Bow & arrow	Spear	Club, stick	Knives / machetes / axes	Crossbow	Catapult/slingshot	Blowpipes	Fire	Trad.snares	Net	Hand	Others	Reference
Asia																		
China, 2015/6	x	x																Chang <i>et al.</i> (2017)
India, Indigenous	x	x		x	x	x	x											Aiyadurai (2007); Aiyadurai <i>et al.</i> (2010)
India, 2006	x	x	x	x				x			x				x		x	Gubbi and Linkie (2012)
India, 2002	x																	Kaul <i>et al.</i> (2004)
India, 2002	x	x																Kaul <i>et al.</i> (2004)
India, Shertukpen, 2012	x			x														Velho and Laurance (2013)
Indonesia, 2011	x	x		x	x													Luskin <i>et al.</i> (2014)
Indonesia, 2005/6	x	x		x		x	x											Pangau-Adam <i>et al.</i> (2012)
Indonesia, 1995–9	x	x										x			x			Riley (2002)
Malaysia, Semaq Beri, 1978/9									x			x						Kuchikura (1988)
Malaysia, Temuan, 2004	x				x						x	x						Naito <i>et al.</i> (2005)
Myanmar, 2002/3	x	x			x					x								Rao <i>et al.</i> (2005)

Vietnam, Katu, 2011	x		x		x										MacMillan and Nguyen (2014)
Latin America															
Bolivia, Brazil, Colombia, Ecuador, Peru, Suriname, Venezuela, Indigenous, review	x				x				x						Jerozolinski and Peres (2003)
Brazil, mixed,	x	x		x	x								x		Alves <i>et al.</i> (2009)
Brazil, Kaxinawa, 2006–9	x								x				x		de Araujo Lima Constantino (2015)
Brazil, Indigenous, 2001/2	x														de Mattos Vieira <i>et al.</i> (2015)
Brazil, 2004/5	x			x					x						Jean Desbiez <i>et al.</i> (2011)
Brazil, Guajá	x			x		x			x						Forline (1997)
Brazil, 1973/4	x			x	x										Smith (1976)
Ecuador, Huaorani, 2002	x		x				x	x		x		x	x	x	Franzen (2006)
Ecuador, Huaorani	x			x			x	x							Lu (1999)
Ecuador, Huaorani, 1989/90							x			x					Rival (2003)
Ecuador, Huaorani,	x						x			x					Yost and Kelley (1983)
Ecuador, Shuar, 2001–3	x	x		x				x	x			x			Zapata-Ríos <i>et al.</i> (2009)
Latin America, Indigenous, review	x			x		x				x			x		Redford and Robinson (1987)
Latin America, Mestizos, review	x			x											Redford and Robinson (1987)

(cont.)

Table 3.1 (cont.)

Country, population, study period	Firearms	Modern snares	Explosives	Dogs	Traps	Bow & arrow	Spear	Club, stick	Knives / machetes / axes	Crossbow	Catapult/slingshot	Blowpipes	Fire	Trad.snares	Net	Hand	Others	Reference
Mexico, Maya	x			x					x									Jorgenson(1993)
Nicaragua, Mayangna and Miskito, 2004/5	x			x														Koster(2008b)
Nicaragua, Mayangna, Miskito,	x			x			x		x									Koster(2007)
Panama, Mestizos, Buglé, Ngöbe, 1999/2000	x			x	x	x					x							Smith(2008)
Peru, Machiguenga, 1988–91							x											Alvard (1993a, 1995b,)
Peru, Piro, 1988–91	x						x											Alvard (1993a, 1995b)
Peru, Matses	x			x		x	x		x									Romanoff(1984)
Worldwide																		
Review (bats)	x				x	x		x			x				x	x	x	Mickleburgh <i>et al.</i> (2009)
Total	93	72	2	41	42	36	40	18	18	9	8	9	2	5	30	19	25	
Percentage	77	60	2	34	35	30	33	15	15	7	7	7	2	4	25	16	21	

Friant *et al.* (2015) report that techniques included traps (75%), guns (71%), machetes (71%) and dogs (18%). Elsewhere, they refer to 'hunting with a gun and dog', raising the question of how the prey was killed. Since hunters with dogs typically use other hunting technologies at the same time (Koster 2009) and the use of ammunition is expensive, the question is how to interpret the data listed in publications. In the case of Friant *et al.*'s study (2015), did dogs kill 18% of prey and guns kill 71% or were guns even more important by killing 89% of prey? Hunting with nets is a similar problem because it remains often unclear how the netted animals were killed. Dounias (2016) points out that spears are mainly used to deliver the coup de grace to animals cornered by dogs or nets and are rarely used as the sole hunting technique, but studies are often not clear whether spears are supporting net hunting or constitute separate strategies. Most studies imply but do not clearly indicate whether snares refer to modern snares that use wire cable made of metal or nylon. Snares made with plant fibres were recorded alongside snares made using metal wire in the Republic of Congo (Kitanishi 1995). Marrocoli *et al.* (2019) refer to snare hunting throughout their document without specifying whether modern or traditional snares are used, but their reference to the Congolese law forbidding hunting with metal snares implies that the snare hunting in question refers to modern ones. Only three studies explicitly referred to traditional snares or snares made from vegetable fibres. Use of snares is generally illegal. Although all studies were careful to work on the basis of anonymity, the response especially regarding snares might be biased and may underestimate the general use of trapping with this method. Casual and unreliable reporting is a general problem with questionnaires, especially when illegal methods are involved. For example, in the state of Arunachal Pradesh in India, hunters reported 11 mammalian species hunted during formal interviews but another 22 species were observed during casual visits, festivals and informal discussions (Aiyadurai *et al.* 2010). Notwithstanding these shortcomings, several key features are discernible from Table 3.1, as examined below.

3.3.1 Hunters Use Many Different Technologies

Almost all studies list more than one technology used, their mix depending on the type of animals hunted and local traditions (Fig. 3.4). This variation is best illustrated by the broad spectrum of how bats are caught and killed. Bats are common wild meat items in Africa and Asia, but are rarely targeted in South and Central America with the exception



Figure 3.4 (a) Asurini do Tocantins tribe member from the region between the Xingu and Tocantins rivers holding bow and arrow (WIN-Initiative/The Image Bank Unreleased/Getty Images); (b) Huaorani hunter from Ecuador using blowgun in forest (WIN-Initiative/The Image Bank Unreleased/Getty Images); (c) Bayaka or Aka tribesman holding spear in a forest in the Central African Republic (Timothy Allen/The Image Bank Unreleased/Getty Images); (d) Yangoru Boiken bat catcher retrieves a giant fruit bat from his net in the foothills of Mount Turu, East Sepik Province, Papua New Guinea (Timothy Allen/The Image Bank Unreleased/Getty Images).

of one Indigenous tribe, the Nambiquara of Western Brazil, who actively hunt three Phyllostomid bat species for food (Jenkins & Racey 2009; Mickleburgh *et al.* 2009; Setz & Sazima 1987). Bats are usually hunted either at roosting sites or at feeding sites by a wide variety of methods – bait and hook, bamboo poles with thorns or fish hooks on the end, barbed burrs of some plant species, birdlime, bow and arrow, by hand, catapults and slingshots, fire, firearms including guns, rifles and airguns, funnel traps to catch bats emerging from caves, hand nets, kites with hooks, nylon lines and ropes with hooks, snares, specialized large nets or fishing nets at roost or feeding trees, sticks, stoning and thorny bushes (Mickleburgh *et al.* 2009).

3.3.2 Techniques Differ between Neighbouring Villages and Regions

Hunting techniques seem to be determined by a mix of tradition, prey species and their densities, but also by the motivations of the hunters themselves. Mbuti Pygmy hunters of the Ituri forest in the Northeastern Congo Basin can be divided according whether they preferentially use bows and arrows or net hunting (Carpaneto & Germe 1989, 1992; Ichikawa 1983; Terashima 1983). The use of bows and arrows is the original subsistence hunting strategy of all the Mbuti Pygmies and involves either solitary hunts in which the archer walks in the forest or lies in ambush, and communal beat-hunt hunting, the so-called *mota*. This Mbuti Efe subgroup in the northeastern parts of the Ituri forest is in social contact with local Sudanic Lese agriculturalists and has adopted iron arrowheads and spear blades from the Lese but never engages in net hunting. The Mbuti Swa use nets alongside bows and arrows. Living in the central, southern and western parts of the Ituri forest, they are in social contact with local Bantu Bira and Ndaka agriculturalists, from whom the Swa have adopted net technology when they invaded the forest about 1,000–3,000 BP.

