

# Ethnography and ethnohistory support the efficiency of hunting through endurance running in humans

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Eugène Morin <sup>1,2</sup>✉ & Bruce Winterhalder <sup>3</sup>

Humans have two features rare in mammals: our locomotor muscles are dominated by fatigue-resistant fibres and we effectively dissipate through sweating the metabolic heat generated through prolonged, elevated activity. A promising evolutionary explanation of these features is the endurance pursuit (EP) hypothesis, which argues that both traits evolved to facilitate running down game by persistence. However, this hypothesis has faced two challenges: running is energetically costly and accounts of EPs among late twentieth century foragers are rare. While both observations appear to suggest that EPs would be ineffective, we use foraging theory to demonstrate that EPs can be quite efficient. We likewise analyse an ethnohistoric and ethnographic database of nearly 400 EP cases representing 272 globally distributed locations. We provide estimates for return rates of EPs and argue that these are comparable to other pre-modern hunting methods in specified contexts. EP hunting as a method of food procurement would have probably been available and attractive to Plio/Pleistocene hominins.

The hominin lineage is characterized by considerable selection for bipedal locomotion<sup>1–3</sup>. While the literature on the emergence of the walking gait in humans is extensive, much less is known about the evolution of the biomechanically distinct running gait. We present mathematical modelling and extensive ethnographic and ethnohistoric data that support the endurance hunting hypothesis formulated four decades ago<sup>4</sup>. It contends that the challenges of procuring medium- and large-sized mammalian game provided the locus of selection for the traits that enhanced endurance running in Plio/Pleistocene hominins.

Compared with cursorial mammals, humans are unimpressive sprinters, able to maintain a maximal running velocity of  $\sim 10 \text{ m s}^{-1}$  in elite sprinters for  $\sim 20 \text{ s}$ , after which performance fades rapidly due to physiological limits on adenosine triphosphate (ATP) resynthesis and the associated switch from anaerobic to aerobic metabolism<sup>5,6</sup>. Cursorial mammals have much higher maximal running speeds—up to  $26.5 \text{ m s}^{-1}$  in Thomson's gazelle (*Gazella thomsoni*) and  $29 \text{ m s}^{-1}$  in the cheetah (*Acinonyx jubatus*)—and can maintain them sometimes over

minutes<sup>7</sup>. However, despite our poor sprinting abilities, humans are highly adept at slower-paced endurance running over long distances, with some athletes accomplishing the feat of running daily marathons (42.195 km) over one or more months. The skeletal muscles of our pelvic area and hindlimbs differ from those of most other mammals, including chimpanzees and gorillas. We tend to have a higher percentage of slow-twitch, fatigue-resistant rather than fast-twitch fibres<sup>8,9</sup>. With reduced power output and lower contraction rates, a greater proportion of slow-twitch fibres in locomotor muscles reduce energy expenditure<sup>10–12</sup>, which helps humans combat hypoxia to maintain a relatively stable metabolic state while running over extended distances.

A second issue for endurance behaviours is metabolic heat dissipation. Overheating can have lethal consequences in animals<sup>13,14</sup>. During vigorous exercise, humans primarily eliminate heat using eccrine sweat glands, a recent evolutionary adaptation limited to the catarrhine lineage<sup>15</sup>. We do this unusually well. Humans can dissipate heat more quickly than most other species because we can sweat copiously—up

<sup>1</sup>Department of Anthropology, Trent University, Peterborough, Ontario, Canada. <sup>2</sup>PACEA, Université de Bordeaux, Pessac, France. <sup>3</sup>Anthropology and Graduate Group in Ecology, University of California, Davis, Davis, CA, USA. ✉e-mail: [eugenemorin@trentu.ca](mailto:eugenemorin@trentu.ca)

to  $3.7 \text{ l h}^{-1}$  in marathon runners<sup>16</sup>, earning us the label, ‘sweaty ape’<sup>17,18</sup>. The effectiveness of cooling by sweat evaporation is enhanced by our high density of eccrine glands—ten times that of chimpanzees—and our diminutive, unpigmented vellus body hair<sup>15,19</sup>. Ungulates that can sweat, such as horse, donkey and camel, do so via the apocrine gland system, which is less effective in part due to markedly lower sweating rates and because evaporation in wet fur occurs at some distance from the skin, which impedes transfer of heat away from the body and results in higher water loss<sup>20,21</sup>. Most other mammals also exhibit less effective systems of heat transfer, including panting<sup>13,22</sup>.

Enquiries into the evolutionary forces that might have favoured the evolution of these traits in humans and how they relate to endurance running are longstanding. Although brief statements of the endurance hunting hypothesis were published earlier or about the same time<sup>23–26</sup>, it was Carrier<sup>4</sup> who first expanded the idea into a full theory. We focus on Carrier’s formulation but use the terminology of endurance pursuits (EPs) for consistency with the foraging theory distinction between search and pursuit<sup>27</sup>. In Carrier’s proposal, bipedal locomotion adapted to the thermal challenges of a tropical environment opened a new predatory niche: relentless, hours-long running pursuits after prey in hot weather. Expansion into this new niche was facilitated by physiological adaptations that gave humans endurance advantages. For instance, humans can take more than one breath per stride and have more flexible breathing patterns than quadrupeds whose locomotor and respiratory cycles are strictly coupled while trotting or galloping, thus posing severe limits on their thermoregulation<sup>28</sup>. Carrier’s model contends that through endurance running, humans were able to drive prey into hyperthermia by forcing them to run at uneconomic gaits in hot weather. Because this hunting tactic does not require advanced tools, EPs would have been a relatively productive and safe method for securing exhausted prey before the emergence of complex weapons.

Expanding on Carrier’s model, Bramble and Lieberman reviewed the derived traits that underlie the ability to run long distances. These derived traits were first perceptible in early *Homo* at least 1.8 million years ago<sup>1</sup> and include a relatively longer leg, a larger gluteus maximus muscle, an expanded Achilles tendon, a developed plantar arch in the foot and larger joints able to handle higher stresses in the lower extremity, among others<sup>29</sup>. By facilitating endurance running, these traits would have expanded scavenging opportunities for ephemerally available carcasses; they also made possible the ability to engage in persistence hunting. In support of the EP hypothesis, research has shown that hot weather EP hunts focused on large game were still practiced occasionally and with success by San foragers (Kalahari Desert, Botswana)<sup>30,31</sup>. Studies using simulations<sup>22,32,33</sup> and/or ethnographic data<sup>34</sup> have confirmed that neither heat dissipation nor the costs of carcass transport are major impediments to this hunting tactic<sup>35</sup>. Continuing investigations of the physiological traits possibly associated with the evolution of endurance running have also been supportive<sup>29,36,37</sup>. However, the amount of energy spent in the activity and limited ethnographic observations have been reasons for continuing skepticism<sup>36,38</sup>.

