

1 **A case of suspected chimpanzee scavenging in the Issa Valley, Tanzania**

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11 **Abstract**

12 Like humans, chimpanzees (*Pan troglodytes*) are well-known for their vertebrate and
13 invertebrate hunting, but they rarely scavenge. In contrast, while hunting and meat
14 consumption became increasingly important during the evolution of the genus *Homo*,
15 scavenging meat and marrow from carcasses of large mammals was likely also an
16 important component of their subsistence strategies. Here, we describe a confrontational
17 scavenging interaction between an adult male chimpanzee from the Issa Valley and a
18 crowned eagle (*Stephanoaetus coronatus*), which resulted in the chimpanzee capturing
19 and consuming the carcass of a juvenile bushbuck (*Tragelaphus scriptus*). We describe
20 the interaction and contextualise this with previous scavenging observations from
21 chimpanzees.
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24 **Keywords**

25 Meat-eating; Carcass theft; Inter-specific competition; Raptor; Hominin subsistence
26 strategies; Hominin evolution
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37

38 **Introduction**

39 Despite rich comparisons between human and chimpanzee (*Pan troglodytes*)
40 hunting techniques (Boesch and Boesch-Achermann 2000; Domínguez-Rodrigo and
41 Pickering 2003), scavenging has been attributed almost exclusively to modern humans
42 (Bunn 2001; Domínguez-Rodrigo et al. 2009) and early hominins (Thompson et al.
43 2019). Scavenging behaviour is broadly defined as the acquisition and consumption of
44 organic tissue (e.g., meat, bone, etc.) from carcasses of vertebrates that were not killed
45 by the scavenger.

46 Hominins are hypothesised to have begun consistently obtaining meat by
47 scavenging in the Plio-Pleistocene (Shipman 1986; Blumenschine 1991; Blumenschine
48 and Cavallo 1992), either passively (Blumenschine 1991; Blumenschine and Cavallo
49 1992; Pante et al. 2012) or confrontationally (O’Connell et al. 2002). A passive
50 scavenging event involves the scavenger reaching a carcass following the departure of
51 the original predator and was likely the basic pattern of scavenging for early hominins
52 (Blumenschine 1991). A confrontational scavenging event is characterised by the
53 scavenger displacing the original predator from the carcass and is inherently more risky
54 for the scavenger.

55 Both types of scavenging behaviour also occur in wild chimpanzees (Morris and
56 Goodall 1977; Goodall 1986; Watts 2008; Hosaka 2015; Hosaka and Ihobe 2015;
57 Nakamura et al. 2019). Here, we follow the above definitions and separate
58 confrontational scavenging into either power scavenging (Bunn 2001) or carcass theft
59 (Watts 2008). Power scavenging involves the displacement of a species known to prey
60 on chimpanzees, e.g., leopards (*Panthera pardus*) (Boesch 1991; Boesch 2009) and
61 increases the chance of injury for both chimpanzees and the predator. Carcass theft

62 involves the displacement of a species that does not prey on the scavenger (Watts 2008),
63 e.g., raptors or medium-sized carnivores like civets (*Civettictis civetta*), caracals
64 (*Caracal caracal*), and baboons (*Papio* spp.). The species displaced during
65 confrontational scavenging is typically referred to as either the ‘original predator’ or
66 ‘confronted species’, with the latter being more suitable when predation is difficult to
67 infer.

68 In most cases, confrontational scavenging results in relatively early carcass
69 access, whilst passive scavenging usually results in late access (Watts 2008). Both the
70 risks and the expected payoffs are higher for confrontational scavenging as successful
71 confrontational scavenging is more likely to lead to the acquisition of fleshed carcasses
72 that yield greater caloric reward. Conversely, late access, usually via passive
73 scavenging, typically results in the retrieval of a defleshed carcass and provides minimal
74 caloric gain (Blumenschine 1991).