The impact of the motivation to hunt with different methods is demonstrated by the four different ethnic groups living around the Banyang-Mbo Wildlife Sanctuary in southwestern Cameroon (Willcox & Nambu 2007). The Mbo are almost exclusively hunters and gatherers while the Banyangi are hunters, gatherers and also cash-crop farmers. Both groups use shotguns and wire snares at almost the same rate (Banyangi 55% and 37%, respectively; Mbo 56% and 38%, respectively). The Bakossi and Basossi primarily farm cash crops (coffee and cocoa) and do not hunt, but their cash income allows them to buy domestic meat,

wild meat and fish. In the oil palm plantation-dominated landscapes of Sumatra motivations and weapon choice are also aligned with the different ethnic groups (Luskin *et al.* 2014). Subsistence hunting is predominant in Javanese immigrants and Malay smallholder farmers, who used snare hunting and air rifles to hunt macaques and wild boar for both pest control and consumption. Professional Chinese and Batak hunters specialized in herding wild boar into wire net traps for subsequent sale. Social and cultural reasons are also the motivations for weekly large social day hunts with dogs by ethnic Minangkabau. Finally, wealthy members of a sport hunting group used hunts with firearms from pick-up trucks at night for sport.

The choice of weapon can depend on which prey hunters pursue. For example, Rogan *et al.* (2017) demonstrates that prey size and weapon choice are significantly correlated with firearms preferred for large game. Optimal foraging theory (Chapter 4) predicts a broad prey profile when a less efficient hunting technology is used compared to a narrower profile for firearms. Indeed, Aché bow hunters' prey profile is broad and includes less profitable species typically not targeted by shotgun hunters (Alvard, 1993; Hill & Hawkes 1983). Although firearm usage is not always correlated with the mean body mass of the target prey (Fa & García Yuste 2001; Gonedélé Bi *et al.* 2017), the general trend is the focus on large animals, one of the main threats against wildlife in Central Africa (Kümpel 2006). This is especially problematic for arboreal primates which are preferentially targeted with firearms (Bobo *et al.* 2015; Mittermeier 1987). Dounias (2016) reports that Fang hunters shoot 82% of harvested primate biomass, although firearms contributed 37% of the hunted biomass overall. Traditional weapons may be superior for animals moving in large groups since silent weapons such as blowguns allow the pursuit of several group-members unlike rifles which will invariably disperse the targeted group after hearing the shot (Peres 1990). However, shotguns can be used to kill several animals in large dense groups that remain in the same location, for example, the shooting of numerous individual mandrills who will remain on a refuge tree without dispersing, (see Fa and García Yuste (2001).

Prey density can also determine the hunting methods employed. In a study of hunting in two villages by Indigenous Central African foragers, Lupo and Schmitt (2017) observed that although hunters used the same range of technology there were differences in the frequency of hunting strategies depending on prey density. Hunters from the village in whose area the mean encounter rates with blue duikers, a preferred prey species,

was low, would use more individualized technologies such as hand capture, spears and snares. Village hunters from the area with overall high wildlife encounter rates would use nets more often, predominantly targeting blue duikers. In two adjacent Community Hunting Zones in Cameroon, the more densely populated and thus the more heavily hunted zone would be primarily hunted using firearms, providing 79% of the hunted prey, whereas the less densely populated zone was targeted by snares, providing 82% prey (Bobo *et al.* 2015).

3.3.3 Firearms Are the Dominant Hunting Technology Today

Firearms were used in three quarters of the study sites in Table 3.1. Wild animals are hunted with shotguns, rifles, airguns, modern automatic weapons such as the AK47 (Barnett 2000a) and ancient muzzle-loader guns (Barnett 2000a; Martin *et al.* 2013; Sirén & Wilkie 2016). There is limited information to determine when firearms started being used for hunting in the tropics. In Gabon, guns were traded in the late 1800s, but they only became common in the 1960s (Bernault, 1996, cited in Walters *et al.* 2015). In the Congo Basin, guns were imported from the 1840s onwards, but they did not become widespread until the twentieth century (Savorgnan de Brazza, 1888, cited in Dounias 2016). Technical advances in the mid 1800s, such as the invention of the breech-loading rifle, spread slowly because of the cost and restrictions imposed by the colonial masters. The price of gunpowder also remained prohibitive and delayed the advance of firearms for hunting until the 1930s (Dounias 2016). The subsequent change from black gun powder to the much more powerful smokeless powder improved hunting efficiency substantially as it dramatically increased shooting distance and, thus, outcompeted bows and arrows (Faure, 2002, cited in Dounias 2016). The final technical innovation making firearms highly detrimental for wildlife has been the introduction of flashlights (Dounias 2016), and more recently the even more efficient LED lights (Bowler *et al.* 2019). Lighting allows hunting at night, preferred by many hunters (e.g. Ahmadi *et al.* 2018; Holmern *et al.* 2006; Yasuoka *et al.* 2015) because many prey species are more easily detected due to eye reflection of light. Moreover, species such as duikers freeze when targeted by flashlights, making them especially easy prey for night hunters (Yasuoka *et al.* 2015).

Despite the cost of firearms having come down dramatically and the availability of relatively cheap, locally produced weapons, initial purchase and cost of ammunition remains prohibitive for many people in the

tropics (Sirén & Wilkie 2016). Gun hunting is the prime activity of soldiers and of wealthier individuals, often from regional cities, such as in Madagascar (Golden 2009) and Cameroon (Yasuoka 2006b). In many hunter-gatherer societies, gun hunting appears only secondary to snaring because of the higher cost and the greater skill involved (Kümpel 2006; Kümpel *et al.* 2008). This is borne out for most studies on Indigenous Peoples where there is quantitative data (Table 3.1). For example, Baka Pygmy hunters need to sell six duiker carcasses to buy a single rifle cartridge (Yasuoka 2006b). None of the Aka Pygmy hunters owned firearms, but most of their non-Pygmy neighbours owned shotguns and sometimes rifles (Kitanishi 1995). To overcome the problem of excessive costs of hunting with firearms, three strategies are often adopted. First, many hunters reload their cartridges with locally produced gunpowder (de Mattos Vieira *et al.* 2015) or use muzzle-loaders (Sirén & Wilkie 2016). Second, Baka Pygmy and Aka Pygmy hunters provide services for their richer, non-Pygmy neighbours who provide them with firearms and ammunition in exchange for meat (Duda *et al.* 2017; Kitanishi 1995; Yasuoka 2006b; Yasuoka *et al.* 2015). Here the main parts of a carcass are kept by the owner of the ammunition, thus making the social relationships between the parties involved also a strong social regulator (Hayashi 2008). In the case of the Aka Pygmies, the hunter is given the head, neck and internal organs plus two cigarettes (Kitanishi 1995). Third, increased market participation can increase cash income and make firearms and ammunition more affordable (Levi *et al.* 2011a). For those who decide to follow this avenue, the extra cost forces hunters to maximize the amount of meat per shot (Jerolimski & Peres 2003), and to provide meat for sale rather than for their own consumption.

There are also social barriers against adopting hunting with firearms, especially amongst hunter-gatherers. Baka Pygmy hunters fear conflicts with the owners and lenders of guns, fear anti-poaching controls, fear the physical risks posed by old weapons and often do not have the required skills to use firearms (Duda 2017; Duda *et al.* 2017). On the other hand, firearm hunting bestows high social status. In Baka Pygmy society, shotgun hunters are often considered 'the best hunters' (Duda 2017). When Baka hunters have access to guns, their success can exceed the success of non-Pygmy hunters dramatically (Fa *et al.* 2016). Where poaching carries the risk of detection, such as in protected areas, firearms are generally avoided as gunshots alert ranger patrols to the presence of the hunter (Gandiwa 2011). A new development in areas where hunting with firearms is illegal is the replacement of firearms by running prey

down with motorbikes or horses and then killing the animals with axes, clubs, spears or machetes to avoid the sound of shots, for example, in Tanzania (Kiffner *et al.* 2014) and Botswana (Rogan *et al.* 2017).

