The Essential Definition of Intelligence: Evolutionary and Developmental Origins of the Survival Domain

Hye-Eun Yoon (Selly)

Independent Researcher, Bucheon, Gyeonggi-do, Republic of Korea

*** Corresponding Author:** Hye-Eun Yoon (Selly) selly@sellyes.org

Keywords: intelligence; survival domain; adaptation; comparative cognition; hominin evolution; cultural evolution

Abstract

Intelligence is often treated as a vertical scale of cognitive sophistication, with human-like language, abstraction, planning, tool use, and self-report occupying the upper end. This framing risks reducing diverse biological capacities to their proximity to human cognition, while the opposite tendency risks expanding intelligence until it becomes indistinguishable from adaptation in general.

This paper proposes a reframing of intelligence as **survival-domain choice-space operation.** On this view, intelligence refers to the capacity of an organism to discriminate, select, combine, and modify survival-relevant options within a species-specific ecological problem space. The framework distinguishes simple adaptation from intelligence by requiring state-dependent operation over multiple possible survival paths.

It then applies this definition to comparative cases, including collective, social, non-social, and boundary systems. Through an evolutionary reconstruction of the *hominin lineage*, the paper traces how the human survival domain became organized around mixed locomotion, bipedal commitment, forelimb availability, object manipulation, social learning, and cumulative cultural transmission. Human-like intelligence is interpreted as the outcome of this transition, through which survival options became increasingly externalized into tools, practices, symbols, and institutions.

The paper further argues that long human development provides implementation time for entering this culturally externalized domain, while curiosity and creativity function as domain-expanding operations. The resulting account offers a non-vertical framework for comparing intelligence across species and within humans, without treating human development as a universal standard.

1 Introduction

Biological organisms do not face the same survival problems. Each species occupies a distinctive problem space shaped by its body, sensory ecology, metabolic demands, social organization, and mode of environmental access. Some species interpret their surroundings through echolocation. Others rely on distributed nervous systems and tactile–motor manipulation. Some stabilize survival conditions through collective environmental modification. Humans, in turn, have developed language, abstraction, long-term planning, symbolic transmission, and social rule formation as central components of their adaptive repertoire.

Yet these human-specific capacities are often compressed into a single term: intelligence. Once this compression occurs, intelligence can begin to appear as a vertical scale, with human-like language, abstraction, planning, tool use, and self-report treated as the upper end of cognitive development. The familiar expression “higher intelligence” reflects this tendency. It does not merely describe difference. It implies a hierarchy in which other forms of biological competence are evaluated by their proximity to human cognition.

This framing raises a basic conceptual difficulty. If each species is adapted to a different survival problem space, then intelligence cannot be understood only by asking how closely an organism approximates human capacities. The question must be posed differently: *what is intelligence, and under what conditions should a biological capacity count as intelligent?*

1.1 Background and Related Work

The study of intelligence has developed across several traditions. Psychometric approaches have treated intelligence as measurable variation in cognitive performance, often organized around general intelligence, IQ, or the g factor (Spearman, 1904). These approaches have been powerful for intra-human comparison, but their reference frame remains largely human and task-based.

Other traditions have challenged this narrowness. Multiple-intelligence and domain-specific accounts have emphasized that cognitive competence is not exhausted by abstract reasoning (Gardner, 1983/1998). Comparative cognition has further expanded the field by examining tool use, social learning, spatial memory, communication, causal sensitivity, and problem solving across non-human species (Shettleworth, 2010). This work has weakened simple human exceptionalism by showing that many animals display flexible and ecologically meaningful forms of cognition.

Embodied and ecological approaches have added another corrective by arguing that cognition is shaped by bodily organization, sensorimotor coupling, and environmental affordances (Gibson, 1979/2014; Varela et al., 1991/1993). From this perspective, organisms do not solve abstract problems in isolation. They act within structured ecological contexts that make some actions possible, costly, or unavailable.

More recent debates over plant cognition, basal cognition, and collective intelligence have extended the boundary problem further (Bonabeau et al., 1999; Calvo et al., 2020; Lyon et al., 2021). Plants, microorganisms, and animal groups can exhibit signal integration, adaptive plasticity, distributed regulation, and coordinated problem solving. These cases are important because they prevent intelligence from being tied too narrowly to human-like cognition or even to nervous systems alone. At the same time, they make the concept more difficult to delimit.

Taken together, these literatures have loosened the older image of intelligence as a single human-centered faculty. What remains unresolved is how to compare intelligence across species without either ranking all capacities by human-likeness or expanding intelligence until it becomes indistinguishable from adaptation.

1.2 Limitations and Problem Statement

Existing approaches have weakened the assumption that intelligence is a single human-centered faculty, but they have not fully removed the scale implicit in that assumption (Call & Tomasello, 2008; Gardner, 1983/1998; Shettleworth, 2010). Diverse biological capacities are still often rearranged under intelligence as one upper-level category. As a result, species-specific abilities are frequently evaluated by their proximity to human-like abstraction, language, planning, tool use, or self-report. The expression “higher intelligence” captures this residual verticality.

This creates a category problem. A capacity may be highly organized within one species’ ecological problem space while appearing limited when measured against another species’ survival domain. Echolocation, distributed tactile manipulation, food caching, social coordination, or collective environmental regulation should not be ranked primarily by their similarity to human cognition (Shettleworth, 2010). They must be interpreted in relation to the survival problems they solve and the bodily and ecological constraints under which they become adaptive.

The opposite risk is indiscriminate expansion. If every adaptive trait or response is called intelligence, the concept loses discriminatory force (Calvo et al., 2020; Lyon et al., 2021). Protective coloration, fixed reflexes, tropisms, and metabolic regulation may be adaptive without being intelligent. The problem addressed here is therefore definitional: intelligence should be neither restricted to human-like cognition nor expanded to adaptation in general. The relevant question is what kind of survival problem space an organism inhabits and what kind of choice-space it can operate within that domain.

1.3 Proposed Reframing and Structure of the Paper

This paper reframes intelligence as survival-domain choice-space operation rather than as a single vertical scale of cognitive sophistication. Intelligence, in this sense, refers to the capacity to discriminate, select, combine, and modify survival-relevant options within an ecological problem space. It begins where environmental pressure generates more than one survival-relevant option and the organism can operate among those options in a state-dependent manner.

The contribution is threefold. First, the paper separates intelligence from adaptation by defining intelligence as state-dependent operation over survival-relevant choice-space. Second, it provides a non-vertical framework for comparing species-specific capacities without ranking them by similarity to human cognition. Third, it applies this framework to hominin evolution and human development, interpreting tool use, social learning, curiosity, and creativity as expansions of a culturally externalized survival domain.