Acceptance of the EP hypothesis has faced two main challenges. The elevated cost of running over walking has been viewed as a potential concern by advocates of the EP hypothesis (ref. 1, p. 351) and as a more serious impediment by skeptics (ref. 39, p. 90; ref. 40, p. 359). Although some of these studies acknowledge that a large game capture may offset potential differences in metabolic costs, the higher efficiency of an optimal walking pace has seemed to preclude evolution of a running gait for hunting. A second challenge to the EP hunting tactic is its rarity among recent and contemporary foragers, the few recorded occurrences being limited to the hot, open environments of the American Southwest, Southern Africa and Australia (citations in ref. 41). Other reservations that have been levelled against the EP hypothesis include the difficulty of tracking prey in the savanna-woodlands biotopes occupied by early *Homo*<sup>38</sup> and laboratory evidence<sup>39,40</sup> contradicting Carrier’s suggestion that the cost of running a given distance is nearly

constant as a function of velocity in humans, unlike ungulates. Were the per km cost independent of velocity as Carrier hypothesized<sup>4</sup>, a hunter would incur no cost increase by electing a running pace uniquely disadvantageous to the animal being pursued.

Here we present a behavioural ecology perspective and an expanded ethnohistoric and ethnographic dataset that together provide theoretically situated and empirically strengthened support for the EP hypothesis. We make four points: (1) we demonstrate using mathematical modelling that EPs can generate favourable foraging energy return rates; (2) we show that there is substantial ethnohistoric and ethnographic evidence that hunting by EP was frequently practiced by a wide range of small-scale societies occupying diverse habitats; and we provide (3) empirical information concerning the factors that give hunters undertaking an EP advantage over his or her prey, as well as (4) quantitative evidence that EP return rates that are possible in principle are achieved in practice. Evolutionary ecology analysis of endurance running can advance understanding of evolutionary changes in our gaits, biomechanics and thermoregulation, and inform a recreational activity enjoyed by millions of people today.

## Results

### Comparative appraisal of walking and running pursuits

The net acquisition rate for pursuit and handling ( $R_p$ , termed  $R_{p\text{prey}}$  in ref. 42) of a resource establishes its value, its ranking relative to other resource possibilities, its potential contribution to overall foraging efficiency if captured, and the opportunity cost of passing it by in favour of searching for and pursuing resource types of higher value<sup>27,43</sup>. This is shown in the formula:

$$R_p = \frac{E_p - c_p t_p}{t_p} \text{ or, expressed in units, } \frac{\text{kcal}}{\text{h}} = \frac{\text{kcal} - \left(\frac{\text{kcal}}{\text{h}} \times \text{h}\right)}{\text{h}}, \quad (1)$$

where  $E_p$  is the edible value of the prey,  $c_p$  is the rate of pursuit energy expenditure and  $t_p$  is the pursuit time required, all values representing averages.  $R_p$  directs us to ask: if undertaken, will an EP return sufficient energy for the time invested to elevate the overall efficiency of the food quest? Foraging theory suggests that endurance pursuits can be favoured because in certain circumstances they have the potential of generating net acquisition rates comparable to or better than other foraging methods. More efficient foraging frees up time for other important activities, including socializing, reproduction and alliance building.

Using the  $R_p$  formula, we can generate semi-realistic estimates of the benefit-to-cost attributes of a pursuit as a function of walking or running velocities. Figure 1 depicts  $R_p$  for a gemsbok (*Oryx gazella*, a medium-sized ungulate commonly hunted in Southern Africa) as a function of gait and average pursuit velocity. The use of an average for velocity recognizes that in any pursuit, pace varies; it may slow to examine tracks or speed up when prey flight direction can be predicted. We envision especially long pursuits as a mix of walking and running gaits and velocities. The 4 to 32 km distances represent various possibilities for how far a pursued game animal might travel within a day before becoming debilitated by exhaustion, overheating, dehydration, projectile-delivered poison or a similar cumulative impairment. The upper end of the X axis is anchored around the average endurance running velocities observed for ‘recreational joggers’,  $3.2\text{--}4.2 \text{ m s}^{-1}$  ( $11.5\text{--}15.1 \text{ km h}^{-1}$ ) (ref. 1, p. 345).

$R_p$  is less at longer distances, as anticipated; perhaps unanticipated,  $R_p$  increases rapidly as hunter pursuit velocity increases. Assuming success and assessed in terms of distance, faster pursuits have the advantage, sometimes by orders of magnitude. This point is easily lost if attention on the greater rate of energy expenditure ( $c_p$ ) while running distracts from the lessened time ( $t_p$ ) required for the hunter to overtake the prey. We use a walking forager expenditure rate of

58.5 kcal km<sup>-1</sup> at 4 km h<sup>-1</sup> and a running rate of 69.0 kcal km<sup>-1</sup> at 10 km h<sup>-1</sup> (see Supplementary Fig. 1, Methods and Supplementary Information) to represent in Fig. 1 (arrow a–b<sub>1</sub>) a common proposal by EP advocates: if circumstances (for example, high heat) give the EP hunter an advantage over the fleeing prey, the result may be a shorter pursuit. In this hypothetical case, a walking pursuit of 4 km h<sup>-1</sup> requires 8 km, but the same pursuit at a running pace of 10 km h<sup>-1</sup> requires only half the distance (4 km), and R<sub>p</sub> for the running pursuit jumps 5-fold, from 59,930 kcal h<sup>-1</sup> to 300,128 kcal h<sup>-1</sup>. Similarly, arrow a–b<sub>2</sub> shows that the hunter can increase R<sub>p</sub> by 1.24× (from 59,930 to 74,515 kcal h<sup>-1</sup>) even if the running pursuit requires 16 km, double the capture distance of walking. This gain is achieved because substantially reducing the ‘duration’ of a pursuit can have a greater impact on R<sub>p</sub> than a moderate increase in expenditure rates. Finally, arrow a–c depicts a 16 km pursuit achieved by a mix of walking at 4 km h<sup>-1</sup> for two-thirds of the time and running at 10 km h<sup>-1</sup> for the remainder. The mixed gait pursuit achieves an average velocity of 6 km h<sup>-1</sup> and a return rate elevated by nearly 50% (29,848 kcal h<sup>-1</sup> to 44,767 kcal h<sup>-1</sup>). In Supplementary Fig. 2, we present a similar plot of velocity-dependent results for an 8 km pursuit of prey ranging in size from a jackrabbit (2 kg live wt) to a moose (600 kg live wt).

The more energy-expensive tactic—running—can beat a walking pursuit, sometimes quite substantially, because the additional energy expenditure of running is of little consequence to R<sub>p</sub> for any but the smallest of prey. We note that factors that appreciatively affect mobility costs (body size, fitness, load, slope, substrate texture, temperature) will act on both a walker and a runner, to little effect on the comparison we emphasize here. The net cost difference of a switch from walking to running at these velocities (69.0 – 58.5 = 10.5 kcal km<sup>-1</sup>) would reduce the food value of a gemsbok pursued for 40 km from 160,436 to 160,016 kcal, a negligible amount of -0.3%. However, the time cost of a 40 km pursuit, walking to running, drops from 10 to 4 h, generating an R<sub>p</sub> advantage of -250%. From a foraging theory perspective, it is not surprising that Plio/Pleistocene hominins might exhibit evidence of selection for endurance pursuits.