Firearm use in the surveyed studies can vary from none to all hunters using firearms and none to all animals killed with firearms, indicating that a multitude of factors impact gun use. There is a general, but not uniform, trend of increasing gun usage over time. Gill *et al.* (2012) visited the same site during a period of rapid national economic growth in Equatorial Guinea and reported that hunters using guns increased from 2% in 2003 to 22% by 2010. Percentage of animals taken by shotgun rose over a 14-year period on Bioko Island in Equatorial Guinea (Cronin *et al.* 2010). In Cameroon, gun use increased, replacing snares, in both a 15-year study in the Lebialem Division, in the southwest of the country (Wright & Priston 2010) and in three villages near the Dja Biosphere Reserve (southeast Cameroon) between 2003 and 2016 (Ávila *et al.* 2019).

Gun use differs amongst ethnicities, reflecting changes in socio-economic systems and lifestyle. Shotgun use in Aka Pygmy hunters increased as a percentage of livelihood activities from 5–29% in 1992/3 to 18–56% in 2007/8. By contrast, their farmer–fisher neighbours kept shotgun use at a similar level; 7–29% in 1992/2 and 7–27% in 2007/8 (Riddell 2013). Yasuoka *et al.* (2015) report on gun use of Konabembe in Cameroon in two adjacent areas and found that at one site 17% of hunters used guns (killing 16% of prey) whilst at a second site 58% of hunters used guns and killed 70% of prey. The two sites differed in their prey density, species composition, forest disturbance, hunting pressure and human density, but it remains unclear what caused the difference in gun use.

In Liberia, ancestral hunting methods have all disappeared and have been replaced by cable snares and shotguns since the civil conflict from 1989 to 2003 (Bene *et al.* 2013). Similarly, civil conflicts which have ravaged the Congo Basin for decades have collapsed many economies and the easy access to firearms may have enabled even more wild meat hunting. In the Amazon Basin, Western contact has led to a rapid change from traditional methods to guns and dogs across all Indigenous societies (Jerzolimski & Peres 2003). Amongst the Huaorani living in the Yasuní National Park, Ecuador, changes in hunting practices were reported in Papworth *et al.* (2013b). The only two South American studies that did not record the use of firearms were both from the 1980s and are for the Huaorani in Ecuador (Rival 2003; Yost & Kelley 1983). All studies from the 1990s and 2000s reported the use of firearms (Franzen 2006; Lu 1999).

There is clear evidence that hunting with guns is much more efficient than hunting with bow and arrow or blowpipes in terms of the number of animals killed at least in the short term. Alvard and Kaplan (1991) compared two Indigenous communities in southeastern Peru, one of which hunted with guns and the other with traditional bow and arrow. Shotgun hunters had relatively short pursuits, averaged 1.3 shots per kill, killed prey often with a single shot, and had uniformly high return rates ranging between 1.2 and 1.5 kg per hour of hunting. In contrast, bow hunters had relatively long pursuits, averaged 30 shots per kill, often missed their target or wounded but did not kill the prey and had low return rates of 0.10 kg per hour of hunting. Wherever there is a mix of modern and traditional hunting technology used, guns attain higher prey kills in study sites in South America (Alvard & Kaplan 1991), Africa (e.g. Baka Pygmy hunters, Duda *et al.* 2017) and Asia (e.g. in Arunachal Pradesh, northeast India Aiyadurai *et al.* 2010).

The problem with hunting with guns lies in its long-term impact on prey populations if commercial hunting is the main aim. Guns allow the killing of many more animals in a shorter time than traditional hunting methods. When prey is hunted for hunters' own consumption only, the increased efficiency afforded by guns reduces the required time for subsistence hunting and can allow hunters to reinvest spare time in other activities. When prey is being sold, however, the time saved can be invested in killing more animals. When animals and prey are not privately but communally owned, the Tragedy of the Commons dictates that as many animals as possible should be killed, leading to severe overhunting and unsustainability (Chapters 4 and 5).

3.3.4 Modern Snares Are the Second Most Utilized Hunting Technology Globally

Traditional snares are encountered rarely, with only five study sites reporting snares made of vines, mostly from the last century (Carpaneto & Germe 1989; Dounias 2016; Fa *et al.* 2016; Kitanishi 1995; Tessmann, 1913a). Modern cable snares were used in 57% of study sites. Snare hunting is rare in the Neotropics, where only 2 out of 20 study sites listed them as a hunting technique, compared to 75% in Asia and 68% in Africa. Although snares appear to be a major cause of prey declines across tropical Asia, information on snare hunting is still sketchy (Gray *et al.* 2018; Harrison *et al.* 2016). Their relative absence in the Neotropics might be related to the generally lower prey population densities of forest mammals,



Figure 3.5 Blue duiker caught using nylon rope snares in Bioko Island, Equatorial Guinea (photo: M. Grande-Vega).

making snares comparatively unprofitable (Fa & Purvis 1997; Peres 2000). However, although snares are illegal in most countries in Africa, they still account for most prey killed, as well as biomass, compared to firearms (Fa & Peres 2001). Their popularity is based on the fact that the material used, wire or nylon cord (Fig. 3.5), is easy to obtain, inexpensive, durable and strong enough for larger animals. Snares can be set under cover of darkness and their low detectability makes them a prime choice for poachers (Gandiwa 2011; Knapp 2012; Lindsey *et al.* 2011b). Snare hunting also requires relatively little skill compared to guns, but experienced hunters may be much more successful than inexperienced ones (Kümpel 2006). In some cases, wire can be stolen from wildlife and domestic fences, as in the Savé Valley Conservancy in Kenya, where rangers removed almost 85,000 snares, all of which were thought to have been made from the perimeter fence (Lindsey *et al.* 2015). In Zimbabwe, stolen telephone copper cables

and steel wire from a veterinary fence along a National Park have been used (Gandiwa 2011).

As for firearms, snares have become more popular over time. Wire cable was introduced in Cameroon after the Second World War and has almost totally replaced vegetal fibre, which rots with moisture, or elephant hair that is only suitable for small prey, although snares made of rattan are still used for small prey (Dounias 2016). As a result, the Fang in Cameroon have changed from more traditional methods to focus on snares, now accounting for 54% of the hunted prey biomass (Dounias 2016). Traditionally, Baka Pygmies used mainly spears for hunting (Bahuchet 1992), but wire snares were introduced in the 1960s after contact with neighbouring cultivators to replace traditional, plant-based snares (Hayashi 2008; Yasuoka 2006b; Yasuoka *et al.* 2015). Nowadays, cable snares are the most common hunting technique amongst Pygmy hunters including Baka since this allows for a larger number of captures, therefore suitable for commercial wild meat production (Hayashi 2008; Noss 2000).

Snares are typically set, left unsupervised and then checked periodically (Fig. 3.5). The passive nature of snaring allows farmers to set and check snares in and at the margin of their fields. Their passive nature can result in indiscriminate capture of animals (Becker *et al.* 2013; MacMillan & Nguyen 2014) although relatively targeted setting of snares is possible (Coad 2007). The non-selectiveness is demonstrated by sex ratios of 1:1 in any captured species as predicted in a study in Equatorial Guinea (Fa & García Yuste 2001). Although daily checks are desirable from an animal welfare point of view, longer periods appear to be the norm rather than the exception. For example, Baka hunters checked snares on average every three days (Yasuoka *et al.* 2015). The consequence of leaving snares unchecked or checking these sporadically can lead to significant animal welfare issues and loss of carcasses. But even when checked regularly, animals may suffer from injury and stress. Up to a quarter of total captures can be lost to scavengers and decomposition (Noss 1998b), and around one third of animals can escape with injury (Lindsey *et al.* 2011b). In Zimbabwe, 59% of snared animals were found rotten or scavenged, 27% recovered by scouts and only 14% were extracted by poachers out of the 2,398 animals recorded as killed in snares from August 2005 to July 2009 (Lindsey *et al.* 2011b). In hunting zones around a study village in the Dja Biosphere Reserve in Cameroon, snare density was inversely related to distance from the village, but despite a 64% lower snare density in the farthest hunting zone compared to the closest zone, overall capture rate was four times higher and the number of rotting carcasses three times

greater in the farthest zone (Muchaal & Ngandjui 1999). Dobson *et al.* (2019) modelled the amount of usable harvest when 20 snares are checked daily versus only once over a 30-day snaring period to find a three-fold increase for the daily-check scenario.