Section 2 defines survival-domain choice-space operation and its boundary conditions. Section 3 reconstructs hominin intelligence as a survival-domain transition. Section 4 examines human development and non-vertical cognitive profiles. Section 5 discusses curiosity, creativity, anthropocentric definitions of intelligence, and the status of human development as a reference case rather than a universal standard.

2 Intelligence and Survival Domain

2.1 Definition and Boundary Conditions

This paper defines intelligence as an adaptive combinatorial operation for survival optimization within a species-specific ecological problem space. A survival domain refers to the range of differences, relations, and combinatorial possibilities that an organism must discriminate and operate upon in order to maintain viability within its ecological conditions (Gibson, 1979/2014; Shettleworth, 2010; Varela et al., 1991/1993).

This definition does not identify a survival domain with mere adaptive fit to environmental pressure. A survival domain exists when environmental pressure generates more than one survival-relevant option and the organism can discriminate, select, combine, or modify those options in relation to its state, resources, risks, energetic conditions, and ecological relations. These operations should not be read as human-like deliberation projected onto other organisms. They refer to the ways in which a living system uses its own bodily structure to discriminate and organize the options made available within its survival domain (Gibson, 1979/2014; Varela et al., 1991/1993). Intelligence, in this sense, is not adaptation in general. It is the state-dependent operation of selectable survival paths. The scope of a survival domain can be specified through the following criteria:

- Does the organism face a recurrent ecological problem space?
- Does it possess bodily structures capable of operating within that problem space?
- Does it discriminate relevant differences in internal state or environmental condition?
- Are there at least two available response paths?
- Does the selection among those paths affect survival, stabilization, reproduction, resource access, or risk avoidance?
- Is there combinatorial flexibility beyond a purely physical reaction or genetically fixed automatic pattern?
- Can the capacity be explained by the organism's own problem space rather than by its proximity to another species' abilities?

This distinction separates intelligence from simple adaptation. Many traits and responses are adaptive because they have been shaped by selection or because they contribute to survival. However, not every adaptive trait constitutes intelligence. Protective spines, camouflage, simple tropisms, reflexes, and fixed action patterns may be adaptive without requiring state-dependent operation over a choice-space (Lorenz, 1981). By contrast, tool use, route selection, hunting strategy, social coordination, and flexible problem solving involve the discrimination and organization of multiple possible survival paths.

Table 1. Distinguishing Simple Adaptation from Survival-Domain Intelligence

Dimension	Simple adaptation	Survival-domain intelligence
Role of environment	Selection pressure	Condition that generates options
Role of organism	Trait or response is selected	Organism selects among options in a state-dependent manner
Core structure	Survival-contributing response	Discrimination, selection, and combination of multiple paths
Temporality	Evolutionary accumulation or fixed response	Situation-sensitive selection and adjustment
Examples	Spines, camouflage, simple tropism	Tool use, route choice, hunting strategy, social coordination, problem solving

Note. The distinction concerns the presence of state-dependent choice-space operation, not behavioral complexity alone. "Simple adaptation" and "survival-domain intelligence" are ideal-typical categories; some biological cases may occupy boundary positions.

Plants provide an important boundary case (Calvo et al., 2020; Calvo & Trewavas, 2021; Colaço, 2022). Growth direction, chemical signaling, and resource allocation may belong to the broad edge of survival-domain organization. However, classifying these processes as intelligence requires more than adaptive environmental responsiveness. It requires evidence that the plant operates among multiple survival-relevant paths through state-dependent selection or combinatorial modification. For this reason, plants are treated here as boundary cases for distinguishing adaptive regulation from survival-domain intelligence. Simple tolerance responses, threshold-based fortification, or automatic changes in growth and reproduction are not sufficient for intelligence in the present sense. Plant cases become relevant only when multiple survival-relevant paths are integrated and modulated in a state-dependent manner. A plant case would satisfy the present criterion more strongly if external environmental variation were shown to modulate competing internal priorities, such as growth, defense, reproduction, and resource allocation, in a temporally flexible and state-dependent manner.

A brief formal intuition for this criterion is provided in Supplementary Material A, where survival-domain intelligence is described as reproducible modulation of choice probabilities by internal state and external condition in relation to survival-relevant outcomes.

2.2 General Types of Survival Domains and Comparative Cases

The survival-domain framework does not classify organisms by how closely they approximate human cognition. It asks what kind of survival problem space a system inhabits, what options that space makes available, and how the organism or group operates among those options. On this basis, several broad types of survival domains can be distinguished.

Table 2. General Types of Survival Domains

Type	Survival domain	Adaptive operation
Collective species	Group size, sensory access, energetic cost, colony or group structure	Group-level combinatorial operation through local rules and environmental traces
Social species	Self-related information, relationships, rank, affiliation, group stability	Combinatorial operation among self-preservation, kin preservation, and group-level stability
Non-social species	Independent survival, territory, resource access, predator avoidance	Combinatorial operation prioritizing territory, direct survival, and immediate resource control

Note. Survival domains differ according to the ecological problem space in which adaptive options become available. The table summarizes broad forms of survival-domain organization by asking what kind of choice-space is generated and what kind of adaptive operation is required. The collective-species row is informed by work on swarm intelligence, collective cognition, and social organization in animal groups (Bonabeau et al., 1999; Couzin, 2009; Wilson, 1975).

This typology is intentionally coarse. It does not imply that collective, social, and non-social species form mutually exclusive categories, nor that one type is cognitively superior to another. Many organisms occupy mixed domains. For example, a social carnivore may combine territory defense, cooperative hunting, kin investment, and rank-sensitive behavior. A solitary species may nevertheless exhibit complex spatial memory or object manipulation. The value of the typology lies in shifting the comparative question. Intelligence is not inferred from human-likeness, but from the organization of survival-relevant options within each domain.

The octopus is a useful case. If intelligence is measured by similarity to human social learning, cumulative culture, language, or institutional transmission, octopus cognition may appear as an anomalous exception. Under the survival-domain framework, however, it is not anomalous. It reflects a different route through which intelligence can be specialized. Octopuses operate through a distributed nervous system, flexible arms, tactile exploration, and rapid sensorimotor manipulation (Carls-Diamante, 2022; Godfrey-Smith, 2016; Hochner, 2012; Olson & Ragsdale, 2023). Their intelligence is not a reduced version of human intelligence, but a form adapted to a sensory–motor manipulation domain.