75 Significant archaeological evidence shows that by ~1.8-2 Myr ago, hominins
76 were likely gaining regular access to fleshed carcasses of small and medium-sized
77 bovids (Yravedra et al. 2020). However, disagreement persists concerning the point at
78 which hominins gained access to carcasses. Blumenschine (1991) suggests that
79 “maximisation of marrow (fat) yields, not flesh (protein) yields, was the criterion
80 shaping decisions about carcass processing”. That is, bone marrow via late access was
81 likely the primary food source provided by scavenged carcasses. Others point to
82 evidence for the existence of early access scavenging in hominins at *Homo erectus*
83 deposits, such as Olduvai (FxJj 50) and Peninj sites in Tanzania (Blumenschine 1991;
84 Domínguez-Rodrigo 2002), as well as from *Homo erectus* deposits in Gona, Ethiopia
85 (Domínguez-Rodrigo et al. 2005). Pervasive across these sites are the high frequencies

86 of cut marks, combined with low frequencies of carnivore tooth marks on upper-limb
87 and pelvic bones from archaeofaunal remains of medium and large Bovidae species
88 such as impala, gazelle, and wildebeest (Bunn et al. 1980) – indicative of hominin
89 scavenging and modification (i.e., butchery).

90 Moreover, insufficient evidence exists of the projectile technology necessary for
91 Plio-Pleistocene hominins to hunt prey of these sizes: Oldowan and early Acheulean
92 technologies raise questions about their adequacy in this role (Stiner 2002). Domínguez-
93 Rodrigo and Barba (2006) conclude that hominins ~1.75 Myr ago had systematic early
94 access to carcasses and, if access was not facilitated by hunting, other strategies such as
95 confrontational scavenging might have facilitated the capture of fleshed carcasses
96 (O’Connell et al. 2002). Regardless of how the early versus late access debate is
97 resolved, contemporary explanations for early access are hunting (Domínguez-Rodrigo
98 et al. 2021) and confrontational scavenging (Ferraro et al. 2013).

99 Wild chimpanzee confrontational scavenging in the form of carcass theft
100 described at Gombe, Tanzania, and Tai Forest, Ivory Coast (Table 1) may represent one
101 potentially significant component of a subsistence model for a chimpanzee-human last
102 common ancestor (LCA) or early hominins, and a precursor to increasingly complex
103 and aggressive Plio-Pleistocene behaviour i.e., the ‘home-base hypothesis’ (Isaac 1971)
104 and the ‘hunting hypothesis’ (Washburn and Lancaster 1968; Stanford and Bunn 2001).
105 Now assume that an LCA lived in a tropical, deciduous woodland mosaic, with a mix of
106 open (grassland) and closed (riparian forest) vegetation (reviewed in Andrews 2020),
107 like the modern, open-habitats of some extant chimpanzees (Drummond-Clarke et al.
108 2022). In that case, we may expect similar subsistence strategies in the form of
109 confrontational carcass thefts.

110 *Chimpanzee scavenging*

111 Wherever chimpanzees have been studied long-term, reports of meat-eating
112 have followed, including a diverse vertebrate diet. Chimpanzees frequently hunt (Mitani
113 and Watts 2001) and consume at least 51 mammal species (Watts in press), which
114 include arboreal primates like red colobus monkeys (*Procolobus* spp.; Hobaiter et al.
115 2017) and bushbabies (*Galago senegalensis*; Pruettz and Bertolani 2007), as well as
116 terrestrial mammalian species like bushpig (*Potamochoerus larvatus*) and bushbuck
117 (*Tragelaphus scriptus*; Stanford 1996). Despite decades of long-term research at
118 multiple communities across chimpanzee distribution (Nakamura et al. 2015; Boesch et
119 al. 2019; Emery Thompson et al. 2020), less than two dozen observations of scavenging
120 have been described, compared to thousands of successful hunting bouts.

121 We have limited data on the frequency with which different chimpanzee
122 communities scavenge for food and how they react to finding carcasses. M-group
123 (Mahale) chimpanzees have been observed scavenging some carcasses immediately
124 upon possession (Nakamura et al. 2019) and have even deprived a leopard of access to a
125 carcass (Nakamura et al. 2019). Equally, Mahale chimpanzees have also shown
126 hesitation toward carcasses presumed to have been predated by a leopard (Hosaka et al.
127 2014). Mahale chimpanzees are analogous to their Ngogo (Uganda) and Gombe
128 counterparts in that they occasionally demonstrate a reluctance to consume carcasses of
129 prey and non-prey species (Nishida 1994; Nakamura et al. 2019). Reports from Ngogo
130 describe a general curiosity toward carcasses (Watts 2008), while Gombe (Tanzania)
131 chimpanzees sometimes ignore them entirely (Goodall 1986).