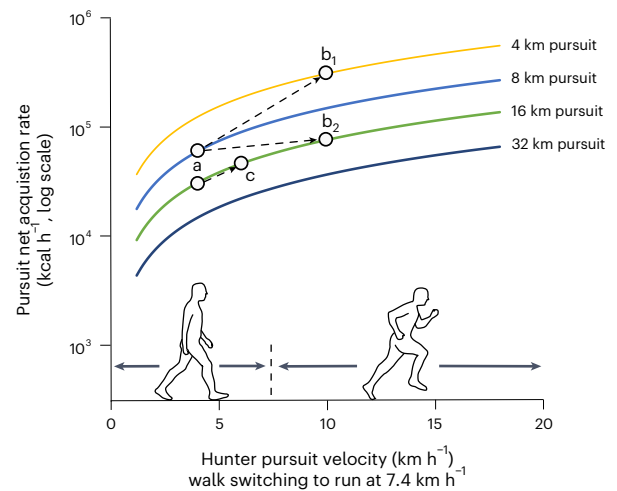
We note that Fig. 1 will also predict an increase in R<sub>p</sub> from a reduction in velocity, if a slower perhaps more stealthy pursuit appreciably shortens the distance to a capture or increases its odds of success. This would be represented in Fig. 1 by an arrow pointing upward to the left. As discussed below, the response of R<sub>p</sub> to increasing or decreasing pursuit velocity depends on situational factors, among them forager tactics and technology, environmental context and prey capabilities and behaviour.

Increasing pursuit velocity over fixed distances can dramatically elevate return rates. Even small amounts of running in a mixed gait pursuit can have significant effects. For game larger than 5–10 kg, the differential energy cost (in kcal h<sup>-1</sup>) of running relative to walking has a negligible impact on R<sub>p</sub>, whereas the effect of reduced pursuit duration is large. We expand on this point by developing a simple approximation for R<sub>p,r</sub> > R<sub>p,w</sub>, the condition for a running pursuit to be more valuable than a walking pursuit. We begin with

$$\frac{E_p - t_{p,r}c_{p,r}}{t_{p,r}} > \frac{E_p - t_{p,w}c_{p,w}}{t_{p,w}}, \tag{2}$$

where E<sub>p</sub> is the edible energy (kcal) of the game animal, t<sub>p,r</sub> is the time (h) required and c<sub>p,r</sub> is the energy expenditure (kcal h<sup>-1</sup>) for a successful running pursuit; t<sub>p,w</sub> and c<sub>p,w</sub> are the analogues for walking. Assuming that (E<sub>p</sub> – t<sub>p</sub>c<sub>p</sub>) is positive and multiplying both sides of equation (1) by  $\frac{t_{p,w}}{(E_p - t_{p,r}c_{p,r})}$ , we rearrange terms to:

$$\frac{t_{p,w}}{t_{p,r}} > \frac{E_p - t_{p,w}c_{p,w}}{E_p - t_{p,r}c_{p,r}}. \tag{3}$$



**Fig. 1 | Modelled pursuit net acquisition rate for *Oryx gazella* as a function of hunter velocity and gait for 4–32 km pursuit distances.** As the hunter’s pace increases, time to a capture at a particular distance declines and net energy (kcal) return rates grow. Dashed arrow a–b<sub>1</sub> compares a walking pursuit undertaken at 4 km h<sup>-1</sup> for 8 km to a running pursuit at 10 km h<sup>-1</sup> that, because it exhausts the gemsbok more quickly, secures a capture in only 4 km. The net acquisition rate jumps 5-fold, from 59,930 to 300,128 kcal h<sup>-1</sup>, the pursuit taking only 24 min. Dashed arrow a–b<sub>2</sub> shows that an increase in R<sub>p</sub> can be positive even if it provokes a pursuit twice as long, the 8 km walking return of 59,930 becoming 74,515 kcal h<sup>-1</sup> over 16 km of running (1.24×). Dashed arrow a–c compares a 4 km h<sup>-1</sup> walking pursuit for 16 km to a pursuit of the same distance in which the forager devotes 1/3 of the pursuit duration to a 10 km h<sup>-1</sup> running pace; net acquisition rate rises from 29,848 kcal h<sup>-1</sup> walking to 44,767 kcal h<sup>-1</sup> mixed walking and running, a 1.5× improvement. Note that the Y axis is on a log scale; parameter values, their sources and a description of calculations depicted appear in Methods and Supplementary Information.

Because the terms (t<sub>p,w</sub>c<sub>p,w</sub>, t<sub>p,r</sub>c<sub>p,r</sub>) are not very different from one another and probably small relative to E<sub>p</sub>, we simplify to

$$\frac{t_{p,w}}{t_{p,r}} > 1. \tag{4}$$

Equation (3) is the exact condition for a running pursuit advantage; equation (4) returns a close approximation indicating that irrespective of distance any successful running pursuit of medium or larger game that requires less time than would have been invested in successfully walking that pursuit will probably have a higher return rate.

The conditions above for running pursuit advantage assume a successful hunt, whether running or walking. To more explicitly recognize the general effect of pursuit success {0 < p<sub>r</sub>, p<sub>w</sub> ≤ 1}, we can define t<sub>p,w</sub> and t<sub>p,r</sub> as average pursuit time ‘irrespective of capture’ and modify equation 4 as:

$$\frac{t_{p,w}}{t_{p,r}} > \frac{p_w}{p_r}. \tag{5}$$

Equation (5) recognizes that time to a capture must be adjusted by success rates. As before, algebra and rearranging terms returns the approximate success-dependent condition for superiority of running pursuits:

$$\frac{t_{p,w}}{t_{p,r}} > \frac{p_w}{p_r}. \tag{6}$$

Equation (6) highlights the degree to which running pursuits can sacrifice success rates and still remain the R<sub>p</sub> choice over walking.

For instance, even if  $p_w = 0.80$  and  $p_r$  only one half of that, then if a walking pursuit also takes more than twice as long, running will still be favoured. Equation (3) can be similarly modified for an exact version of this result.

### Distribution of EPs in space and time

Our search through ethnohistorical and ethnographic sources (see Methods) yielded a database of 391 hunt descriptions consistent with an EP tactic (examples in Table 1 and Supplementary Table 2; all instances are listed in Supplementary Data 1; excerpts addressing specific results are presented in Supplementary Tables 3, 4, 6–8 and 10). The sample is more than an order of magnitude larger than previously known; it was assembled through a research design focused on the discovery of new ethnohistoric material taking advantage of the increasing conversion of paper documents into digital, word-searchable sources (Supplementary Information 1.1.3–1.1.4). Of these descriptions, 277 derive from ethnographic and ethnohistorical texts and 114 are from the Culture Element Distribution (CED) surveys undertaken in the 1930s and 1940s by the University of California. The full Supplementary Data 1 spans all continents except Antarctica (Fig. 2). The global distribution and abundance of EPs in early records is in stark contrast to their paucity in the post-1950 ethnographic literature. Allowing for occasional dating ambiguity, 85.7% of the cases in our dataset predate 1950 and most refer to events that occurred before the twentieth century. Despite a sparser record, the 23 descriptions for the period AD 1527–1702 suggest that EP hunts were practiced by a wide range of societies in, and presumably before, the early contact period, a point corroborated by several more recent sources (see excerpts in Supplementary Table 2, #51, 87, 129 and 247, and Supplementary Table 3).