Table 3. Human and Octopus Intelligence as Distinct Survival-Domain Forms

Dimension	Human	Octopus
Main route	Cultural accumulation and social learning	Distributed nervous system and tactile–motor manipulation
Information structure	Externalization through language, tools, institutions, and norms	Distributed bodily control and local sensorimotor exploration
Survival strategy	Group transmission and cumulative modification	Individual exploration and immediate object manipulation
Form of intelligence	Cultural–symbolic survival domain	Sensorimotor manipulation survival domain

Note. Human and octopus intelligence are compared as distinct survival-domain forms, highlighting differences in dominant problem spaces and adaptive operations.

This comparison illustrates the central point of the framework. The question is not whether the octopus is "as intelligent as" the human in a general sense. The question is what kind of problem space it inhabits and what kind of operations are required within that space. The same logic applies to echolocating bats, caching corvids, social primates, migratory birds, and collective insects (Shettleworth, 2010). Their capacities should first be read as domain-specific solutions to recurrent survival problems, not as partial approximations to human cognition.

2.3 The Human-Specific Survival Domain

Human intelligence should therefore be understood not as a higher capacity located only inside the individual brain, but as a species-specific strategy for externalizing and expanding the survival domain. Humans do not merely solve problems through neural computation. They extend the space of selectable survival paths through tools, language, norms, institutions, symbolic systems, teaching, and cumulative culture (Boyd et al., 2011; Vaesen, 2012).

This externalization is central. Tools allow the body to act beyond its immediate anatomical limits (Vaesen, 2012). Language allows information to be stabilized, transmitted, recombined, and detached from the immediate situation; cumulative cultural processes allow successful variants to persist beyond individual lifetimes (Mesoudi & Thornton, 2018; Tomasello, 1999). Norms and institutions organize expectations across individuals and generations. Teaching and imitation reduce the cost of rediscovering solutions individually. Cultural accumulation allows successful variants to persist beyond the life of a single organism. In this sense, the human survival domain is not simply broader because humans possess more "general intelligence." It is broader because humans build external structures that preserve and expand the range of possible actions.

Several biological and developmental conditions make this strategy especially important. Human survival capacities are concentrated less in direct bodily defense and more in endurance, manual manipulation, social coordination, and externalized problem solving (Boyd et al., 2011; Bramble & Lieberman, 2004; O'Neill et al., 2017). Humans are relatively limited in short-burst power, speed, impact protection, tissue regeneration, and specialized defensive structures compared with many predators, large mammals, and armored or highly regenerative animals. They also do not occupy the size and force range of large carnivores.

This vulnerability is not limited to defense. Humans are also unusually dependent on external processing when physiological needs must be met from natural resources. Many herbivores process coarse plant material through specialized gastrointestinal systems and microbial symbiosis, and many carnivores tolerate raw flesh, bones, or carrion to a degree that humans generally cannot (Aiello & Wheeler, 1995; Froidurot & Julliand, 2022). Human staple resources often require washing, cutting, grinding, fermenting, cooking, storage, and social distribution before raw biological materials become reliable food. Cooking and food processing increase digestibility, reduce chewing and digestive costs, and improve net energetic returns, especially for starchy and fibrous resources (Carmody & Wrangham, 2009; Wrangham, 2017). Without such processing, coarse structural fiber, soil contamination, pathogens, toxins, and digestion-resistant tissues can impose substantial physiological risk.

Unlike many species in which juvenile vulnerability is substantially reduced after maturity, adult humans remain dependent on external supports, including clothing, shelter, tools, cooking, cooperative defense, medicine, food storage, and social coordination. These observations do not imply that vulnerability alone caused human intelligence. They suggest that persistent bodily, metabolic, and defensive vulnerability made externalized resource transformation, cooperative protection, and cumulative social learning increasingly valuable within the human survival domain.

Humans also have a long childhood and adolescence, slow maturation, extended dependency, and prolonged learning periods (Bogin, 1999; Lancaster & Kaplan, 2010). These developmental conditions are further stabilized by social care and cooperative breeding arrangements that support prolonged dependency and social learning (Burkart et al., 2009). These features are costly, but they create time for cultural learning, social calibration, tool use, language acquisition, and normative participation. Human intelligence emerges within this extended developmental window, where survival increasingly depends on the ability to inherit, modify, and transmit externally stored solutions.

The human-specific survival domain is therefore cultural-symbolic rather than merely individual-cognitive. Its core operations include social learning, cumulative modification, long-term planning, symbolic communication, rule formation, intergenerational transmission, and tool-mediated environmental transformation. This does not make human intelligence the highest form of intelligence in a universal hierarchy. It makes it a distinctive form of survival-domain operation: one in which selectable options are increasingly externalized into artifacts, practices, institutions, and shared meanings.

3 Hominin Intelligence as a Survival-Domain Transition

If intelligence is understood not as a single vertical scale but as an adaptive combinatorial operation within survival domains, the comparative question changes. In a vertical model, the question is often framed as why other species did not develop tool use, planning, or creativity in the human manner. Within the survival-domain framework, the question is reformulated: what kinds of combinatorial operations each species has optimized within its own survival domain?

Applied to the hominin lineage, this shift in perspective suggests that human-like intelligence was formed through the reorganization of the hominin survival domain. Changes in locomotion, bodily constraint, object manipulation, and social transmission gradually altered the kinds of survival-relevant options available to hominins. Cultural evolution then became one way of stabilizing and transmitting adaptive variants beyond the pace of inherited biological change (Boyd et al., 2011; Mesoudi & Thornton, 2018).

This section reconstructs how shifts in locomotion, bodily constraint, ecological opportunity, and cultural transmission transformed the survival-relevant options available to hominins, making manipulation, external media, social learning, and cumulative transmission increasingly central to the human survival domain.

3.1 Background Foundations

Several background observations are relevant to this reconstruction.

First, humans appear to have reduced short-burst muscular power relative to other great apes. Compared with humans of similar body mass, chimpanzees have been reported to show greater maximum dynamic force and power, with one estimate placing this advantage at approximately 1.35 times that of humans, largely associated with differences in fast-twitch muscle fiber composition (O'Neill et al., 2017). This contrast points to a survival-domain shift in the hominin lineage, from direct explosive strength toward manipulation, endurance, coordination, and increasing reliance on external media (Bramble & Lieberman, 2004; O'Neill et al., 2017).