132 The differences in scavenging tendencies between communities are yet
133 unknown; however, if variation exists in confrontational scavenging, it is likely a result

134 of ecological differences, such as the density of sympatric predators (Nakamura et al.
135 2019). Chimpanzee encounters with predators are rarely observed directly. As a result,
136 indirect accounts of confrontation are often inferred through (chimpanzee) vocalisations
137 within the vicinity of the carcass or posthumously by predation marks, such as
138 lacerations on the body and puncture wounds around the throat (Hiraiwa-Hasegawa et
139 al. 1986; Nishida 1994). It is important to exercise caution when drawing conclusions
140 about scavenging after the event. Leopards typically cache their prey for several days
141 (Bailey 1993), so inferences alone are inadequate for determining whether confrontation
142 occurred or if the carcass was passively scavenged whilst the leopard was away.

143 Only one first-hand account of confrontational scavenging by chimpanzees has
144 been reported (Nakamura et al. 2019). It represents the only power scavenging
145 observation beyond modern humans within the Primate order. The report describes
146 Mahale M-group members depriving a leopard of a blue duiker (*Philantomba*
147 *monticola*) carcass. Chimpanzee carcass theft has been documented 51 times, of which
148 only seven (not including this observation) meet our criteria for Table 1 (see below).

149 Most (n=48) carcass thefts or ‘piracies’ from baboons have been reported from
150 Gombe (in both Kasekela and Mitumba communities) (Gilby et al. 2017). However, we
151 have only included accounts where both the predators and prey were identified, and
152 their interaction was directly observed or reasonably inferred from the circumstances
153 (e.g., via indirect observations and postmortem evidence). It is also compulsory that the
154 carcass be consumed and not provided by researchers or previously hunted by
155 chimpanzees and then abandoned. Consequently, we have cited only a small proportion
156 (n=4) of detailed reports described in Morris and Goodall (1977) and Goodall (1986) in
157 Table 1, summarising the remainder within the text above (Goodall 1986; Gilby et al.

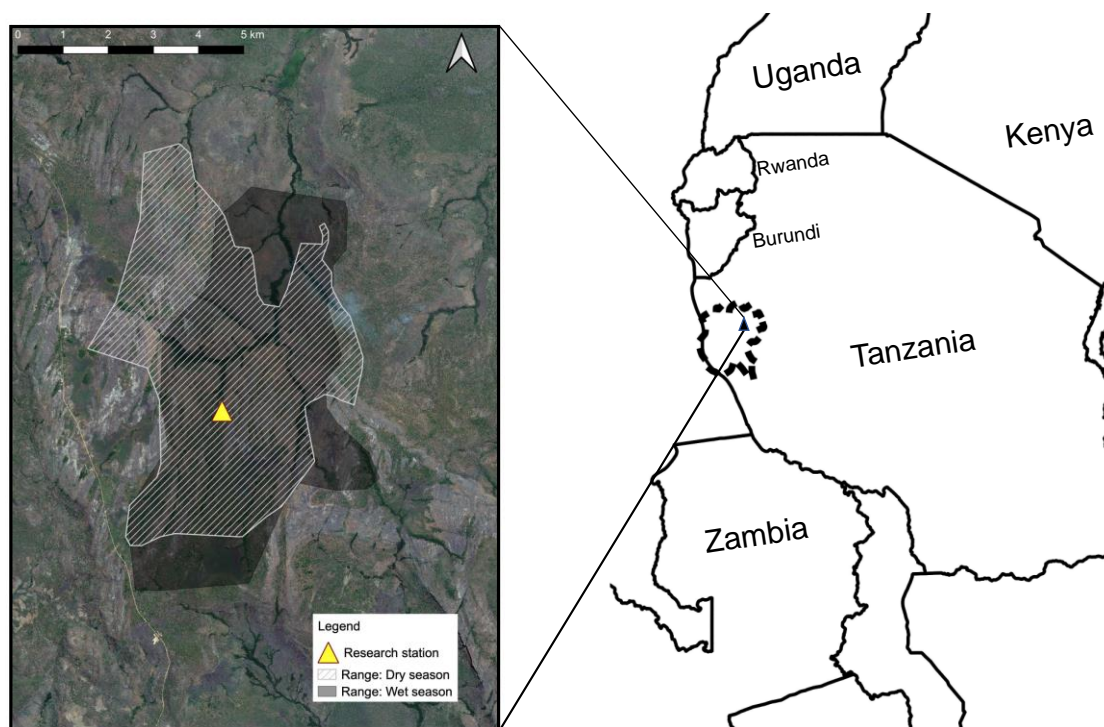
158 2017). Similarly, we acknowledge three carcass thefts at Tai, reported by Boesch and
159 Boesch-Achermann (2000), but have not included them in Table 1 due to the live status
160 of the prey during the scavenging event, which contradicts our scavenging definition.