This point is confirmed by the density of early contact hunter-gatherer societies in precolonial western North America documented by the CED inventories to practice run or wear-down pursuits (Fig. 2 lower left inset and Supplementary Fig. 3). The 17 studies in our dataset were generated by experienced ethnographers using standardized methods for systematically coding presence/absence from pre-existing and largely standardized trait lists. Native American elders were asked whether each trait listed was present or absent in the time of their parents and grandparents. The CED surveys cover contrasting environmental zones, ranging from the taiga and temperate forests of Western Canada to the xeric shrublands and arid deserts of California and the Pacific coastal margin into the Great Basin. The regional coverage encompasses a diverse set of social organizations including small-scale egalitarian groups (for example, Tsilhqot'in (Chilcotin), Dakelh (Carrier), Shoshone, Ute, Paiute) as well as larger stratified societies (for example, Halkomelem [Cowichan], Pomo, Chumash). Deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), elk (*Cervus canadensis*), mountain sheep (*Ovis canadensis*) and bear (*Ursus americanus*) were hunted by these groups using EP strategies.

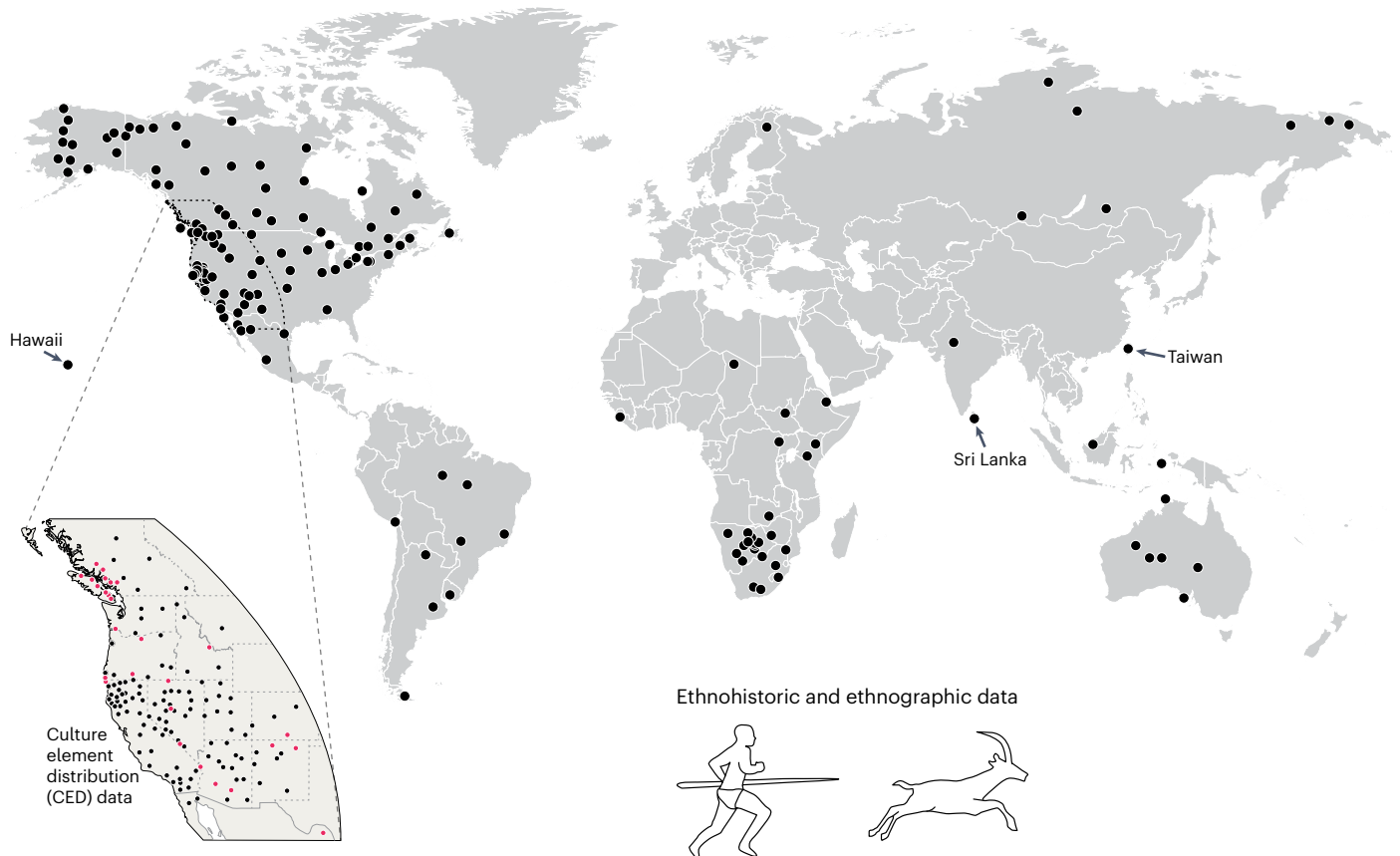
The methods and exhaustive regional coverage of the CED data allow us to assess the degree of confirmation bias likely to affect the rest of our sample. Confirmation bias can arise in analyses based on keyword searches<sup>44–46</sup>. In the CED sample, 141 societies systematically inventoried for EPs in Western North America, 114 (80.9%; Supplementary Table 5, Supplementary Fig. 3 and Supplementary Data 1) are positive for the trait. This confirms that this form of hunting was widespread in the region. More subtle forms of confirmation bias than presence/absence can be assessed from annotations in the overall dataset (recorded in the Supplementary Data 1 excerpts). For instance, 110 sources contain descriptions that shed light on the frequency of occurrence of EPs within a given society (for example, EPs presented as a usual form of hunting when there is crusted snow). In 70.9% of the cases with relevant information (Table 2), the descriptions are consistent with EPs being a habitual activity with delimited seasonal or environmental contexts such as high heat or a crusted snow cover. We return to this point below.

**Table 1 | Sample of excerpts describing EP hunts**

Group, place and time of observation	Description and reference
39. Gwich'in, Northwestern North America, ca. 1850s	"One ancient Indian said to me: In the old days we used to hunt with the bow and spear. Our young men were strong in those days. We hunted the moose by running him down on snowshoes, and we could run all day, such as wolves. Now our young men are become [sic] lazy and feeble. They prefer to hunt the moose in the fall, when he is easy to kill. They ride on their dog-sleds and are afraid to run all day." Ref. 61:24
67. Beothuk, Newfoundland, Canada, 1822	"The capabilities of some of the Indians in hunting seem almost incredible to those who have not seen their powers tried. Some single Indians will run down a stag; when the stag is fat, he is sometimes worth such an arduous pursuit, and it is then only he is liable to be fatigued to exhaustion. The hunter will commence the chase early in the day, and by following it up without intermission, will before night make the stag his prey without firing a shot. The stag at first easily outstrips his pursuer, but after a run of four or five miles he stops and is by and bye overtaken; again he sets off, and again he is overtaken; again, and again, he is overtaken; he lies down fatigued but is again surprised; thus the chase is kept up, until the poor stag, in despair of eluding his pursuer, plunges into a pool or morass to escape, Man at last winning the day." Ref. 62:152–153
229. Coahuiltecas, Texas, United States/Northern Mexico, 1527–1536	"They [the natives] are so accustomed to running that, without resting or getting tired, they run from morning till night in pursuit of a deer, and kill a great many, because they follow until the game is worn out, sometimes catching it alive." Ref. 63:91
286. Wailaki, California, United States, 1901–1919	"They [the Wailaki] were hunters, and, like the Lassik, took deer and elk by running them down. This, of course, does not mean that they outsped them, but that in a relentless pursuit they wore down the endurance of the game, until, unable to feed and perhaps overcome by psychic [sic] depression, it succumbed." Ref. 64:151–152
313. Bororo, Pugu River, Brazil, 1901	"They [the natives] greatly admire hunting with horses and dogs, as well they may, since by their method of hunting they must pursue an animal on foot for hours at full speed." Ref. 65:385
328. Teda, Chad, 1950s	"Course-hunting is popular: the hunter, during the hottest time of day, will pursue an oryx antelope that flees from one shady place to another. Finally it is so exhausted that it lets the hunter come close enough to kill it with a spear." Ref. 66:16–17 (translated by eHRAF)
378. Iban, Borneo, 1856–1858	"Deer are often hunted with dogs, and the former suffer so much from heat that in very oppressive and dry weather the Dayaks declare they can run them down themselves." Ref. 67:248
390. Native Hawaiians, Hawaii, 1882	"The native method of hunting them [the wild goats] is decidedly unique. The goat hunter follows a flock on foot. As he approaches they gallop away over the rocks, leaving the pursuer far behind. But they soon halt, tired and blown by their exertions, while the kanaka keeps on. It becomes a question of endurance between the steady jog-trot of the pursuer and the alternate halts and spasmodic efforts of the pursued. The kanaka wins every time. In the course of a couple of hours the animals are too weary and too much discouraged to flee further. Reaching the first laggard, the hunter breaks its hind legs across his knee, and the remainder of the flock are treated in like manner. Returning upon his track, he skins the animals at his leisure." Ref. 68:137