Second, early hominins appear to have occupied a mixed locomotor survival domain rather than a fully modern bipedal one. Analyses of *Australopithecus afarensis*, including the specimen commonly known as Lucy, have emphasized the coexistence of terrestrial bipedal features and robust upper limbs associated with climbing or arboreal competence (Crompton et al., 2010; Prabhat et al., 2021). Later *Homo erectus* shows stronger alignment with long-distance terrestrial mobility and more human-like lower-limb proportions (Steudel-Numbers, 2006). This pattern places early hominins within a locomotor domain in which climbing, terrestrial movement, posture change, reaching, carrying, and foraging remained jointly relevant.

Third, extant great apes provide a useful comparative background. Large-bodied primates operate under locomotor constraints that differ from those of smaller primates. Body mass, fall risk, energetic cost, substrate stability, food access, and postural control all shape the available movement repertoire. Living great apes combine knuckle-walking, climbing, suspension, vertical postures, and occasional bipedal behaviors according to context. *Ardipithecus ramidus* is often interpreted in a similar mosaic frame, with traits associated with both terrestrial bipedality and arboreal locomotion (Crompton et al., 2010; Prang et al., 2025). These cases support the view that early hominin mobility was organized through a mixed set of arboreal and terrestrial affordances.

Within this mixed domain, bipedalism is better treated as part of a broader locomotor reorganization (Sellers et al., 2005). Early hominin movement involved tree use, ground travel, posture switching, carrying, reaching, foraging, and energetic economy. As the forelimbs became less continuously committed to weight support, braking, and propulsion, their availability for reaching, grasping, pulling, carrying, and manipulation increased. The functional availability of the hands then amplified later selection pressures related to object manipulation, tool use, and social learning.

A broader comparative life-history pattern also matters for this reconstruction. Across vertebrate lineages, species often regarded as cognitively complex tend to combine long lifespan, slow maturation, extended juvenile learning, high parental investment, and limited effective offspring output (Bogin, 1999; Burkart et al., 2009; Lancaster & Kaplan, 2010). Longevity alone is insufficient, as shown by long-lived reptiles with limited post-hatching parental care. The more relevant condition is the convergence of long exposure to changing ecological and social problem spaces with developmental arrangements that allow learned strategies to be acquired, protected, and transmitted. A comparative overview of these life-history configurations across vertebrate classes is provided in Supplementary Material B.

3.2 Survival-Domain Transition Chain

On the basis of these background conditions, the hominin transition can be reconstructed as a plausible survival-domain transition model. The sequence proposed here is not intended as a necessary linear pathway. It identifies a set of pressures that may have accumulated and reinforced one another as the hominin lineage shifted from a mixed arboreal–terrestrial locomotor domain toward a more manipulation-centered and culturally mediated survival domain (Boyd et al., 2011; Crompton et al., 2010; Vaesen, 2012).

The starting point is the bodily burden of large-bodied primates. For a large primate, movement across trees and ground requires more than locomotor displacement. It involves postural control, substrate assessment, fall-risk reduction, reaching, pulling, carrying, and the management of energetic cost. Early hominins likely occupied such a mixed movement domain, in which climbing, terrestrial travel, posture switching, and occasional bipedal positioning were jointly relevant. Within this domain, bipedal posture could increase access beyond ordinary reach height and allow the forelimbs to participate repeatedly in reaching, grasping, pulling, gathering, and carrying.

These repeated uses gradually reduced the hand's primary commitment to locomotor support, including weight bearing, braking, directional change, shock absorption, and propulsion. As more support and transport demands were transferred to the hindlimbs, the forelimbs became increasingly available for tactile exploration, precision handling, object transport, and object combination (Kivell, 2015; Vaesen, 2012). The available problem-solving space therefore widened from direct bodily action toward action sequences involving external things.

The hindlimbs then took on a more specialized role in support, balance, and terrestrial movement. Longer lower limbs, efficient stride mechanics, shock absorption, and stable hip–knee–foot organization would have been favored in a domain where carrying, foraging, and longer-distance travel became more important (Bramble & Lieberman, 2004; Steudel-Numbers, 2006). Lower-limb elongation can therefore be interpreted as a structural expansion of the bipedal movement repertoire. It increased feasible options for load-bearing, turning, balance recovery, and energy-efficient movement across uneven terrestrial environments.

This reorganization also changed the relative value of muscular performance. Explosive upper-body strength remained useful, but it became less central as endurance, postural stability, coordinated manipulation, and external mediation gained adaptive importance (Bramble & Lieberman, 2004; O'Neill et al., 2017). The body became increasingly organized for carrying, moving, selecting, combining, and modifying objects rather than relying primarily on direct force. In this sense, the relative decline of short-burst muscular power in humans can be understood as part of a broader shift in functional priority, not as simple physical weakening.

Object manipulation then altered the role of the environment. Once stones, sticks, plant materials, carcasses, containers, shelters, and eventually fire could be transported, positioned, combined, or modified, external materials became part of the available survival strategy. Tool use in this context is not just a technical behavior. It marks the incorporation of external media into survival-domain operation (Orban & Caruana, 2014; Vaesen, 2012). Problems could be solved through object-mediated sequences rather than immediate bodily action alone.

This placed new demands on learning and control. Object-mediated behavior requires sequencing, timing, error correction, affordance recognition, and the stabilization of repeated action patterns. These demands are functionally connected to motor sequence learning, executive control, and cerebellar and basal-ganglia contributions to action organization (Baladron et al., 2023; Doyon et al., 2009). Within this framework, such mechanisms are not isolated "higher" abilities. They are components of a survival domain in which manipulation and external mediation became increasingly central.

Social learning changed the temporal structure of this domain. Useful object-action relations did not have to be rediscovered independently by every individual (Boyd et al., 2011; Mesoudi & Thornton, 2018). They could be observed, imitated, corrected, modified, and transmitted. This allowed acquired variants to persist beyond a single attempt or a single lifetime. Cultural evolution thereby supplemented inherited biological change by stabilizing solutions in tools, practices, routes, gestures, norms, and eventually symbolic systems.

Curiosity and creativity can be located within this same transition. Curiosity increases exploration at the boundary of available options, especially where uncertain relations may become useful. Creativity recombines materials, actions, and meanings into new possible strategies. These capacities become adaptive when survival increasingly depends on discovering, preserving, and recombining externalized solutions.

The transition chain can therefore be summarized as a cumulative reorganization: large-bodied mixed locomotion increased the importance of posture switching, reaching, carrying, and environmental access; forelimb availability supported manipulation; greater terrestrial bipedal commitment specialized the hindlimbs for support and transport; external materials became mediating structures in action; social learning preserved useful variants; and cumulative culture widened the survival domain beyond the individual body and lifetime. Human-like intelligence, in this reconstruction, emerges as a culturally externalized mode of survival-domain operation.