Two main categories of snares exist – foot snares and neck snares, – whereby the latter constitute the vast majority (Kümpel *et al.* 2009; Noss 2000; Yasuoka *et al.* 2015). When animals are entangled with their heads in neck snares, they are normally strangled to death. Larger animals can be caught by their feet in neck snares. After an animal steps into a typical foot snare, a bent rod springs loose, causing a wire fastened to the rod to wrap around the animal's foot and lift it into the air (Yasuoka *et al.* 2015). Animals larger than those targeted by any type of snare can still be caught but can escape – often with injuries. The two methods are characterized by different prey profiles. For example, in a study in Equatorial Guinea carnivores were only captured in neck snares and rodents solely in foot snares, but a large proportion of duikers were caught in both types though some were also shot (Kümpel *et al.* 2009). Ungulates, rodents and carnivores are relatively more vulnerable to snares than to firearms (Fa & García Yuste 2001). Medium-sized mammals are significantly more vulnerable to snaring (Duda *et al.* 2017; Fa *et al.* 2005; Fa & García Yuste 2001; Noss 1998b). Rodents, for example, represented 92% of snared animals in southeastern Cameroon (Bobo *et al.* 2015). A review of 36 tropical moist forests sites in seven countries in West and Central Africa revealed higher harvest rates for snared than for shot species, significantly smaller body size of snared *versus* shot species, higher extraction rates for terrestrial *versus* arboreal species, higher extraction rates for fast and medium speed species *versus* slower ones and higher extraction rates for frugivore–herbivores *versus* other dietary categories (Fa *et al.* 2005).

Snares are typically set along trails and often in clusters. Densities can vary widely with values of up to 56/km² as reported from Equatorial Guinea (Fa & García Yuste 2001). In a private property near the Savé Valley Conservancy in Zimbabwe, 1.16 and 0.68 snares/km² were removed in 1998 and 1999, respectively, but the number increased dramatically to around 90 snares/km² per year from 2005 to 2009 after the settlement of adjacent land (Lindsey *et al.* 2011b). Whilst almost 85,000 snares were detected in a period of eight years in the Savé Valley Conservancy, 170,000 snares were removed from just two protected areas in Vietnam and Cambodia between 2011 and 2015 (Gray *et al.* 2018). The effects of snaring can be chilling. In Asia and in Africa,

snaring is a major contributor to defaunation (Becker *et al.* 2013; Gray *et al.* 2018; Noss 1998b). This not only affects target species but also by-catch. Becker *et al.* (2013) analysed by-catch data from 1,038 antipoaching patrols in Zambia's Luangwa valley focusing on savanna elephants and large carnivores, to show that additional mortalities of 32% for elephants, 20% for adult (>4 years) male lions and 14–50% of adult and yearling pack members of African wild dogs were inflicted.

3.3.5 Traditional Hunting Technology Generally Augments Modern Technology Today

In only 15% of sites in Table 3.1 neither firearms nor cable snares were used. This proportion is biased towards traditional hunting methods such as bow and arrow and nets because 11 of the 19 sites in the table stem from a single study on Mbuti Pygmies in the DRC that documented a different mix of hunting technologies at different sites (see Fa *et al.* 2016). Here, we introduce the five most important traditional techniques: spears, dogs, bow and arrow, nets and blowpipes.

3.3.5.1 Spears

Spears are the oldest hunting weapons discovered and predate the emergence of modern man. As outlined above (see Section 3.2.1) the 400,000 year old Schöningen spears were likely used for thrusting or hand-thrown at close quarters (Shea 2006; Thieme 1997; Fig. 3.6). Virtually all historically known hunter-gatherers used spears but none employed spears alone without projectile weapons (Churchill 2014). In an extensive survey of small-scale hunter-gatherer societies across the world, Churchill (1993) observed that almost all had spears in their arsenal, but only half used them for terrestrial hunting. Other uses include hunting marine mammals, spearing fish, warfare and defence from predators. Most spears are thrusting spears and only some groups in Australia and Tasmania are known to use thin, light spears to hunt wallabies and kangaroos. Excluding these thin spears, the distance when thrown is 5.7 ± 0.9 m (Churchill 1993) or up to 20 m (Milks *et al.* 2019), depending on the thrower's skill. Typical use of thrusting spears is as a dispatching tool after prey has been driven by hunters, with or without accompanying dogs, into a disadvantaged position when using nets, snow drifts or geographical features such as valleys, rocks and swamps, or have been caught in traps. Spears were used as part of pitfall traps, but this technology has been replaced by snaring (Lewis & Phiri 1998). The



Figure 3.6 Spear II. The 2.30 m long spear is shown to the left of an incomplete pelvis of a horse, and the base has been broken off. Inset shows a detail of the tip of spear II. Scale in cm. (From Thieme 1997; reprinted with permission from Springer Nature.)

spearthrower, also called the atlatl, is a tool that uses leverage to throw a spear or dart at longer distances with a range of about 40 metres (Churchill 1993). The earliest known example is from the upper Palaeolithic in the Dordogne, France; it is made of reindeer antler and dated approx. 17,500 BP (Cattelain 1989). As a hunting weapon, it is used for marine mammals and waterfowl in Oceania, the Arctic and part of the Americas, but terrestrial hunting is known only from Australia (Cattelain 1997; Churchill 1993).

Spears have been reported for wild meat hunting in Africa, the Americas and Asia (Table 3.1). In the early twentieth century, spears were extensively used by the Fang during collective hunting expeditions (Tessmann 1913a). Like weapons of war, spears were richly carved and ornamented, thus expressing a special cultural importance. Elevation into the mythical level was also observed elsewhere, such as the Huaorani in South America. With the advent of firearms, spears were slowly replaced and the Fang do not have spears in their arsenal any longer (Dounias 2016). Today, spears are a Pygmy

specialty in the rainforest where non-Pygmy people do not use them, but are also still encountered in Madagascar, Eastern Africa savannas and amongst the San in the Kalahari desert (Dounias 2016; Fa *et al.* 2016; Golden 2009; Holmern *et al.* 2006; Ikeya 1994). Pygmy groups use spears to kill larger and more aggressive mammals like elephants, African buffaloes, bushbucks, gorillas and wild pigs or as a dispatching tool, especially in net hunts and whenever any opportunity arises (Bahuchet 1992; Carpaneto & Germi 1989; Hayashi 2008; Kitanishi 1995; Yasuoka 2006a).

3.3.5.2 *Dogs*

Wild and domestic animals have been widely used as ‘auxiliary animals’ to assist in foraging generally and hunting in particular (Dounias 2018). Several birds of prey, ungulates, elephantids and felids have been tamed as hunting auxiliaries. For example, horseback falconry is still actively performed in Central Asia today and can be traced back to the second millennium BCE (Soma 2012). Indian hunters used tamed Indian antelope and Indian gazelle as decoys by sending them into a wild herd with nooses attached to their horns. Once an intruder was engaged by a wild animal its horns would easily become entangled with the tame animal’s noose and could then be easily caught (Menon 2000). Similarly, tame female Asian elephants serve as decoys in Sri Lanka, India, Myanmar, Cambodia and Thailand, to attract wild individuals into places where they can more easily be trapped (Baker & Manwell 1983).

Domestic dogs are the undisputedly most important hunting auxiliary worldwide. Hunting has been discussed as one of the principle factors motivating the domestication of the dog from the wolf (Lupo 2011; Olsen 1985). Hunting dogs are used by numerous subsistence hunters in a broad range of locations and habitats across the world (Koster 2009). An exception appears to be in the tropical New World, where many Amazonian societies apparently lacked dogs until the historical period, though dogs may have been brought to South America by Paleoindians (Fiedel 2005). However, because bones do not preserve well in Neotropical settings it is difficult to make firm conclusions from the absence of archaeological evidence (Koster 2009). Hunting with dogs is both a traditional and a modern technology. Parallel to the introduction of firearms many of the previously isolated Neotropical societies acquired dogs (Koster 2009). Dogs are now common throughout Latin America, emphasizing their versatility and importance for hunting. Dogs were likely introduced to the Mbuti Pygmy hunters by agriculturalists (Carpaneto & Germi 1989) and have recently been used more frequently by numerous societies

(Barnett 2000b; Franzen 2006; Ikeya 1994). For example, hunting with dogs was once only of relatively low importance for the San in the Kalahari, but became more common as hunting with bow and arrows declined. This increase has been facilitated by a general increase in the dog population, by the ease of using these animals, by the convenience of having accompanying dogs when walking long distances and by the increase in market demand in a developing commercial economy (Ikeya 1994). In Table 3.1, the percentage of hunts with dogs varied dramatically from no dogs to 86% by Mayangna and Miskito hunters in Nicaragua (Koster 2008b) and 85% of hunts alongside hunters on horseback in the Brazilian Pantanal (Jean Desbiez *et al.* 2011). While Piro shotgun hunters brought dogs on only 3% of the hunts, the Machiguenga bow hunters living just 90 km away brought dogs on three quarters of their hunts (Alvard & Kaplan 1991); this difference may have been caused by different prey densities (Koster 2009). Among poachers, for example on farmland in KwaZulu-Natal, South Africa, some prefer using dogs over other methods such as hand-weapons, in this case 'knobkerries', traditional strong, short wooden clubs with a heavy rounded knob on one end used by Southern African tribes (Grey-Ross *et al.* 2010). Hunting with dogs in some areas includes more women and juveniles than in other forms of hunting, which are primarily dominated by adult males (Koster 2009).