161 Here, we present the first observation of confrontational carcass theft in the Issa
162 Valley (Figure 1) and contextualise it with previous descriptions from other
163 communities. Our observation offers a second example of a chimpanzee-raptor
164 confrontation but differs in an important way from the one reported at Tai over two
165 decades ago (Boesch and Boesch-Achermann 2000). Issa chimpanzees (*Pan troglodytes*
166 *schweinfurthii*) live in a savanna mosaic woodland and thus provide a more ecologically
167 relevant model for hominin evolution (Drummond-Clarke et al. 2022).

168 Table 1 Published accounts of inferred and observed power scavenging and carcass theft across chimpanzee communities
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Type	Community	Scavenger age/sex	Scavenged species	Confronted species	Citation
Power scavenging	M-group (Mahale, Tanzania)	adult female	blue duiker (<i>Philantomba monticola</i>)	leopard (<i>Panthera pardus</i>)	Nakamura et al. 2019
		–	red colobus (<i>Procolobus tephrosceles</i>)	leopard (<i>Panthera pardus</i>)	Hosaka 2015
Carcass theft	Kasekela (Gombe, Tanzania)	adult male	blue duiker	smaller-sized predator: e.g., civet or honey badger	Hosaka and Ihobe 2015
		adult male	bushbuck	olive baboon (<i>Papio anubis</i>)	Morris and Goodall 1977
		adult male	bushbuck	olive baboon (<i>Papio anubis</i>)	
		adult male	guinea fowl (<i>Meleagris numida</i>)	olive baboon (<i>Papio anubis</i>)	
	Ngogo (Kibale, Uganda)	adult female	bushbuck	olive baboon (<i>Papio anubis</i>)	Goodall 1986
		adult male	red duiker (<i>Cephalophus natalensis</i>)	olive baboon (<i>Papio anubis</i>)	David Watts, pers. comm., 22 Jan 2023
		adult male	blue duiker	olive baboon (<i>Papio anubis</i>)	

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 171 *Note.* Scavenging accounts were subject to the following criteria: accurate predator and prey identification, direct observation of interaction or reasonable inference
 172 based on circumstance, and the scavenging of a carcass not provided by researchers or previously hunted by chimpanzees and then abandoned



174 Figure 1 Issa community home ranges during the wet (shaded) and dry (lined) season from
 175 2018-2020 are shown within the broader Greater Mahale Ecosystem (GME) (dotted outline)
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178 **Methods**

179 *Study site and subjects*

180 The Issa Valley lies within the Tongwe West Forest Reserve, western Tanzania.
 181 Vegetation is characterised as a mosaic habitat of deciduous miombo woodland
 182 (dominated by *Brachysteria* and *Julbernardia*), interspersed with thin strips of riparian,
 183 evergreen forest (7% landcover), small patches of seasonally inundated grasslands, and
 184 rocky outcrops (Drummond-Clarke et al. 2022). Besides chimpanzees, the area hosts a
 185 rich diversity of small (D'Ammando et al. 2022) and medium-large (Piel et al. 2019)
 186 mammalian wildlife, including sympatric predators such as leopard, lion (*Panthera leo*),
 187 spotted hyena (*Crocuta crocuta*), and wild dog (*Lycaon pictus*). Chimpanzees have

188 preyed on various species, including blue duiker, bushbuck, and klipspringer
189 (*Oreotragus oreotragus*) (Ramirez-Amaya et al. 2015; Moore et al. 2017; Piel and
190 Stewart, unpublished data). The community have been habituated since 2018 and at the
191 time of the observation, the community comprised 32 individuals (13 male and 12
192 female adults and subadults, along with seven dependent offspring) and ranged over at
193 least 36km² (Giuliano et al. 2022).