Numbers on the left column correspond to those in the full Supplementary Data 1.

Non-CED sources from the region of CED coverage report only 44 societies as practicing EPs (Supplementary Fig. 3). This apparent under-reporting of EPs in non-CED sources may have several explanations: because they occurred routinely only in limited contexts, EPs would frequently have been missed by short-term ethnohistoric



**Fig. 2 | Societal locations ( $n = 158$ ) with ethnohistorical or ethnographic evidence of hunting using an EP tactic and locations.** Lower left inset: locations for CED data ( $n = 114$ ) from western North America (see Supplementary Information). The CED data are presented separately because systematic regional coverage of presence/absence for trait list information does not exist

for other world regions; black dots represent a society positive for EPs; red are negative for it. Societies appearing more than once in our sample ( $n = 90$ ) are represented by only one dot; some data points ( $n = 29$ ) are missing due to a lack of precise geographical information.

**Table 2 | Prevalence of EPs by region as suggested by a qualitative analysis of the excerpts**

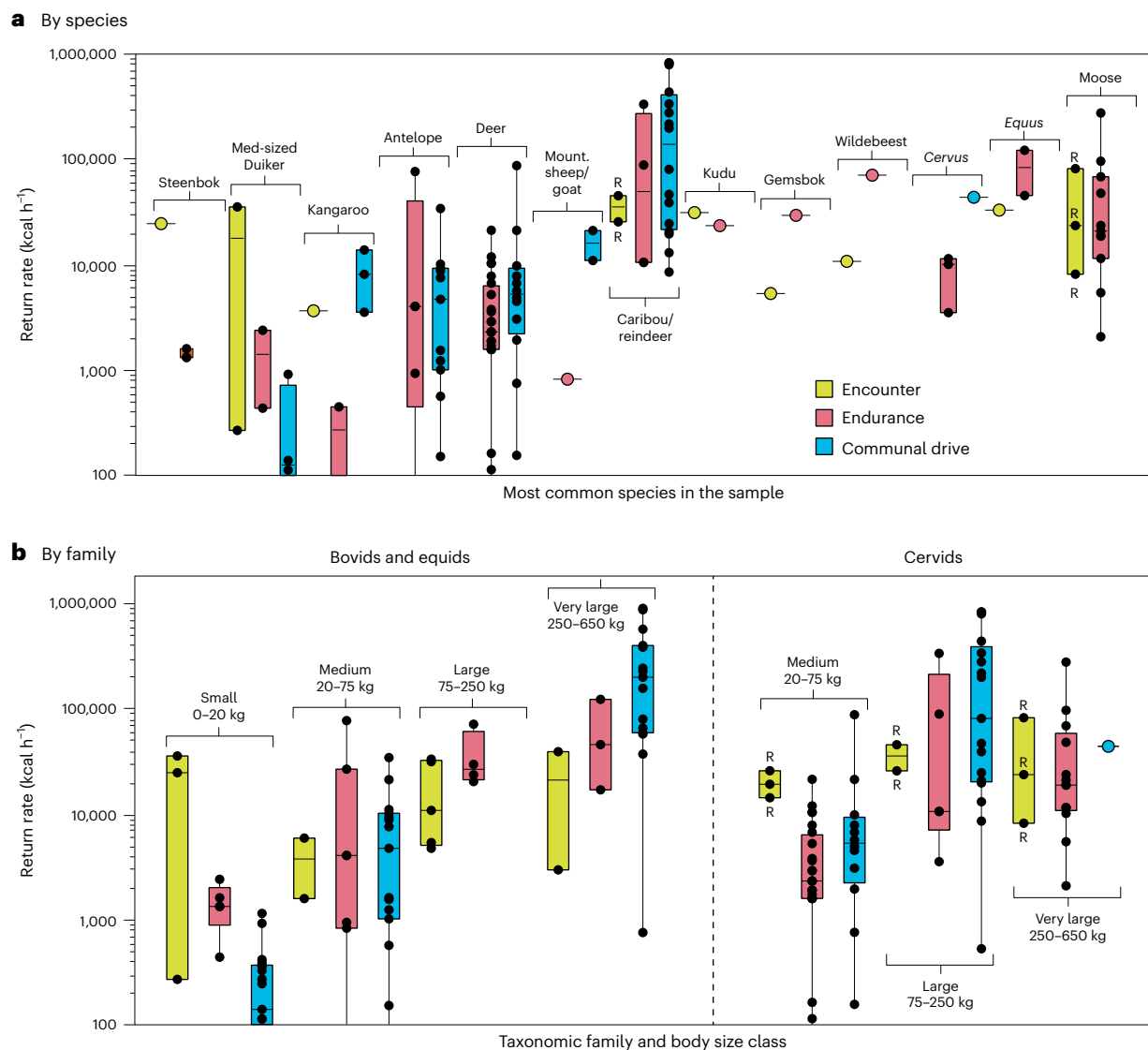
	Rare (Rare and seasonal)		Common (Common and seasonal) <sup>a</sup>		Total	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
North America	22 (5)	27.5 (6.3)	58 (40)	72.5 (50.0)	80	100.0
Europe and NE Asia	1	50.0	1 (1)	50.0 (50.0)	2	100.0
NE Asia			7 (7)	100.0 (100.0)	7	100.0
Africa	8	44.4	10 (2)	55.6 (11.1)	18	100.0
Australia	1 (1)	33.3 (33.3)	2 (1)	66.7 (33.3)	3	100.0
Total	32 (6)	29.1 (5.5)	78 (51)	70.9 (46.4)	110	100.0

Values in parentheses specify the subsample of EPs that were performed seasonally. <sup>a</sup>‘Common’ and ‘Common seasonally’ includes cases where EPs are described as being ‘Frequent’ and ‘Frequent seasonally’, respectively.

observers. Foragers were likewise reluctant to take Westerners, perceived as being slow and noisy encumbrances (Supplementary Table 4), with them on this type of hunt. Most ecologically oriented ethnographies are based on post-1950s observations which were recorded after EPs had largely ceased as a method of pursuing game. However, where we have a reliable, systematically collected sample (CED coverage of western North America), we can say that EPs were a common form of hunting practiced in specific contexts by most societies situated across a wide range of habitats. For the rest of the world, the available sample is much sparser, but adequate to show that EPs at minimum were globally distributed. The diversity and proficiency of hunter-gatherer methods and the demonstrable foraging efficiency advantages of EPs in the right contexts suggest to us that the larger global sample of EPs is greatly

under-represented and/or remaining to be discovered. Unsurprisingly, EP descriptions are few in regions such as southern Eurasia where most forager societies disappeared long before the beginning of the written record. Finally, we note that despite the breadth of our search protocol and our use of keywords that included and excluded running-related terms, the sample includes only a few cases of EPs that exclusively used walking as a pursuit tactic (for example, Supplementary Data 1 #62, 72a, 86; see ref. 38).