Dogs are used to directly kill small prey but, more importantly and more frequently, are used to flush out or corner prey to be dispatched by the hunters or to drive prey into nets or traps. Sometimes, dogs are the only means to target species that are rare or are otherwise not susceptible to other hunting methods. For example, hunters in Lebialem Division, Cameroon, could only locate drills by hunting with dogs (Wright & Priston 2010). Poachers in Zimbabwe primarily target hyrax (100%), warthog (93%), bushpig (85%) and baboons (79%) with dogs, whilst buffalo (100%), zebra (98%), wildebeest (97%), impala (97%) and eland (90%) are primarily killed with snares (Lindsey *et al.* 2011b). Advantages of dogs vary. An increased encounter rate with prey and, thus, a higher efficiency has been described in several studies (Alves *et al.* 2009; Koster 2008b; Nobayashi 2016). Among the San in the Kalahari, dogs are not reported to increase encounter rates, but they decrease handling time between detection and kill of prey such as gemsbok (Ikeya 1994). In Nicaragua, the return rates of hunting tapirs, the largest prey species in the study, with dogs, with rifles, and with both guns and dogs were comparable (Koster 2008b). On the other hand, hunters with dogs encounter more than eight times as many agoutis as hunters without dogs in the same study, indicating that hunting dogs can rival firearms in their overall effectiveness.

3.3.5.3 *Bow and Arrow*

Bows and arrows are used across the world, mainly in traditional hunter-gatherer societies (Table 3.1). The technique is very versatile, allowing ambush, pursuit and disadvantage hunting. Bow hunting allows the hunter to focus on the behavioural characteristics of a given prey species without the constraints of prey size and terrain features encountered when hunting with spears or atlatl (Churchill 1993). However, to kill the prey, the arrow must be precisely lodged between ribs or behind the shoulder blade, thus resulting in short effective distance of 25.8 m on average (Churchill 1993) and in low success rates (Liebenberg 2006). Iron-tipped arrows are deadlier than simple wooden arrows but are heavy and, thus, limited by short distances. Mbuti archers use iron-tipped arrows for terrestrial animals and light wooden arrows, often with poisoned tips, for arboreal prey, because they are light and can be used at larger distances than iron-tipped arrows, but they often require that wounded animals are tracked (Carpaneto & Germi 1989). Mbuti archers hunt either individually or in groups in forest environments (Carpaneto & Germi 1989), but Hadza, the hunter-gatherers of savannahs in Tanzania, usually hunt alone to be able to approach prey in open habitats close enough without being detected to be able to shoot (Marlowe 2005). The prey portfolio of bow hunters differs from gun hunters. When Piro shotgun hunters used bows, they consistently pursued many species ignored when hunting with shotguns (Alvard 1993), which is consistent with foraging theory which predicts a broader prey selection when hunting with less efficient bow technology (Hill & Hawkes 1983). Although bows and arrows are still used by traditional hunters, they are largely been superseded by the more efficient firearms. The specialist knowledge and traditional skills required for bow and arrow hunting, such as how to prepare poison, has often vanished, for example in the Katu ethnic group in Vietnam (MacMillan & Nguyen 2014).

3.3.5.4 *Blowpipes*

Blowpipes, also called blowguns, are long narrow tubes for shooting light darts, seeds or clay pellets primarily used for hunting wildlife. They have been used by many Indigenous Peoples in Eastern regions of North America (Riley 1952), in tropical forests in Southeast Asia (Alvard 1999a; Bennett *et al.* 1999; Kuchikura 1988; Naito *et al.* 2005), South and Central America (Papworth *et al.*, 2013a, b; Riley 1952; Rival 2003; Yost & Kelley 1983), and in Madagascar (Andrianaivoarivelo *et al.* 2012; Jenkins & Racey 2009). Blowpipes are exclusively employed by men who hunt typically alone or in small groups (Naito *et al.* 2005; Rival

2003; Yost & Kelley 1983). The Semaq Beri hunter-gatherers of Peninsular Malaysia sometimes hunt in pairs with one specialized blowpipe hunter accompanied by a 'carrier' who only gathers and carries the killed animals (Kuchikura 1988). Several types of blowpipes exist. In North and Central America, it is a simple tube; in the Guyana region of Northeastern South America, it is a tube fitted into a protective sheath; in the Amazon Basin, it is a composite of two longitudinal half-tubes, but there are also intermediate types (Riley 1952). In Southeast Asia, double tubes are reported in which both the inner and outer tubes are composites of longitudinal half-tubes (Kuchikura 1988). Darts are either not poisoned, in North America, or poisoned with curare, a toxic extract from various plant species including the *Curarea* vine, in South and Central America. In Southeast Asia, poison from the sap of the ipoh tree is used (Kuchikura 1988). The poison is highly effective and relatively fast. In one reported case, it took the curare of 11 darts to bring a puma crashing down from a tree in just over half an hour (Yost & Kelley 1983).

Blowpipes are typically used for overhead hunting of arboreal species, such as bats, birds, primates and squirrels, but terrestrial vertebrates, such as pigs and peccaries, can also be targeted (Piper & Rabett 2009; Rival 2003). The technological differences between the blowpipes and darts and the effectiveness of the poison used impact prey choice of blowpipe hunters as demonstrated by the comparison of the different hunting strategies of the Huaorani of Ecuador (Yost & Kelley 1983) and the Semaq Beri of Malaysia (Kuchikura 1988). The Semaq Beri focus on hunting dusky and banded leaf monkeys but occasionally also kill large-sized Malayan and cream-coloured giant squirrels. Middle-sized and small-sized squirrels and birds are, however, ignored. In contrast, the Huaorani's prey included not only monkeys such as the Venezuelan red howler monkeys but also birds of all sizes (nearly 45% of the total catches) and ground-dwelling animals (15% of catches), whereby small-sized animals of less than 2 kg contribute nearly 60% of the total number of animals killed. The Huaorani's blowpipes are longer and produce higher velocities and higher penetration for their darts than those of the Semaq Beri. Success rate for the Huaorani is approximately 2.4 times higher and return rate 4 times higher. Crucially, the preparation time for darts is half for Huaorani than for Semaq Beri allowing the Huaorani to carry and use more darts than the Semaq Beri (100–300 *versus* 10–50, respectively). Thus, the Huaorani do not conserve darts and shoot even at small birds of less than 50 g including hummingbirds whereas the Semaq Beri save darts until they encounter large primates, their prey of choice.

Blowpipe hunter groups produce a diversity of blowpipe darts depending on the prey. Some dart types are easy to make in great

quantities and can be used without moderation; some others should not be lost and are saved carefully for appropriate prey.

3.3.5.5 *Nets*

Hunting with nets mainly occurs in three main contexts. First, nets have been reported to be used to hunt bats and birds. For example, bat hunting is practiced in Benin, Cameroon, Madagascar and the Seychelles in Africa, and in India, Indonesia, Malaysia, Myanmar, Philippines, Thailand and Vietnam in Asia (Golden 2009; Jenkins & Racey 2009; Mickleburgh *et al.* 2009; Riley 2002; Struebig *et al.* 2007). Specialized mist nets are used in China, India, Indonesia and Laos (Mickleburgh *et al.* 2009). Second, nets can be components of traps, either underground for small mammals or as net traps to capture terrestrial mammals. Third, net hunting of terrestrial animals has been practiced by a variety of Indigenous Peoples in the Congo Basin (Dupré 1976) and is today a specialty of some Pygmy populations. Up to the 1950s, the Fang used nets, but abandoned them for modern hunting technology (Dounias 2016; Koch 1968). According to Dounias (2016), it is not surprising that 'Pygmies have become the natural depositories of net hunting since this activity exacerbates egalitarian values like mutual aid, food sharing, social links between communities, spatial mobility and demographic fluidity.' Mbuti Pygmies use large collective beat-hunts with women as beaters (Carpaneto & Germe 1989). The nets are between 1 m and 1.5 m high and between 30 m and 100 m long and belong to the man who wove it (Ichikawa 1983). Animals are driven into a circular array of individual nets where men hide near their own nets ready to kill the game running towards them. Those Mbuti who sell their prey animals to Muslim Bantu kill the animals by cutting their throat with a knife in order to adhere to Muslim requirements for slaughter (Carpaneto & Germe 1989). The gender role in the Aka is opposite to the Mbuti as the adult and adolescent men set the nets and beat the bush, whereas women capture the animals caught in the net, waiting around the nets; sometimes they lead net hunting and also beat the bush when no adult men participate in the hunt (Bailey & Aunger 1989; Kitanishi 1995; Noss 2000). In Gabon, game was driven into nets by fire, but this practice has been abandoned and fire is mainly being used to promote growth of grass to which grazing game is attracted (Walters *et al.* 2015). Whilst the Mbuti specialize in net hunting and the Aka use nets alongside cable snares, the sympatric Efe do not practice net hunting (Carpaneto & Germe 1989; Fa *et al.* 2016; Kitanishi 1995). Bailey and Aunger (1989) argue that the Efe