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195 **Results**

196 On 24 October 2021, S. Baker and a field assistant were following a party of
197 nine chimpanzees, including five adult males (IM, SA, KI, BO, MA), one adult non-
198 estrous female (BA), and three subadult males (DH, WI, MO). IM has been the highest-
199 ranking male in the Issa community since 2018, followed by SA and KI. BO and MA
200 are middle and low-ranking males, respectively. The party was crossing a riparian forest
201 at 1345h when IM abruptly ran to the left out of the forest and into a (woodland) area of
202 long grass. Researchers heard no vocalisations, and other party members continued
203 travelling in the same direction as they were previously. In the moments immediately
204 following, S. Baker observed a large raptor take flight from where IM now stood with
205 the carcass (in mouth). Researchers were situated favourably as the bird took flight and
206 confidently recalled its physical characteristics, identifying it as a mature crowned eagle
207 (*Stephanoaetus coronatus*). Note: Observers did not detect laceration marks or puncture
208 wounds on the carcass that indicated an attack by the raptor; IM was moving too
209 quickly after he obtained the carcass, and once in the tree, the melee between group
210 members shrouded the carcass from view. At this point, all the other chimpanzees in the
211 party ran toward IM, who ran at speed to climb a nearby tree, and the others followed,

212 except for MO, remaining near the base of the tree. Later, we confirmed that the carcass
213 was a juvenile bushbuck (*Tragelaphus scriptus*), approximately 45 cm in head-body
214 length. The bushbuck was lifeless when first observed but appeared intact and without
215 deformation. Once in the tree (1350h), IM lost control of the carcass to an unidentified
216 individual, and the five adult males (IM, SA, MA, BO, KI) began to compete for meat,
217 accompanied by vocalisations (screams and hoots). KI procured a limb during the
218 aggression, and the subadult male WI descended to the ground to retrieve a scrap that
219 fell. Moments later (1353h), IM took back control of the carcass and was subject to
220 intermittent begging behaviour (vocalisations and gestures – Gomes et al. 2019),
221 primarily from males MA and SA and female BA for the following hour; only BA was
222 allowed access to the meat. The remainder was entirely consumed by IM (Figure 2),
223 who carried the carcass until 1530h. At that point, he dropped it, and WI retrieved and
224 carried it for 60 minutes until 1630h when researchers lost contact with the party. In
225 total, four individuals were observed to consume the meat, and only the skull remained
226 (which researchers did not collect) when the party was last observed.



Figure 2 IM consumes the bushbuck carcass (credit: S. Baker/GMERC)

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255 **Discussion**

256 With our description of a rare carcass theft at Issa, we contribute a new case of
257 confrontational scavenging in chimpanzees from western Tanzania. This confrontation
258 concerns the theft of a bushbuck carcass from a crowned eagle. Researchers were able
259 to identify the confronted raptor species by its distinct physical characteristics: legs and
260 flanks were blotched/ barred and closely spotted with black and white; underwing
261 coverts had a bold chestnut colouration, spotted lightly with black; and primary
262 underwing feathers were barred in black and white (Ferguson-Lees and Christie 2001).
263 Although the moment of the theft was not directly observed, we can infer its occurrence
264 due to the simultaneous flight of the crowned eagle from where chimpanzee IM was

265 first observed holding the carcass. Due to the speed and direction in which IM travelled
266 after scavenging, observers were unable to identify potential injuries on the carcass that
267 alluded to predation by the raptor. Moreover, researchers detected no putrid odours after
268 directly trailing IM and the carcass, suggesting that the bushbuck recently died.

269 Whilst possible, it is unlikely, that IM and the raptor converged on a live animal
270 simultaneously. The chimpanzees were followed consistently – across a semi-open
271 woodland habitat – immediately preceding the point at which IM was observed with the
272 carcass. Despite good visibility, no interaction was witnessed between the bushbuck and
273 raptor, i.e., the raptor was not observed descending to the ground, nor were any
274 vocalisations heard prior to researchers arriving at the scene. Therefore, it is most likely
275 that the eagle had already preyed upon the bushbuck prior to the arrival of the
276 chimpanzees when IM confronted and chased the eagle from the carcass.

277 It is plausible to assume that the crowned eagle captured and killed this bushbuck.
278 The crowned eagle is a diurnal raptor (Nagy and Tökölyi 2014), a pursuit predator not
279 recognised to scavenge prey (Potier et al. 2017). Crowned eagles are a known predator
280 of (immature) bushbuck-sized antelope (Reeves and Boshoff 2016), a prey species of
281 Issa (Piel and Stewart, unpublished data), Gombe (Newton-Fisher 2007), and Mahale
282 (Hosaka et al. 2001; Hosaka et al. 2020) chimpanzees. Given these inferences, we may
283 determine that the requirements of a confrontational carcass theft were met: (1) the
284 carcass was fleshed and the tissue consumable, (2) the species likely previously in
285 command of the carcass was a crowned eagle, a predator species non-threatening to
286 chimpanzees, and (3) the dominant male chimpanzee (IM) likely chased the eagle off to
287 gain access to the carcass. The event resulted in the complete consumption of the
288 carcass, supporting the existence of confrontational scavenging in Issa chimpanzees, the