Study of the sample gives us other insights. EP hunts are not limited to open environments as suggested by earlier analyses based on much smaller ethnographic samples<sup>38</sup>. Fully 156 descriptions (39.9% of Supplementary Data 1) derive from groups occupying forest biomes, including habitats such as taiga and rainforests. To an almost equal



**Fig. 3 | Estimated pursuit or pursuit and handling return rates for three types of hunt.** The three types of hunt: encounter, endurance pursuits (EPs) and communal drive hunts (CDHs) are arrayed by: (a) species and (b) taxonomic family and body size class. Note that the Y axis is on a log scale. The EP values were calculated assuming a success rate of 75%; an 'R' identifies cases in which

rifles were used. EP rates come from Supplementary Data 2. Encounter and CDH values are based on refs. 42,49, reduced by an amount equal to forager energy expenditure (pursuit costs of transport) to match the metric used for the EP data (see Supplementary Information 1). Values <100 kcal h<sup>-1</sup> are not shown.

degree, EP hunts are associated with open settings ( $n = 164$ , 41.9%), but more rarely, with biomes of mixed or intermediate vegetation ( $n = 71$ , 18.2%). According to the CED survey data, the proportion of groups with positive evidence of EPs increases as one moves from closed (32/48 or 66.7%) to mixed (27/32 or 84.4%) to open environments (55/61 or 90.2%; Supplementary Table 5). In the full dataset, most EPs unfold in a common pattern embedded in a flexible hunting strategy: (1) the hunter encounters a prey that cannot be approached within the range of their weaponry, (2) a pursuit is initiated and the endurance-paced hunter is rapidly outdistanced; (3) after a sprint, the prey pauses its flight to shelter and/or recuperate and the hunter through persistent running, perhaps with occasional interruptions to rest and/or search for tracks, catches up; (4) the animal again flees, perhaps to find refuge in shade, thickets or to seek water; (5) the sprint–pause cycle repeats, the animal's flight initiation distance steadily diminishing until the exhausted prey is overtaken and can be approached and dispatched, often without resistance (concerning the latter point, see Supplementary Data 1, #14, 28, 69, 72b, 76, 80,

123, 137, 239, 296, 309, 338, 341). The mule deer pursuit described in ref. 47 illustrates this pattern vividly.

EP hunts may involve one or more pursuers, with individuals cooperating in tracking or acting in relays. In a wide range of mobile forager societies, emphasis on endurance running occurs early in a prospective hunter's life and is promoted through games and races. Connections to warfare and rituals are important (Supplementary Table 6). Although some descriptions stress the hunter's exceptional athleticism, a majority suggest usual practice of EP in specific, seasonally recurring contexts (Table 2).

The prey most frequently mentioned in our sample are ungulates of medium and large size: deer (*Odocoileus* sp.,  $n = 154$ ), elk/red deer (*Cervus* sp.,  $n = 54$ ), moose (*Alces alces*,  $n = 45$ ), caribou/reindeer (*Rangifer tarandus*,  $n = 35$ ), pronghorn (*Antilocapra americana*,  $n = 32$ ), bison (*Bison bison*,  $n = 16$ ), eland (*Taurotragus oryx*,  $n = 13$ ), steenbok (*Raphicerus campestris*,  $n = 10$ ), horse/zebra (*Equus* sp.,  $n = 9$ ), gemsbok (*Oryx gazella*,  $n = 7$ ), mountain sheep (*Ovis canadensis*,  $n = 7$ ), kudu (*Tragelaphus strepsiceros*,  $n = 5$ ), giraffe (*Giraffa camelopardalis*,  $n = 5$ )

and kangaroo (possibly *Macropus* sp.,  $n = 5$ ). Carnivores, including bear (*Ursus* sp.,  $n = 14$ ), small felids (*Felis/Lynx*,  $n = 5$ ), cheetah (*Acinonyx jubatus*,  $n = 4$ ), wolf (*Canis lupus*,  $n = 3$ ) and fox (*Vulpes* sp.,  $n = 3$ ), are also targets of EPs.

### Factors giving EP hunters advantages over their prey

Prominent among the factors that humans exploit to their advantage in an EP, either separately or in combination are: (1) substrates that substantially impede, debilitate or increase energy expenditure of the prey relative to the hunter and (2) ambient environmental conditions (for example, heat) to a degree that cumulatively induces exhaustion and debility in a game animal harried by a persistent predator. In contrast, besides their endogenous advantages, humans can use technology to alleviate the adverse effects of substrate and climate. Foot gear, snowshoes, protective clothing and water-carrying devices are examples.

While the hominin evolutionary version of the EP hypothesis has largely focused on tropical settings and hot weather pursuits<sup>4,30,38</sup>, 30.7% of our descriptions are hunts that take advantage of snow cover. Most are described as occurring at a fast pace. Snowshoes and skis make it possible to overtake an exhausted prey, especially when the snow is deep or crusted. Thus, EPs might have been practiced by hominin groups such as the Neandertals occupying cool latitudes. At low latitudes, water-sogged substrates, soft sand, ground covered with sharp or abrasive rocks or excessive surface-level temperatures and radiant heat all ease game capture. Hooves burned by scorching sand or chafed by wet sand will markedly shorten pursuit distance. Some ungulates regularly flee in an arc (excerpts in Supplementary Table 7), allowing the hunter to reduce their energy expenditure, save time and close distance by cutting across the chord. To illustrate this circling tendency, according to a GPS-based map<sup>30</sup>, Karoha (a San hunter in Botswana) ran a total of 25.1 km while pursuing a kudu, yet dispatched the animal only 1.5 km away from the starting point. The animal presumably ran a greater distance. In a related tactic, the hunter, occasionally aided by signals from an accomplice perched on an elevated overlook, surveys the landscape to predict the movement of animals driven to seek locations offering water, concealment or shelter. Hunters can sometimes steer the nearly exhausted animal towards the hunter's camp or home base where it will be killed, minimizing transport costs (Supplementary Table 8). Such tactics are probably widely known to EP hunters and associated with substantial gains in performance that have not been factored into previous assessments of the EP hypothesis.