never adopted net hunting because their neighbouring farmers do not use them whereas the Mbuti adopted net hunting from their neighbours. Baka pygmies might have used nets in the past, but do not carry out net hunting today (Hayashi 2008; Yasuoka 2006b). In general, net hunting is declining and being replaced by snare hunting even amongst the Aka and Mbuti because of higher individual returns of snare hunting, greater involvement in formal employment and agriculture, and enforcement of regulations in protected areas (Noss 1997). However, it has not been abandoned completely because of the growing demand for wild meat (Noss 1997) and its suitability for illegal hunting, such as in communities adjacent to National Parks (Gandiwa 2011).

3.4 The Hunters

The typical profile of a hunter corresponds to any adult male with most hunters being around 25–50 years old (Bene *et al.* 2013; Fimbel *et al.* 1999; Kamins *et al.*, 2011a; Martins & Shackleton 2019; Paillet *et al.* 2009; Pangau-Adam *et al.* 2012; Rogan *et al.* 2018; Wright & Priston 2010). Women hunters are generally very rare (Rogan *et al.* 2018) but can sometimes contribute to traditional hunting by checking traps, contributing to dog and net hunting (Sections 3.1.2 and 3.2.5.5) and helping to make weapons (Duda *et al.* 2017; Fimbel *et al.* 1999; Smith 2005). Amongst Baka Pygmies, all shotgun hunters and most snare trappers are men but half of the traditional hunters can be women (Duda *et al.* 2017). Except for the remaining hunter-gatherers, hunting wild meat is typically a secondary occupation alongside farming or employment and full-time hunters are rarely encountered, typically less than 10% (Ahmadi *et al.* 2018; Bene *et al.* 2013; Loibooki *et al.* 2002; Paillet *et al.* 2009; Pangau-Adam *et al.* 2012; Rao *et al.* 2005; Spira *et al.* 2019; Tumusiime *et al.* 2010). Socio-economic variables and a hunter's personal profiles, such as skills, income security, number of dependants and physical ability, are typically correlated with hunting behaviour (Kümpel *et al.* 2009). For example, Rogan *et al.* (2018) report from South Africa that in contrast to other studies, households with some form of formal employment were 1.6 times more likely to hunt than unemployed households and seasonal employment had the strongest correlation with the likelihood of hunting. In Uganda, the probability for an individual to set snares in the forest decreased with rising levels of formal education and subsistence farmers were 10 times more likely to set snares as compared to those who had some other main occupation (Tumusiime *et al.* 2010).

Marlowe (2005) used the most extensive dataset of known Indigenous forager and hunter-gatherer societies worldwide contained in Binford (2001). The majority of these societies were located in sub-Saharan Africa, India and Southeast Asia, Australia, South America and North America. Marlowe observed that the percentage contribution of hunting to their diet was positively correlated with local group area and how often camps moved. Figure 3.7a displays the relationship between area size and percentage hunting, whereby area size is log-transformed, and percentage hunting was logit transformed (logit is the appropriate transformation for percentages). The correlation coefficient is $r = 0.66$ with $n = 257$, explaining 43% of the observed variance. Using the dataset, we also analysed the relationship between population density and hunting and found a strong negative correlation with $r = -0.63$ with $n = 338$, explaining 40% of the variance (Fig. 3.7). Local group area and population density are also negatively correlated with $r = -0.90$ with $n = 258$, explaining 81% of the variance. Fitting a linear model with both population density and local group area size as independent variables, reveals no significance for the former ($p = 0.5$) but significance for the latter ($p < 0.0001$). In other words, it is local group area size which best explains the percentage of hunting in the diet. Less land corresponds with higher input from agriculture and fishing.

In the wild meat literature, hunting by children is rarely mentioned (Bonwitt *et al.* 2017). However, children learn hunting skills often from an early age and they also can actively engage in the hunting of wild meat. The vast cultural and environmental diversity of hunter gatherers results in a variety of learning and teaching subsistence skills during childhood. A meta-analysis of the anthropological literature has demonstrated several common trends across different societies (Lew-Levy *et al.* 2017). Across these, learning foraging begins in infancy when children are taken to foraging expeditions and when they are given toy versions of the tools used in hunting, such as baskets, spears and bows. Children then transition through multi-age playgroups where social peer-to-peer learning is important, but they also continue to observe their parents' subsistence activities and learn through participation. Small-animal hunting and trapping is primarily learned in playgroups. While children can become proficient at small-animal hunting relatively early in life, more complex hunting methods to take down larger animals are normally taught by adults, not necessarily the parents, from adolescence onwards. Learning to hunt big game may continue through life. There is a controversial debate whether teaching takes place in small-scale societies, including among foragers, but some research suggests that teaching rarely occurs (MacDonald 2007). However, in many hunter-gatherer societies, hunting

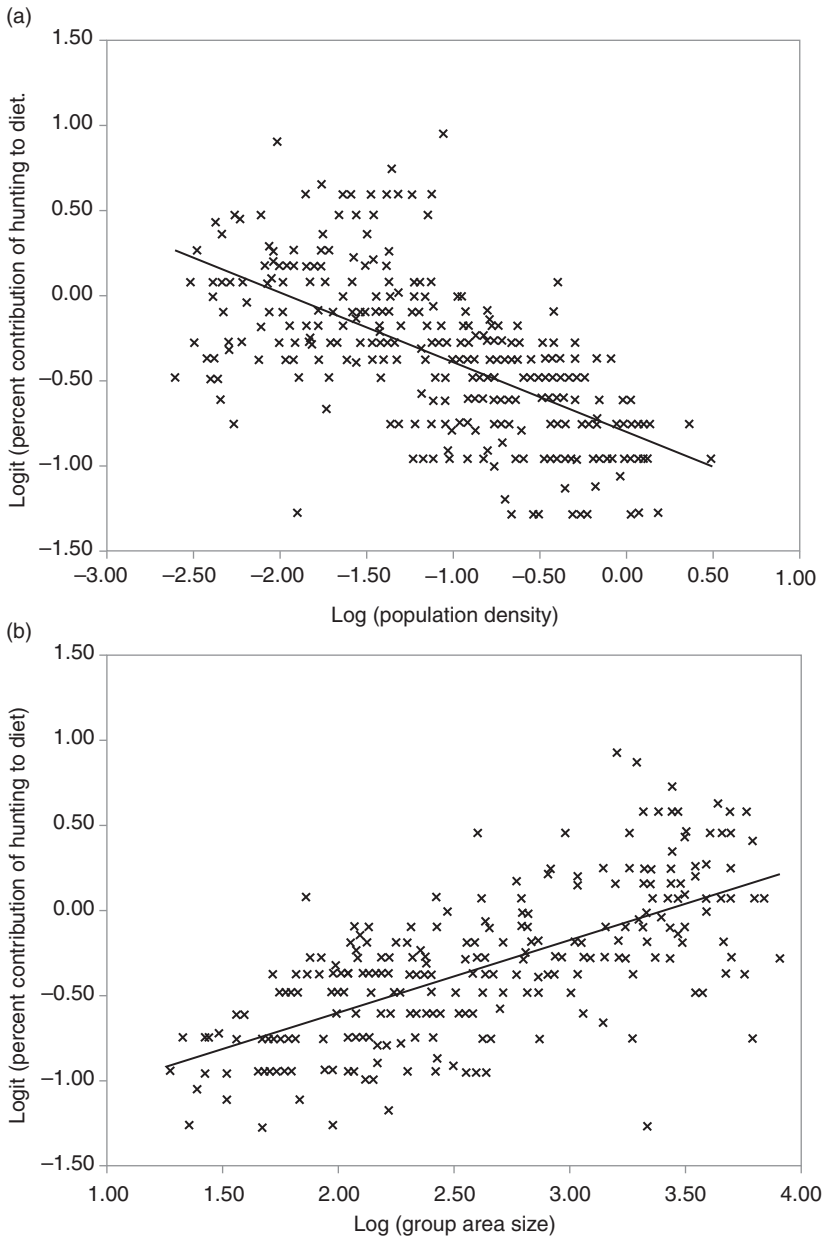


Figure 3.7 (a) Local group area size *versus* percent hunting contribution to diet; (b) population density *versus* percent hunting contribution to diet (data from Binford 2001).