289 first recorded at Issa since habituation was completed in 2018. Crucially, if we
290 acknowledge that chimpanzees are capable of confrontational scavenging, then
291 previously published ‘hunts’ may have been scavenging unseen by human observers
292 who arrived after the event. Nakamura et al. (2019) contend that aggressive scavenging
293 events could be underrepresented in the literature due to longstanding assumptions that
294 chimpanzees hunt and do not scavenge.

295 We propose that the ecology of the area influences the frequency of these
296 behaviours. For example, we see disproportionately higher densities of leopards at
297 Mahale despite a relatively low density of medium-sized ungulates (Nakazawa 2020),
298 allowing for greater exposure to fresh carcasses recognisable as food. Leopards are
299 regularly encountered on remotely-triggered cameras at Issa (Piel and Stewart,
300 unpublished data), but no density data have been reported.

301 Specific ecological conditions (predator-prey abundances) likely affected the
302 confrontational scavenging behaviour of extant chimpanzees versus extinct hominins
303 ~1.7 Myr ago. The differences in abundance and diversity of carcass and predator may
304 have led to correspondingly higher frequencies of medium-to-large carcasses available
305 for hominins (Van Valkenburgh 2001), increasing the opportunity and prevalence of
306 confrontational scavenging.

307 Issa chimpanzees live in a predominantly open habitat, characterised by
308 woodland and grasslands and one that resembles reconstructions of early hominin (e.g.,
309 *Ardipithecus*) paleohabitats (White et al. 2009). Chimpanzee dietary ecology, especially
310 hunting, has long been used to inform our understanding of hominin evolution, namely
311 how prey was attained and the complexity of group cooperation required to meet this
312 goal (Stanford 1996; Sponheimer and Lee-Thorp 1999). In contemporary hunter-

313 gatherer populations, scavenging can comprise up to 20% of meat intake during some
314 periods of the year (Hadza: O'Connell et al. 1988).

315 Debate surrounds the method with which early hominins acquired large animal
316 carcasses: the prevalence of confrontational scavenging (Pante et al. 2015; Thompson et
317 al. 2019) compared to hunting (Domínguez-Rodrigo et al. 2021). Watts (2008) suggests
318 confrontational scavenging provided a vital stepping-stone to hominin hunting – a
319 transition that would propel humans from ‘marginal scavengers’, reliant on the
320 ‘leftovers’ of carnivores (Shipman 1986), to successful hunter-scavengers proficient in
321 aggressively securing fleshed carcasses from large predators (Bunn et al. 1986).

322 Additional accounts of confrontational scavenging in extant nonhuman primates,
323 especially those in open-habitat communities, would expand behavioural insights into
324 the ecological opportunities and limitations conceivably encountered by early hominins
325 in similar habitats (O'Connell et al. 2002). The Issa Valley is particularly suited to
326 provide a realistic (mosaic) woodland scavenging model of chimpanzees, as it is an
327 analogous environment to which early hominins were adapted (Stanford and Bunn
328 2001).

329 Whether confrontational scavenging, as described at nearby Mahale and now at
330 Issa, reflects a regional cultural tendency or an opportunistic strategy is unknown and
331 cannot be better understood without numerous future observations. Furthermore, each
332 new observation of scavenging by nonhuman primates helps us to understand the role of
333 scavenging in extant species and, hopefully, in the future, the role of the local
334 environment in predicting scavenging behaviour. Future research could use systematic
335 statistical analyses of scavenging patterns across the *Pan* distribution to determine the
336 role of habitat in influencing scavenging behaviour, especially in the context of human

337 evolution. Due to the combination of abundant terrestrial mammalian wildlife, a diverse
338 guild of large carnivores, and inter-specific spatial overlap at Issa, we predict similar
339 scavenging observations in the future.

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Declarations

345 All authors contributed to the study's conception and design. SAB performed data collection.
346 SAB wrote the first draft of the manuscript, and AKP and FAS commented on and edited
347 subsequent versions. All authors read and approved the final manuscript. No funding was
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