3.3 Anatomical and Functional Implications

Three anatomical implications follow from this reconstruction.

First, mixed locomotor repertoires in large-bodied primates. Although small primates can display temporary bipedal posture or short bouts of bipedal locomotion, large apes more prominently combine quadrupedal movement, climbing, suspension, terrestrial travel, posture switching, and occasional bipedal posture within their survival strategies (Crompton et al., 2023; Hammond et al., 2025; Richmond et al., 2001). Body mass, fall risk, substrate stability, food access, and energetic cost make this parallel organization especially important. Early hominin bipedalism is therefore best read as a reorganization of this mixed movement domain (Crompton et al., 2010, 2023).

Second, lateral hindlimb tension structures may provide a useful clue for distinguishing locomotor domains. The relevant point is not whether a given fascial structure is anatomically present or absent in a strict sense. The issue is how visibly and functionally the hip-to-lateral-thigh tension line is organized in relation to movement. In cursorial terrestrial animals, lateral fascial and tendon structures are often strongly expressed because straight-line propulsion, elastic energy storage, rapid directional change, and speed are central. In small and medium-sized primates, arboreal movement favors joint mobility, rotation, grasping, suspension, jumping, and balance across three-dimensional substrates. In large apes, greater body mass makes support, posture change, joint stability, and trunk–pelvis control more important than speed. In humans, this organization is transformed again. Committed bipedalism reorganizes the hindlimb around body support, shock absorption, balance, propulsion, and upright stabilization. Related structures such as the fascia lata and iliotibial band remain important; the human iliotibial band, for example, has been analyzed as a structure specialized for elastic energy storage relative to chimpanzee fascia lata (Eng et al., 2015). Within the present framework, this supports interpreting hindlimb organization as part of upright stabilization and long-distance bipedal efficiency.

Third, the divergence between hand and foot morphology reflects the division of survival-domain functions after locomotor reorganization. In primates, three-dimensional movement, posture switching, support, grasping, and manipulation became increasingly important relative to straight-line terrestrial propulsion. In the human lineage, this pattern was reorganized around committed bipedalism, lower-limb stabilization, hand specialization, and efficient terrestrial travel. The hand became increasingly suited to segmentation, freedom of movement, thumb opposition, wrist rotation, tactile sensitivity, and fine motor control (Kivell, 2015; Vaesen, 2012). The foot became increasingly suited to stability, lever efficiency, shock absorption, aligned toes, arch formation, and reliable support during upright locomotion. Comparative evidence linking relative thumb length with brain size across primates supports a broader coevolutionary association among manual dexterity, sensorimotor control, and encephalization (Baker et al., 2025). In this sense, the hand and foot are not merely different anatomical endpoints. They express different solutions within the same survival-domain transition: one toward manipulation and external mediation, the other toward stable bipedal support and efficient terrestrial movement.

3.4 Differentiation of Survival Domains within the Primate Lineage

The same framework clarifies differentiation within the primate lineage. Body size, diet, social structure, habitat, locomotion, competition, and developmental tempo generate different problem spaces, which in turn favor different forms of competence (Fleagle, 2013; Shettleworth, 2010).

Table 4. Differentiation of Survival Domains within the Primate Lineage

Lineage	Main survival domain	Developed capacities
Gorilla	Large body size, herbivorous diet, relatively stable group structure	Physical size, threat display, social hierarchy
Chimpanzee	Forest–ground mosaic, hunting and gathering, competitive social life	Tool use, coalition formation, aggressive cooperation
Bonobo	Resource-rich environment, reduced feeding competition, social bonding	Sexual and affective conflict regulation, social buffering
Orangutan	Arboreal life, semi-solitary ranging, broad spatial demands	Spatial memory, individual problem solving, slow life history
Gibbon	Arboreal movement, small body size, branch-to-branch travel	Brachiation, agility, pair-centered social life
Early hominin	Mosaic environment, terrestrial movement, forelimb availability, carrying	Bipedalism, tool use, social learning, cumulative culture

Note. Primate lineages occupy different survival domains shaped by body size, habitat, locomotion, diet, social structure, and developmental tempo; the table provides a simplified comparative summary rather than a full review of primate ecology and cognition (Fleagle, 2013; Shettleworth, 2010; Tomasello & Call, 1997).

Early hominins occupy a mosaic survival domain in this comparison. Terrestrial movement, forelimb availability, carrying, object manipulation, and social learning became increasingly consequential within this domain. This configuration helps explain why tools, transport, cumulative learning, linguistic transmission, and long-term planning later became central components of the human survival domain.

4 Developmental Causality and Human Variation

4.1 Long Development, Social Learning, and Cultural Shelter

Human development provides a developmental counterpart to the evolutionary reconstruction above. The long human developmental period is not simply a delay before mature intelligence appears. It is the implementation time required for entering a culturally externalized survival domain. Human children must learn not only how to move, perceive, and regulate their own bodies, but also how to use tools, follow rules, interpret social signals, acquire language, participate in shared practices, and inherit solutions generated before their own lifetime (Boyd et al., 2011; Tomasello, 1999).

Several developmental features make this possible. Human childhood and adolescence are unusually extended (Bogin, 1999). Early neural organization remains highly plastic, with prolonged maturation of long-range connectivity and executive control (Johnson, 2001). Social learning, imitation, repeated practice, and guided correction allow children to acquire survival-relevant operations without discovering them independently (Boyd et al., 2011; Tomasello, 1999). Tool use and language further expand the set of available actions, while norms and institutions stabilize expectations across individuals. In this sense, the child does not merely develop intelligence inside the brain. The child is gradually inducted into an externalized problem space composed of artifacts, meanings, practices, and social constraints.

This process depends on protection. A long learning period is viable only when the organism is sheltered from the full cost of immediate failure (Burkart et al., 2009; Lancaster & Kaplan, 2010). Emotional safety, caregiver regulation, and culturally structured environments lower the cost of exploration. When questions are permitted and errors can be corrected without catastrophic consequences, curiosity becomes a developmental operator: it pushes the child toward the boundary of the current survival domain. Repeated exploration then stabilizes neural circuits, motor routines, linguistic forms, social expectations, and practical skills.

Cultural shelter therefore has a specific function in the present framework. It protects developmental vulnerability long enough for survival-domain operations to be learned, practiced, corrected, and transmitted. Human intelligence becomes possible through this protected interval, where biological immaturity is converted into time for social learning, technical skill, symbolic participation, and domain expansion.