skills are generally taught through direct instructions, likely because of the complexity of hunting, demonstrating that teaching does indeed exist amongst these societies (Lew-Levy *et al.* 2017). For example, San boys learn hunting skills through play, from five years old onwards, by imitating their playmates and not by overt instruction from adults (Imamura 2016). While they learn the use and construction of tools through observational learning and trial and error, teaching is very rare and, if it happens, it is limited to older children assisting younger children in tool making. Similarly, Chabu children in Ethiopia start learning to spear hunt at young age, 6–7 years of age, through role-playing and collaborative learning with their peers; they also actively listen to stories and verbal instructions from their fathers and learn skills by active participation under guidance of adults, mostly uncles (Dira & Hewlett 2016).

Regarding active hunting, an example are older children and juveniles in the Serengeti National Park and adjoining protected areas, who hunt small animals irrespective whether they are boys or girls (Magige *et al.* 2009). In a survey of rural children in the Eastern Cape of South Africa, 62% of the children surveyed were supplementing their diets with wild foods by gathering and by hunting, predominantly by setting snares (McGarry & Shackleton 2009). In a study on Fang People in Cameroon, snare hunting in forest edges, agroforests, swiddens, fallows or home gardens near or within or near villages (so-called garden trapping) is an activity exclusively conducted by children (Dounias 2016). Children maintain the trapping and snaring knowledge, which is technically highly diversified, with little intervention from adults. Such hunted wild meat is generally eaten by the children as snack food and constitutes a valuable part of their diet. Also children of the Baka Pygmies in Cameroon participate in snare hunting not only for garden trapping but also together with adults during hunting expeditions in forest camps (Hayashi 2008). Importantly, Baka children can conduct snare hunting by themselves whilst adult men devote days to spear-hunting expeditions (Yasuoka 2014). The non-overlap between children and adult hunting is also observed in village children in Sierra Leone, who regularly hunt from about 7 years of age, but focussing, in contrast to adults, on small animals using traps and nets (Bonwitt *et al.* 2017). Boys were more likely to hunt than girls and they hunt alone or, especially for net hunting, in small groups.

3.5 Cultural Hunting Aspects

Hunting is shaped by prey type, density and distribution (i.e., the OFT, Chapter 4) and by cultural behaviours. Here we highlight the importance of

food taboos and how costly signalling and taste of meat can determine which species are hunted and which are ignored. Taboos are considered here for they reveal ongoing changes affecting traditional hunting practices and the shift into more commercial hunting that not only deplete wildlife, but also deteriorate cultural systems that give a high value to animals. Another cultural factor is the taste of meat, which can bias prey selection contrary to the predictions of the OFT. Costly signalling in the context of hunting is hunting of prey that is dangerous or otherwise costly to hunt in terms of time, material investment, risk of failure and the opportunity to engage in more efficient foraging, but awards the specialized hunters an enhanced social status and reproductive advantage (Bahuchet 1990; Putnam 1948).

Food taboos and taboos against killing certain animal species were widespread amongst small-scale traditional societies worldwide. McDonald (1977) reviewed food taboos amongst South American hunter-gatherers and found such taboos in all of the 11 societies under investigation. Food taboos are also reported from additional sites in South America (Jerzolimski & Peres 2003; Redford & Robinson 1987; Rival 1993), Africa (Hall *et al.* 1998; Inogwabini *et al.* 2013; Jimoh *et al.* 2012; Wright & Priston 2010), the Indian subcontinent (Aiyadurai *et al.* 2010; Velho & Laurance 2013), Inuit in Canada and Alaska (Burch 2007), Southeast Asia (Tuck-Po 2000) and virtually everywhere in the world. De-tabooing is widespread and reported in many studies, such as brocket deer in Central America (Hames & Vickers 1982), the tapir in South America (Rival 1993), the bonobo in Africa (Inogwabini *et al.* 2013) or the gaur, Himalayan serow and tiger on the Indian subcontinent (Velho & Laurance 2013). Taboos are often connected with religious belief (Meyer-Rochow 2009). For example, Machiguenga hunters believe that certain monkeys (especially large adult males) and other prey species have vengeful spirits that can ‘take revenge’ on the hunter’s family (da Silva *et al.* 2005). This association between religious belief and taboos triggers changes and disappearance of taboos once people or societies convert. For example, a shift towards Christianity in Indigenous communities of Arunachal Pradesh probably led to an erosion of hunting taboos (Aiyadurai *et al.* 2010). When Christianity replaced the traditional system of beliefs about predator–prey relations in Inuit, the taboo vanished which previously significantly constrained the pursuit, processing and consumption of prey, vanished (Burch 2007). In Africa, many who belong to a Western religion now see some of these taboos as satanic (Jimoh *et al.* 2012), demonstrating that the taboos have no inner connection with conservation. When taboos are based on religion, it does not guarantee protection. For example, in Cameroon the belief that people

can transform into animals is widespread. Although 83% of those that believed in transformation did not shoot apes for fear of killing a person, there are others that had killed apes despite knowing about this traditional belief (Wright & Priston 2010). Moreover, those that spoke of the belief were in the minority and the belief in animal totems has especially declined among the younger generation (Etiendem 2008 cited in Wright & Priston 2010). Erosion of taboos other than by religion is widespread. Jerozolimski and Peres (2003) have demonstrated that a shift from large to small-bodied prey species has taken place in the Neotropics and that taboos seem to play a minor role in determining the overall composition of target species. Increased consumption of meat previously avoided amongst the Yuqui community of Bolivia expresses how cultural attitudes change when preferred prey becomes scarce (Jerozolinski & Peres 2003). Bonobos were not hunted historically in the DRC because of traditional taboos but the introduction of money, commodity hunting and commerce has caused bonobos to now be killed (Inogwabini *et al.* 2013). This change might have been triggered by immigration of newly established ethnic groups that did not have such taboos. Finally, taboos might have spiritual or medicinal purposes, which have nothing to do with conservation. Alternatively, some taboos might have evolved as a means to prevent hunters from wasting time searching for game species that are difficult to find (Jerozolinski & Peres 2003).

Taboos and the avoidance of some wild meat species have in common that the species are not hunted despite OFT's prediction that some of these species should be exploited. For example, Machiguenga hunters in the Amazonian Peru prefer large primates while avoiding deer and ocelot (Shepard 2002); Piro in the Amazonian Peru never pursue otters, sloths, and pumas (Alvard 1993); and Kaxinawá and Katukina prefer peccaries while otters, kinkajous, rats, and marsupials are considered inedible (Kensinger 1995a). Mayangna and Miskito hunters in Nicaragua generally focus on prey types that are in the optimal diet set and kill giant anteaters and northern tamanduas to protect their dogs, but they do not eat the meat despite both species being in the optimal diet set (Koster 2008b, 2008a). Mayangna and Miskito hunters also pursue the sympatric, similar sized, black-handed spider monkey and mantled howler monkey differentially despite both being in the optimal diet set (Koster *et al.* 2010). Spider monkeys are predominantly frugivorous and howler monkeys are primarily folivorous, which may determine the different taste of their meat for humans (Shepard 2002). The taste of the meat of howler monkeys is unappealing to the hunters and the species is generally not pursued during hunts (Koster *et al.* 2010). Moreover, several

carnivore species including ocelots, pumas, jaguars and tayras are not pursued and eaten as they appear unpalatable to the hunters because these species eat raw meat which hunters associate with potentially harmful pathogens (Koster *et al.* 2010). Similar to howler monkeys in Nicaragua, black colobus monkeys in Gabon are normally not pursued due to their meat's bad taste despite their being easy to hunt because of their inactivity and large size (Brugière 1978). Nevertheless, they are heavily hunted if other, preferred species have become overhunted.