Our data suggest that prey can be driven into hyperthermia even in moderate weather. This seems particularly true for deer (by far the most common species in our dataset), a panting animal with an inefficient system of heat dissipation<sup>48</sup>. Other factors mentioned as increasing the probability of success in EPs include running after impaired, undernourished, old, very young and/or fat- or pregnancy-encumbered animals; targeting ruminants in the dry season when digestion is easily disrupted or in seasons when animals are harassed by insects or infested with parasites. The habit of certain species to use beaten tracks in snow or to move towards preferred shelters also appears to increase the odds of capture by making the course of the animal more predictable. Other sources emphasize that in hot weather, excessive drinking by thirsty animals had a positive effect on the probability of a kill. San hunters also take advantage of wet ground because tracking is easier, and of the full moon to hunt the animal at daybreak when they are tired<sup>30</sup>.

### Quantitative comparisons with other methods

Mathematical modelling shows that EPs can be an efficient method of hunting. Nonetheless, to help explain its global distribution, what remains to be determined is whether the payoffs of EP tactics match or exceed those of other methods of prey procurement. To proceed with these comparisons, we used the information contained in the ethnohistorical database, which permitted deriving a quantitative estimate of EP  $R_p$  in 71 instances. We adjusted these estimates using both

**Table 3 | Average and standard deviation of EP return rates,  $R_p$ , for species represented in Supplementary Data 1**

Game animal	$n$	Live weight (kg)	$R_p$ (average)	$R_p$ (s.d.)
Steenbok ( <i>Raphicerus campestris</i> )	3	11.5	1,411	160
Duiker ( <i>Sylvicapra grimmia</i> )	2	18.5	1,412	1,381
Pronghorn ( <i>Antilocapra americana</i> )	5	40.0	17,139	33,373
Deer ( <i>Odocoileus</i> sp.)	24	56.8	4,374	4,935
Caribou/reindeer ( <i>Rangifer tarandus</i> )	4	102.5	110,912	153,190
Elk/red deer ( <i>Cervus</i> sp.)	3	318.0	8,340	4,234
Horse ( <i>Equus ferus</i> )	2	438.0	83,806	54,268
Moose ( <i>Alces alces</i> )	11	600.0	53,586	79,164
Kangaroo (possibly <i>Macropus</i> sp.)	2	25.0	270	251
Fox ( <i>Vulpes lagopus</i> )	2	2.5	242	173
Feral cat/lynx ( <i>Felis/Lynx</i> )	2	7.7	1,907	1,595

The species shown have a minimum of two observations; 75% probability of success assumed. See Supplementary Information 1 and Data 2 for how these data were generated.

a conservative 50% and a less conservative 75% success rate for prey capture (Supplementary Information 1 and Supplementary Table 9). Figure 3a presents the 75% results along with pursuit and handling efficiencies for the same or similar species obtained by non-EP encounter hunting and communal drive hunts (CDHs)<sup>42,49</sup>. EP return rates largely overlap those of the two other procurement methods. A plot by taxonomic family and body size confirms the pattern and, by aggregating data points, shows that it is not an artefact of sampling error (Fig. 3b). Lowering the success rate from 75% to 50% reduces the overlap without altering the main pattern (Supplementary Fig. 4). The averaged EP estimates for the species listed in Table 3 exhibit a linear relationship with prey body mass ( $r = 0.81$ ,  $P = 0.0023$ , log-transformed data), although there is no clear increase in EP pursuit efficiency between medium- and large-sized taxa (Fig. 3b).

## Discussion

In its original formulation, the EP hypothesis emphasized the ability of hominins to pursue game economically over long distances in hot weather while dissipating the resulting metabolic heat through rapid evapotranspiration of sweat. African low latitude environments were a focus because they provide the context for the evolution of the associated physiological and anatomical traits. Our results provide general support for the original EP hypothesis. However, they also suggest several important modifications and they significantly expand the environmental, bio-behavioural, technological and archaeological contexts in which EPs are likely to have been performed.

Skeptics and some supporters of the original EP hypothesis have generally assumed that the technique is not very efficient, an assessment seemingly confirmed by the very few contemporary observations of the method. Contrary to that consensus, foraging theory—a productive framework for assessing the economic element of pursuit methods<sup>35</sup>—demonstrates that EPs have, in principle, the potential to be highly efficient<sup>22</sup>. The available observational data on energy benefits and costs are consistent with theory; estimated EP return rates are similar to, and sometimes surpass, those of other techniques of prey acquisition, although caution is advised given that our analyses are subject to reporting bias and are limited by the size of the sample

(Supplementary Fig. 3). In agreement with calculations that suggest considerably lower returns (see above, also ref. 22), EPs conducted at a walking pace are rare in our dataset.

While the frequency and success of EPs in low latitude, open settings give broad credence to the original hypothesis, ethnohistorical and ethnographic sources show that EPs have been a frequent form of prey procurement for a wide array of foraging societies located in diverse environments and seeking multiple species of game. EPs are not restricted to arid open habitats but can occur in partially or fully closed forested habitats stretching from tropical to Arctic latitudes. Although hyperthermia in hot weather is a common factor of successful EPs<sup>22</sup>, it is not a prerequisite. Successful EPs occur at milder temperatures as well, especially in terrain unfavourable to prey evasion. Other contexts are also conducive to EPs, such as targeting young, pregnant or excessively fat animals. Whether EPs are associated with mortality profiles biased towards juvenile and old individuals as suggested by some studies<sup>50</sup> is unclear, our data suggest that a wide range of age classes are taken, the context (for example, in hot weather, on soft wet ground) and state of the animal (for example, whether it is excessively fat, injured or pregnant) on encounter being determinants. In situations not favourable to EPs, techniques such as encounter hunting<sup>42</sup>, ambush hunting<sup>51,52</sup> and communal drives<sup>49</sup> may have been more profitable alternatives.

As initially formulated, the EP hypothesis relied on evidence that the cost of running transport is velocity invariant in bipedal humans but that quadrupeds have an optimal speed for each type of gait<sup>4</sup>. If true, this would give hominins the option of selecting pursuit velocities disadvantageous to their prey. Research since has shown that human runners tend, with some exceptions, to have preferred curvilinear transport costs with an intermediate velocity optimum, although the pattern seems less pronounced than in other mammals<sup>39,40,53,54</sup>. While these cost of transport findings are biomechanically and evolutionarily important, for all but the smallest game species (Supplementary Fig. 2), differences in running and walking human energy expenditure are a relatively unimportant factor in pursuit decisions. The more critical parameters are time investment and probability of pursuit success. Further, nearly all our cases with information on prey flight patterns describe it as intermittent. The EP hunter presumably adopts a comfortable and sustainable, perhaps optimal, running pace, but prey animals seem locked into a flight-initiated, sprint-pause cycle that, in the right circumstances, becomes cumulatively debilitating. Given the presumption that running pursuits will be lengthy with captures occurring far away from the forager's home base, the resulting cost of transporting the carcass could also be disqualifying. However, this argument underestimates the sagacity and skill of hunters who, by carefully steering their prey, are often able to drive it to a desired location before dispatching it (Supplementary Table 8). It also ignores the tendency of many ungulates to flee in an arc, with kills frequently made near the starting point (Supplementary Table 7).