4.2 Non-Vertical Cognitive Profiles within Humans

The survival-domain framework also applies within humans. If intelligence is understood as operation within a specific problem space, then human cognitive variation should not be reduced too quickly to a single vertical ranking. Overall IQ, diagnostic categories, and standardized task performance provide useful information, but they do not exhaust the structure of cognitive competence (Nisbett et al., 2012).

Some individuals may show relative limitations in working memory, abstract verbal reasoning, processing speed, or formal academic tasks while retaining strengths in procedural learning, pattern detection, social signal sensitivity, visual–spatial processing, repetitive task stability, motor routines, or memory within specific domains of interest (Nisbett et al., 2012). Such profiles are especially relevant in discussions of borderline intellectual functioning, developmental disorders, and uneven neurocognitive development. The issue is not simply whether a person is “less intelligent” in general. The more informative question is which survival-relevant or task-relevant domains are available, which operations are stable, and which forms of environmental support allow those operations to become effective (Vygotskij & Cole, 1981).

This does not deny the practical value of general measures. It places them within a broader framework. A single score may summarize performance across selected tasks, but it can obscure the uneven distribution of strengths and constraints across domains. A non-vertical account of intelligence therefore treats human variation as a profile of domain-specific operations: some capacities are limited, some are scaffolded by context, and some may be highly developed in restricted but meaningful problem spaces.

This perspective also has educational and social implications. When intelligence is treated as a single hierarchy, support often aims only to compensate for deficit relative to a general norm. When intelligence is treated as survival-domain operation, support can also identify usable strengths, stabilize environmental scaffolds, and expand the person’s available choice-space. Human variation then becomes part of the same general argument developed across species: intelligence is best understood through the relation between organism, problem space, and available operations.

5 Discussion and Implications

5.1 Curiosity as Boundary Exploration of the Survival Domain

Within the survival-domain framework, curiosity can be interpreted as a regulatory strategy for exploring possibilities that are not yet stabilized within the current domain. It moves the organism beyond immediately required responses and toward uncertain relations that may later become useful (Kidd & Hayden, 2015; Loewenstein, 1994). Curiosity therefore operates at the boundary of the available choice-space.

This boundary exploration is condition-dependent and overlaps with work on intrinsic motivation and curiosity-driven learning (Oudeyer et al., 2016). Curiosity does not emerge with equal strength under all biological states. It requires a degree of safety, energetic availability, and tolerance for prediction error. When the organism is under acute threat, unstable arousal, or severe resource constraint, exploration becomes costly and regulation narrows toward immediate stabilization. A safer regulatory state lowers the cost of exploratory action and allows uncertain possibilities to be tested without catastrophic risk.

In humans, this has a developmental and cultural role. Children ask questions, manipulate objects, test rules, and repeat actions partly because protected environments make such exploration affordable. Curiosity is therefore not only an individual trait. It is a domain-expanding operation supported by safety, time, and cultural shelter.

5.2 Creativity as Combinatorial Expansion of the Survival Domain

Creativity can be interpreted as the combinatorial expansion of a survival domain. It rearranges stabilized rules, materials, actions, and meanings in order to generate pathways that were previously unavailable or difficult to perceive (Muthukrishna & Henrich, 2016). In this sense, creativity does not float above biological adaptation. It operates on the structure of available options.

This role becomes especially important in the human lineage. Humans have long developmental periods, slow maturation, and relatively slow generational turnover. Genetic change alone cannot track rapidly shifting ecological, social, and technical demands. Cultural variation, social learning, and tool use provide a faster adaptive route by allowing new combinations to be generated, tested, preserved, and transmitted within and across generations (Boyd et al., 2011; Mesoudi & Thornton, 2018; Muthukrishna & Henrich, 2016).

Creativity therefore functions as a generator of cultural variation. It expands the survival domain by producing new relations among objects, actions, symbols, and social practices. Some combinations fail, while others become stabilized as tools, methods, norms, institutions, or shared meanings. Human creativity is thus best understood as a survival-domain operation that increases the range of selectable futures.

5.3 Beyond Anthropocentric Definitions of Intelligence

The central implication of this paper is that intelligence should not be evaluated by similarity to human capacities alone. Language, abstraction, long-term planning, tool use, and self-report are important components of the human survival domain, but they do not provide a universal scale for all organisms. Intelligence should instead be understood by asking what differences an organism must discriminate, what relations it must select, and what combinations it can construct within its own ecological problem space.

This shift allows non-human capacities to be described without reducing them to weaker versions of human intelligence. Echolocation, tactile manipulation, caching, migration, social coordination, collective regulation, and tool use each become intelligible within the survival domain that makes them adaptive (Shettleworth, 2010). A bat, octopus, corvid, primate, or social insect does not need to approximate human symbolic cognition in order to display intelligence. Its competence must be evaluated in relation to the options its body, ecology, and social organization make available.

The same point applies to boundary cases. Plants, microorganisms, and collective systems may show adaptive plasticity, distributed regulation, or group-level problem solving (Bonabeau et al., 1999; Calvo et al., 2020; Lyon et al., 2021). These cases should be handled through the boundary criteria developed in Section 2: the key question is whether the system operates among multiple survival-relevant options in a state-dependent or combinatorial manner. This preserves the concept of intelligence without collapsing it into adaptation in general.

5.4 Human Development as a Reference Case, Not a Universal Standard

Human development is especially useful for this framework because it shows how a survival domain can be learned, externalized, and culturally expanded over time. Long childhood, social learning, language acquisition, tool use, emotional safety, and institutional participation reveal how biological immaturity can become a condition for entering a complex cultural-symbolic domain (Bogin, 1999; Boyd et al., 2011; Tomasello, 1999). Human development therefore provides a rich reference case for studying intelligence as survival-domain operation.

Its usefulness as a reference case should be distinguished from universality. Human development is not the standard by which all intelligence should be measured. It is one highly elaborated case in which survival-domain operation depends heavily on symbolic transmission, social scaffolding, and cumulative culture (Boyd et al., 2011; Tomasello, 1999). Other organisms organize intelligence through different bodies, senses, ecological demands, and developmental timings.

This distinction matters for both comparative cognition and human variation. Across species, it discourages ranking organisms by human-likeness. Within humans, it discourages reducing cognitive profiles to a single vertical measure. Human development shows one way in which intelligence can become culturally externalized, but the broader framework asks a more general question: how does a living system construct and operate within the choice-space that its survival domain makes possible?

6 Conclusion

This paper proposed a reframing of intelligence as survival-domain choice-space operation. The aim was to move away from a single vertical model in which intelligence is ranked by proximity to human-like language, abstraction, planning, tool use, or self-report. Intelligence was instead defined as the capacity to discriminate, select, combine, and modify survival-relevant options within a species-specific ecological problem space.