The pursuit of inefficient or expensive prey is a costly signalling strategy (Boone 2017; Hawkes & Bliege Bird 2002) that has been documented in many societies. Costly signalling theory has been applied to explain some seemingly maladaptive cultural practices, such as relatively inefficient or apparently suboptimal foraging behaviours, and generosity by the foragers' motivation to broadcast honest information about their abilities (Hawkes & Bliege Bird 2002). Spearfishing Meriam Islanders violate predictions of OFT when they bypass opportunities to harvest shellfish and focus on inefficient, thus costly, spearfishing instead (Bliege Bird *et al.* 2001). These foraging decisions can be explained by the social status associated with being known as a successful spearfisher. The motivation underlying modern trophy hunting and big-game fishing, which are while rarely costly in terms of danger or difficulty but can be extraordinarily expensive, can be explained by costly signalling (Darimont *et al.* 2017). Turtle hunting by the Meriam Islanders (Bliege Bird & Smith 2005) and torch fishing for dogtooth tuna in the Micronesian Ifaluk atoll are other outstanding examples (Sosis 2000). Differences between the sexes in the use of costly signalling have been documented. Bliege Bird and Bird (2008) showed that in Australian Martu hunters, women will optimize their hunting for consumption, while men will hunt to optimize their social and political status. Hunters involved in costly signalling can improve their reproductive success, enjoy larger networks of allies and/or trading partners, as well as increase their social and political standing (Bliege Bird & Smith 2005; Smith 2004; Sosis 2000). In prehistory there is some evidence that in some situations signallers (hunters) would have gained social and even reproductive benefits. This is the most plausible explanation for prehistoric dolphin hunting, as inferred from faunal collections from several archaeological sites in the California Channel Islands, and Baja California (Porcasi & Fujita 2000). The faunal remains reveal a distinctive maritime adaptation that is more heavily reliant on the riskier capture of pelagic dolphins than on near-shore pinnipeds, a phenomenon that cannot be explained by the OFT. Similarly, OFT does not explain the benefits accrued by big game

hunters living in the whaling community of Lamalera, Indonesia (Alvard & Gillespie 2004). Results indicate that big game hunting provides males a strong selective advantage. Harpooners, and, to a lesser degree, hunters in general reap substantial fitness benefits from their activities. Hunters, especially harpooners, have significantly more offspring than other men after controlling for age. Harpooners marry significantly earlier and start reproducing at an earlier age unlike other hunt group members or non-hunting participants – the technicians and the boat managers. These results are consistent with data from other hunting societies that show significant reproductive benefits for good hunters. Harpooners receive significantly more meat even after controlling for the effort they expend hunting, while at the same time suffer an increased risk of mortality. Some forms of collective hunting do not translate into larger quantities of meat for hunters than for the rest of the group, but this is compensated by obtaining other types of benefits such as, reputation and reproductive success. This public recognition may allow hunters to have more wives, who raise their children better (Blurton-Jones *et al.* 1997), as well as being considered a desirable neighbour and ally (Hawkes 2001). Among cooperative Hadza hunters (Blurton-Jones *et al.* 1997), meat is shared almost evenly between all the households in camp. Men with a higher reputation have higher reproductive success. First, they tend to have wives who produce live children faster because these wives are more efficient foragers than other women. Second, older Hadza men with a high reputation have young wives, usually married after deserting older wife by whom they had fathered children, thus increasing reproductive success. Finally, the costly signalling theory might apply in situations where hunters elect to forfeit hunting profitable prey types if it is linked to social costs. Koster *et al.* (2010) argue it might be preferable to return home empty-handed than to be known as a hunter who must pursue species that are widely disliked because of bad taste of the meat in order to secure an adequate amount of meat.

3.6 The ‘Ecologically Noble Savage’ Debate

From the 1970s to the 1990s the issue of the ‘ecologically noble savage’ was controversially debated but the discussion has abated since the predictions from the thesis were tested using foraging theory for the prey choice by Piro shotgun hunters of Amazonian Peru, demonstrating that there is little evidence supporting the hypothesis (Alvard 1993). Moreover, the hypothesis has become more and more redundant because most hunter-gatherer

societies do not practice their original lifestyle any longer. Thus, the debate appears dated, but we present it here for completion and also to introduce the related concept of ‘autonomous conservation’.

Indigenous, small-scale societies have often been portrayed as natural conservationists who ‘live in harmony with their environment’ (Alvard 1993). For example, McDonald (1977) argues that food taboos facilitate conservation of prey species among South American tropical forest groups. Jean Jacques Rousseau’s romantic view of a ‘noble savage’, the Indigenous person who has not been corrupted by civilization, was extended and adapted to the concept of the ‘ecological noble savage’, the popular belief assuming that ‘primitive’ humans existed in a state of equilibrium with the surrounding natural resources (for overview, see Alvard 1993). Amongst biologists, the hypothesis gained support by Wynne-Edwards’ (1962) assumption of group selection whereby social species evolved adaptations that prevented them from degrading their habitat. Specifically, he assumed that hunter-gatherer remained in balance with their natural resources (Wynne-Edwards 1965). Since, the hypothesis has been thoroughly debunked (Alvard 1993; Krech 1999; Harkin & Lewis 2007; Smith & Wishnie 2000). For example, McDonald’s (1977) argument that food taboos facilitate conservation does not hold as shown by the numerous examples outlined above. Nevertheless, the hypothesis periodically appears in the academic literature, such as in Stoffle (2005): ‘For tens of thousands of years, the people of the New World sustainably used and managed these very old human ecosystems. Those peoples who remained in place for long periods coadapted with their ecosystems causing a new ecological order to emerge – an order often accompanied by increases in biodiversity and biocomplexity.’ The strongest evidence against the ‘ecological noble savage’ hypothesis comes from the test of foraging theory on the prey choice by Piro shotgun hunters (Alvard 1993) and from mammal extinctions over the past 126,000 years (Chapter 6.1; Andermann *et al.* 2020). Foraging theory assumes that foragers will maximize their short-term harvesting rate rather than be driven by a concern for the sustainability of the harvest (Chapter 4). The data show that Piro hunters pursued prey consistent with predictions of foraging theory. They did not show any restraint from harvesting species vulnerable to over-hunting and local extinction. For example, howler and spider monkeys, which are most vulnerable to extinction, were always pursued. One could argue that hunter-gatherers in South America had less time to adapt to the local environment and that, consequently, conservation behaviour should be strongest in Africa, the cradle of humanity. However, the widespread

adoption of firearms and snares by Aka Pygmies, Baka Pygmies and San and the connected increased extraction rates and unsustainability of hunting speak against this notion. The exception is the Mbuti Pygmies, but all studies are from the last century and Mbuti readily adopted the more efficient net hunting after contact with agriculturalist neighbours (see Section 3.3.2).

Much of the debate appears to be centred on the definitions of conservation. It is important to distinguish proactive conservation from epiphenomenal conservation, which Hames (2007) defines as a consequence of a human population's inability to cause resource degradation or a simple observation about long-term equilibrium with resources. In contrast, proactive conservation does not only prohibit or mitigate resource depletion and damage, but it is designed to do so. An extensive review suggests that proactive conservation amongst hunter-gatherers is rare (Smith & Wishnie 2000). However, it is clear that many small-scale hunter-gatherers have extracted prey at sustainable levels, thus fulfilling the definition of epiphenomenal conservation. In general, this appears an epiphenomenon of population density where demand remains sustainable. Where effective population density increases, for example by hunting for the market economy through selling wild meat outside their own group, increased extraction rate occurs and unsustainability is the norm rather than the exception even within hunter-gatherer societies (Chapter 8). In other words, hunter-gatherer societies exhibit all the ingenuity and self-interest as societies elsewhere, except that they belong to the most disenfranchised people of the world (The Lancet 2016).

Related to, but clearly distinct from the 'ecologically noble savage' hypothesis is the recently emerging concept of rural communities taking responsibilities for managing their resources in their own lands (Franco *et al.* 2021) and that recognizing Indigenous Peoples' rights to land, benefit sharing and institutions is essential to meeting local and global conservation goals (Garnett *et al.* 2018), often even forming alliances with conservation bodies (Schwartzman & Zimmerman 2005). The new approach argues that 'local people are effective in protecting large areas in a relatively natural state' (Sheil *et al.* 2015), ensuring that autonomous management can lead to effective conservation. We discuss this in more detail in Chapter 8.