The perception that EPs were inordinately costly may be coloured by contemporary sedentary lifestyles. Research shows that perceived exertion for the same running effort is scored higher by sedentary than by athletic individuals<sup>55</sup>. In contrast, many foragers exhibit physical fitness that matches a physically demanding lifestyle. Mobile foragers of the past probably appraised endurance running skills as critical in hunting and warfare. Mention of community-organized foot races is frequent in our data and, along with EP pursuits, would have offered young males an arena for acquiring prestige. Although they are mentioned as practicing running and participating in foot races (Supplementary Table 6), females are infrequently represented in our EP hunting sample, a point that we will develop in a subsequent paper. The social, sometimes ritual importance placed on endurance running<sup>41</sup> and its association with highly valued resources and activities critical to survival point to the possibility of deep-seated cultural valorization of running in foraging societies.

Finally, although our cases reference foraging events long after the likely initiation of selection for EP capacities, they may contain clues about their possible origin through natural selection. They also aid understanding why the method is currently near extinction. With respect to origins, authors have emphasized that quickly reaching scavenging opportunities is possibly a more feasible avenue for early EP selection than running pursuits after live, cursorial and difficult-to-kill game animals<sup>1</sup>. Opportunities to scavenge actively are sought by mobile foragers such as the Hadza (Tanzania); they were probably more common in the past, at least in East Africa, due to a larger biomass of herbivores in the Plio/Pleistocene<sup>56</sup>.

Whatever the role of scavenging in EP origins<sup>33</sup>, our sample suggests a variety of contexts that might have preadapted Plio/Pleistocene hominins to the use of EP strategies, contexts that probably facilitated our shift towards a more energy-dense diet that included a greater proportion of animal soft tissue. They include: (1) targeting of prey, possibly of small to medium body size, already partially compromised by age, excessive fat depots, disease, hunger or trauma, or with limited abilities to dissipate heat; (2) EPs undertaken only in the most auspicious conditions of weather or substrate; (3) pursuits drawing on skilful anticipation of animal behaviour to lessen demands on hunter capacity; (4) EPs undertaken collaboratively in relays; and/or (5) communal drive hunts—a method documented in chimpanzees and bonobos that involves fast-paced chases<sup>57,58</sup>. Although these cooperative hunts have not been considered in the EP literature, their high returns and reliability, the fact that they are documented in other primates and the frequent long pursuits engaged in some of them suggest that they influenced the evolution of traits associated with endurance running.

Opportunities for evolutionary selection favoring a nascent EP capacity are enhanced by the observation that even small infusions of a running gait into a walking pursuit will significantly elevate its return rate. Favourable EP return rates also beg the question of why EP tactics were almost completely abandoned by the twentieth century. Supplementary Data 1 and the excerpts collated in Supplementary Tables 2–4, 6–8 and 10 suggest several possibilities: declining encounter rates with medium to large prey due to widespread reductions in their population density; the introduction of the horse, a more frequent use of dogs in hunting and especially the diffusion of reliable repeating rifles probably all played a role. The same factors appear to have acted to nearly extinguish the tactic of communal drive hunting<sup>49</sup>. Although EPs are now largely abandoned, our ethnohistorical and ethnographic data, evaluated from the perspective of foraging theory, show that they can be an efficient method of game procurement that would have been available to Plio/Pleistocene hominins.

## Methods

### Search of ethnographic and ethnohistorical sources

Our database was assembled from an extensive survey of digital ethnohistorical and ethnographic documents containing subsistence information on small-scale societies. Over 8,000 memoirs, travelogs, missionary accounts, reports of governmental agencies, monographs, dissertations and published research papers were included. All sources are in the public domain. Except for a small number of online sources, the document files were searched with DEVONthink 3 software, using Boolean operators of word proximity focused on terms such as 'run', 'run down', 'tiring', 'game' and 'animal', with each occurrence manually verified for relevance. French, Spanish, Italian and German keyword analogues also were used, although our access to non-English and non-French sources was limited. Excerpts consistent with an EP were then collated and coded (Supplementary Data 1).

The 'culture element distribution' (CED) checklists for western North America were compiled in the 1930s and 1940s by University of California Berkeley anthropologists in an effort to determine the presence or absence of thousands of cultural features for a regionally



exhaustive sample of Native American societies. Experienced field-workers located and queried elderly informants who were asked to situate their answers in the time of their parents or grandparents, just before contact. EP information was included in 17 of the 19 multisociety reports published by the Berkeley team using rubrics such as ‘Game run down’, ‘Single hunter... runs down on foot’, sometimes with more detailed annotations.

Because few of our ethnohistoric or ethnographic sources provided quantitative information on parameters needed for the calculation of return rates (that is, the duration of an EP, how many hunters were present, the estimated rate of success), we converted semi-quantitative statements into quantitative estimates as described in Supplementary Information 1. Information on our coding of biomes can be found in the same document along with additional details on methods.

### Modelling of return rates

The  $R_p$  curves in Fig. 1 were produced in an Excel spreadsheet using equation (1) replicated at 0.2 km h<sup>-1</sup> increments over the range of 1.2–18.0 km h<sup>-1</sup> hunter velocities for each of the 4 distances (Fig. 1) or 4 species (Supplementary Fig. 2) graphed. We made context-specific conversions between time and distance metrics as required by the input parameters. The 4–32 km range of comparisons represents EPs that might occur at various paces over the course of a day. Species-specific parameters used to calculate return rates associated with the four species modelled in Supplementary Fig. 2 were from ref. 42 Table 3, and are laid out in Supplementary Table 1.

We estimated the energy expenditure of a walking or running hunter using the experimental results of ref. 39 (Fig. 1, p. 87), noting the similarity to earlier estimates used by ref. 1 (Fig. 2b, p. 347). We made two adjustments to the cost of transport values generated by these laboratory-produced equations: (1) we decreased the values by a factor of 0.688 (see ref. 59, p. 41 and ref. 60, p. 213) to allow for the average weight difference between the laboratory sample of ref. 39 of 72.7 kg and our 50 kg model hominin forager; and (2) we increased the values by a factor of 1.30 to account for the substrate difference between the laboratory and field conditions (ref. 59, p. 43). We further adjust equation (1) to allow for a 0.75 capture success rate by inflating the distance covered and time required in each of the 3 successful of 4 pursuits by 1.33. The walking to running comparisons represented by arrows a–b<sub>1</sub>, a–b<sub>2</sub> and a–c were assigned a near-optimal pace for walking (4 km h<sup>-1</sup>) and a (2.5×) multiple of 10 km h<sup>-1</sup> for running, just below the average range of recreational jogging<sup>1</sup>.

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

### Data availability

All data presented in the paper are available in Supplementary Data 1, along with citations to their sources.

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## Author contributions

E.M. and B.W. designed the study, collected the data and wrote the paper.

## Competing interests

The authors declare no competing interests.

## Additional information

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**Correspondence and requests for materials** should be addressed to Eugène Morin.

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Data analysis Data analysis was relatively straightforward. We compiled occurrences of endurance hunting in different types of environments. The data were analyzed in Excel v. 16.78 for mac.

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Study description	Analysis of published ethnohistorical and ethnographic data
Research sample	Approximately 8,000 documents
Sampling strategy	Search for specific terms related to endurance hunting on the internet and in documents using a software called Devonthink 3
Data collection	Occurrences of endurance hunting were collated and assigned to one of three types of environment (closed, mixed and open).
Timing and spatial scale	Our sample covers all continents except Antarctica and spans the period A.D. 1500-2020
Data exclusions	We excluded several cases we had reason to believe were duplicates reported by earlier observers, and several where the description was vague on key points.
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## ChIP-seq

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