This definition separates intelligence from adaptation in general. Many traits and responses contribute to survival, but intelligence requires the operation of multiple possible paths under bodily, ecological, energetic, and relational constraints. The relevant question is therefore not whether one species is generally more intelligent than another, but what kind of survival domain a species inhabits and what kinds of operations become adaptive within that domain.

The hominin case illustrates this framework. Human-like intelligence can be understood as the outcome of survival-domain reorganization involving mixed locomotion, forelimb availability, lower-limb stabilization, object manipulation, social learning, and cumulative cultural transmission. Tools, language, norms, and institutions expanded the human survival domain beyond the individual body and lifetime. Curiosity and creativity then appear as domain-expanding operations: curiosity explores unstable boundary conditions, while creativity recombines existing materials, actions, and meanings into new possible paths.

This framework also changes how human development and human variation are interpreted. Long childhood, social learning, emotional safety, repeated practice, and cultural shelter provide the developmental time through which children enter a culturally externalized survival domain. Within humans, cognitive profiles should be understood through the uneven distribution of domain-specific operations, not only through a single vertical measure.

The broader implication is that intelligence is not a universal ladder. It is a biological strategy organized around the survival problems a living system must solve. Human intelligence is one distinctive form of this strategy, centered on cultural-symbolic externalization and cumulative transmission. Other organisms express different forms through different bodies, senses, ecologies, and social structures. A theory of intelligence should therefore begin from the survival domain in which a capacity becomes meaningful.

Declarations

Competing interests
The author declares that there are no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Authors' contributions
Hye-Eun Yoon: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Validation, Writing - Original Draft, Writing - Review & Editing, Visualization, Supervision, Project administration.

Funding
This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Acknowledgments
None.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process.
During the preparation of this work the author used GPT-5.5 in order to language refinement. After using this tool/service, the author reviewed and edited the content as needed and take full responsibility for the content of the published article.

Ethics Statement
Not applicable. (This study does not involve human subjects or animals.)

Availability of data and material
This article does not report original data, empirical analyses, or computational analyses. No code or data are required to reproduce the arguments presented in this manuscript.

References

Aiello, L. C., & Wheeler, P. (1995). The Expensive-Tissue Hypothesis: The Brain and the Digestive System in Human and Primate Evolution. *Current Anthropology*, *36*(2), 199–221. https://doi.org/10.1086/204350

Baker, J., Barton, R. A., & Venditti, C. (2025). Human dexterity and brains evolved hand in hand. *Communications Biology*, *8*(1), 1257. https://doi.org/10.1038/s42003-025-08686-5

Baladron, J., Vitay, J., Fietzek, T., & Hamker, F. H. (2023). The contribution of the basal ganglia and cerebellum to motor learning: A neuro-computational approach. *PLOS Computational Biology*, *19*(4), e1011024. https://doi.org/10.1371/journal.pcbi.1011024

Bogin, B. (1999). Evolutionary Perspective on Human Growth. *Annual Review of Anthropology*, *28*(1), 109–153. https://doi.org/10.1146/annurev.anthro.28.1.109

Bonabeau, E., Dorigo, M., & Theraulaz, G. (1999). *Swarm intelligence: From natural to artificial systems*. Oxford University Press.

Boyd, R., Richerson, P. J., & Henrich, J. (2011). The cultural niche: Why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences*, *108*(supplement_2), 10918–10925. https://doi.org/10.1073/pnas.1100290108

Bramble, D. M., & Lieberman, D. E. (2004). Endurance running and the evolution of Homo. *Nature*, *432*(7015), 345–352. https://doi.org/10.1038/nature03052

Burkart, J. M., Hrdy, S. B., & Van Schaik, C. P. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *18*(5), 175–186. https://doi.org/10.1002/evan.20222

Call, J., & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences*, *12*(5), 187–192. https://doi.org/10.1016/j.tics.2008.02.010

Calvo, P., Gagliano, M., Souza, G. M., & Trewavas, A. (2020). Plants are intelligent, here's how. *Annals of Botany*, *125*(1), 11–28. https://doi.org/10.1093/aob/mcz155

Calvo, P., & Trewavas, A. (2021). Cognition and intelligence of green plants. Information for animal scientists. *Biochemical and Biophysical Research Communications*, *564*, 78–85. https://doi.org/10.1016/j.bbrc.2020.07.139

Carls-Diamante, S. (2022). Where Is It Like to Be an Octopus? *Frontiers in Systems Neuroscience*, *16*, 840022. https://doi.org/10.3389/fnsys.2022.840022

Carmody, R. N., & Wrangham, R. W. (2009). The energetic significance of cooking. *Journal of Human Evolution*, *57*(4), 379–391. https://doi.org/10.1016/j.jhevol.2009.02.011

Colaço, D. (2022). Why studying plant cognition is valuable, even if plants aren't cognitive. *Synthese*, *200*(6), 453. https://doi.org/10.1007/s11229-022-03869-7

Couzin, I. D. (2009). Collective cognition in animal groups. *Trends in Cognitive Sciences*, *13*(1), 36–43. https://doi.org/10.1016/j.tics.2008.10.002

Crompton, R. H., Sellers, W., Davids, K., & McClymont, J. (2023). Biomechanics and the origins of human bipedal walking: The last 50 years. *Journal of Biomechanics*, *157*, 111701. https://doi.org/10.1016/j.jbiomech.2023.111701

Crompton, R. H., Sellers, W. I., & Thorpe, S. K. S. (2010). Arboreality, terrestriality and bipedalism. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1556), 3301–3314. https://doi.org/10.1098/rstb.2010.0035

Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J., Lehéricy, S., & Benali, H. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioural Brain Research*, *199*(1), 61–75. https://doi.org/10.1016/j.bbr.2008.11.012

Eng, C. M., Arnold, A. S., Biewener, A. A., & Lieberman, D. E. (2015). The human iliotibial band is specialized for elastic energy storage compared with the chimp fascia lata. *Journal of Experimental Biology*, jeb.117952. https://doi.org/10.1242/jeb.117952

Fleagle, J. G. (2013). *Primate Adaptation and Evolution* (3rd ed). Elsevier Science & Technology.

Froidurot, A., & Julliand, V. (2022). Cellulolytic bacteria in the large intestine of mammals. *Gut Microbes*, *14*(1), 2031694. https://doi.org/10.1080/19490976.2022.2031694

Gardner, H. (1998). *Frames of the mind: The theory of multiple intelligences* (10. anniversary ed.). BasicBooks. (Original work published 1983)

Gibson, J. J. (2014). *The Ecological Approach to Visual Perception: Classic Edition* (1st ed.). Psychology Press. https://doi.org/10.4324/9781315740218 (Original work published 1979)

Godfrey-Smith, P. (2016). *Other minds: The Octopus, the Sea, and the Deep Origins of Consciousness*.

Hammond, P., Bobe, R., & Carvalho, S. (2025). The behavioural ecology of hominin locomotion: What can we learn from landscapes of fear and primate terrestriality? *Frontiers in Ecology and Evolution*, *13*, 1473794. https://doi.org/10.3389/fevo.2025.1473794

Hochner, B. (2012). An Embodied View of Octopus Neurobiology. *Current Biology*, *22*(20), R887–R892. https://doi.org/10.1016/j.cub.2012.09.001

Johnson, M. H. (2001). Functional brain development in humans. *Nature Reviews Neuroscience*, *2*(7), 475–483. https://doi.org/10.1038/35081509

Kidd, C., & Hayden, B. Y. (2015). The Psychology and Neuroscience of Curiosity. *Neuron*, *88*(3), 449–460. https://doi.org/10.1016/j.neuron.2015.09.010

Kivell, T. L. (2015). Evidence in hand: Recent discoveries and the early evolution of human manual manipulation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1682), 20150105. https://doi.org/10.1098/rstb.2015.0105

Lancaster, J. B., & Kaplan, H. S. (2010). Embodied Capital and Extra-somatic Wealth in Human Evolution and Human History. In M. P. Muehlenbein (Ed.), *Human Evolutionary Biology* (1st ed., pp. 439–456). Cambridge University Press. https://doi.org/10.1017/CBO9780511781193.032

Loewenstein, G. (1994). The psychology of curiosity: A review and reinterpretation. *Psychological Bulletin*, *116*(1), 75–98. https://doi.org/10.1037/0033-2909.116.1.75

Lorenz, K. Z. (1981). *The Foundations of Ethology*. Springer. https://doi.org/10.1007/978-3-7091-3671-3

Lyon, P., Keijzer, F., Arendt, D., & Levin, M. (2021). Reframing cognition: Getting down to biological basics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1820), 20190750. https://doi.org/10.1098/rstb.2019.0750

Mesoudi, A., & Thornton, A. (2018). What is cumulative cultural evolution? *Proceedings of the Royal Society B: Biological Sciences*, *285*(1880), 20180712. https://doi.org/10.1098/rspb.2018.0712

Muthukrishna, M., & Henrich, J. (2016). Innovation in the collective brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1690), 20150192. https://doi.org/10.1098/rstb.2015.0192

Nisbett, R. E., Aronson, J., Blair, C., Dickens, W., Flynn, J., Halpern, D. F., & Turkheimer, E. (2012). Intelligence: New findings and theoretical developments. *The American Psychologist*, *67*(2), 130–159. https://doi.org/10.1037/a0026699

Olson, C. S., & Ragsdale, C. W. (2023). Toward an Understanding of Octopus Arm Motor Control. *Integrative and Comparative Biology*, *63*(6), 1277–1284. https://doi.org/10.1093/icb/icad069

O'Neill, M. C., Umberger, B. R., Holowka, N. B., Larson, S. G., & Reiser, P. J. (2017). Chimpanzee super strength and human skeletal muscle evolution. *Proceedings of the National Academy of Sciences*, *114*(28), 7343–7348. https://doi.org/10.1073/pnas.1619071114

Orban, G. A., & Caruana, F. (2014). The neural basis of human tool use. *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.00310

Oudeyer, P.-Y., Gottlieb, J., & Lopes, M. (2016). Intrinsic motivation, curiosity, and learning. In *Progress in Brain Research* (Vol. 229, pp. 257–284). Elsevier. https://doi.org/10.1016/bs.pbr.2016.05.005

Prabhat, A. M., Miller, C. K., Prang, T. C., Spear, J., Williams, S. A., & DeSilva, J. M. (2021). Homoplasy in the evolution of modern human-like joint proportions in Australopithecus afarensis. *eLife*, *10*, e65897. https://doi.org/10.7554/eLife.65897

Prang, T. C., Tocheri, M. W., Patel, B. A., Williams, S. A., & Orr, C. M. (2025). Ardipithecus ramidus ankle provides evidence for African ape-like vertical climbing in the earliest hominins. *Communications Biology*, *8*(1), 1454. https://doi.org/10.1038/s42003-025-08711-7

Richmond, B. G., Begun, D. R., & Strait, D. S. (2001). Origin of human bipedalism: The knuckle-walking hypothesis revisited. *American Journal of Physical Anthropology*, *116*(S33), 70–105. https://doi.org/10.1002/ajpa.10019

Sellers, W. I., Cain, G. M., Wang, W., & Crompton, R. H. (2005). Stride lengths, speed and energy costs in walking of *Australopithecus afarensis*: Using evolutionary robotics to predict locomotion of early human ancestors. *Journal of The Royal Society Interface*, *2*(5), 431–441. https://doi.org/10.1098/rsif.2005.0060

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior* (2nd ed). Oxford University Press.

Spearman, C. (1904). "General Intelligence," Objectively Determined and Measured. *The American Journal of Psychology*, *15*(2), 201. https://doi.org/10.2307/1412107

Steudel-Numbers, K. L. (2006). Energetics in *Homo erectus* and other early hominins: The consequences of increased lower-limb length. *Journal of Human Evolution*, *51*(5), 445–453. https://doi.org/10.1016/j.jhevol.2006.05.001

Tomasello, M. (1999). *The Cultural Origins of Human Cognition*. Harvard University Press.

Tomasello, M., & Call, J. (1997). *Primate cognition*. Oxford University Press.

Vaesen, K. (2012). The cognitive bases of human tool use. *Behavioral and Brain Sciences*, *35*(4), 203–218. https://doi.org/10.1017/S0140525X11001452

Varela, F. J., Thompson, E., & Rosch, E. (1993). *The embodied mind: Cognitive science and human experience* (14. print.). MIT Press. (Original work published 1991)

Vygotskij, L. S., & Cole, M. (1981). *Mind in society: The development of higher psychological processes* (Nachdr.). Harvard Univ. Press.

Wilson, E. O. (1975). *Sociobiology: The new synthesis* (pp. ix, 697). Belknap Press of Harvard U Press.

Wrangham, R. (2017). Control of Fire in the Paleolithic: Evaluating the Cooking Hypothesis. *Current Anthropology*, *58*(S16), S303–S313. https://doi.org/10.1086/692113