

Nine Levels of Explanation

A Proposed Expansion of Tinbergen's Four-Level Framework for Understanding the Causes of Behavior

Melvin Konner¹

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Abstract

Tinbergen's classic "On Aims and Methods of Ethology" (Zeitschrift für Tierpsychologie, 20, 1963) proposed four levels of explanation of behavior, which he thought would soon apply to humans. This paper discusses the need for multilevel explanation; Huxley and Mayr's prior models, and others that followed; Tinbergen's differences with Lorenz on "the innate"; and Mayr's ultimate/proximate distinction. It synthesizes these approaches with nine levels of explanation in three categories: phylogeny, natural selection, and genomics (ultimate causes); maturation, sensitive period effects, and routine environmental effects (intermediate causes); and hormonal/metabolic processes, neural circuitry, and eliciting stimuli (proximate causes), as a respectful extension of Tinbergen's levels. The proposed classification supports and builds on Tinbergen's multilevel model and Mayr's ultimate/proximate continuum, adding intermediate causes in accord with Tinbergen's emphasis on ontogeny. It requires no modification of Standard Evolutionary Theory or The Modern Synthesis, but shows that much that critics claim was missing was in fact part of Neo-Darwinian theory (so named by J. Mark Baldwin in The American Naturalist in 1896) all along, notably reciprocal causation in ontogeny, niche construction, cultural evolution, and multilevel selection. Updates of classical examples in ethology are offered at each of the nine levels, including the neuroethological and genomic findings Tinbergen foresaw. Finally, human examples are supplied at each level, fulfilling his hope of human applications as part of the biology of behavior. This broad ethological framework empowers us to explain human behavior-eventually completely—and vindicates the idea of human nature, and of humans as a part of nature.

Keywords Niko Tinbergen · Ernst Mayr · Levels of explanation · Ethology · Behavioral biology · Phylogeny · Ontogeny · Ultimate/proximate causes

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Extended author information available on the last page of the article

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In his 1963 classic "On Aims and Methods of Ethology," Niko Tinbergen named four levels of explanation, also known as the four questions, or levels of causation, or the four whys (Tinbergen, 1963). "Why did the organism do that?"—because of its phylogeny (it's a certain kind of animal), adaptive value (what it was selected for), ontogeny, or elicitors and physiological mechanisms. In this framework, he defined ethology as "the biology of behavior" and stayed within The Modern Synthesis (TMS) in evolutionary biology, even while emphasizing ontogeny. Julian Huxley and Ernst Mayr, both architects of TMS, gave behavior a key role in setting the scene for natural selection, and both had earlier versions of the levels. Neither named a level for ontogeny, but Mayr always emphasized ontogenetic interactions, even while separating ultimate from proximate causation.

Tinbergen wanted all four levels in play. To the question "Why did the whitecrowned sparrow sing that song?" we can answer: (1) its phylogeny gave its ancestors mating songs; (2) singing enhances its reproductive success (RS); (3) it heard its father's song dialect in early life and practiced it in adolescence; and (4) having found a territory that might attract females, it heard other males sing nearby and its forebrain song circuits (enlarged by androgen surges) responded with its own assertive song, Note that this (as in Tinbergen) is a framework, not a theory. The framework is for behavior, and so it is not in competition with TMS or more recent frameworks for all processes in evolution, which are broader (Love, 2017; Meyers & Bull, 2002). But whatever the framework, there is one key logico-deductive theory in evolution: Neo-Darwinian theory, which is necessary, although not sufficient, for directional evolution resulting in adaptation. Natural selection (including sexual and kin selection) maximizes relative RS (fitness) over time, despite many other processes (Darwin 1958). Fitness can be expressed in population-genetic terms (Lewontin, 1974), but it needn't be. Local theories apply at every level of explanation, but Neo-Darwinian theory is the generative logico-deductive system and the ultimate explanation.

Philosophers of biology distinguish between *semantic* and *syntactic* theories (Love, 2017). To the extent that the framework proposed here (or, for that matter, Tinbergen's framework) is a theory, it is semantic, a collection of models and explanations. It contains many local theories (e.g., electrochemistry of the neuronal membrane, learning, chaos and emergence in development, predator-prey relations, optimal foraging), some of which are fully or mainly syntactic (logico-deductive). However, at its core is the syntactic theory of natural selection, just as that theory is at the core of the much broader field of evolutionary biology, which is about much more than behavior.

The multilevel model is also consistent with the framework of Meyer and Bull (2002) for evolution in variable environments. They emphasize *robustness*, which buffers a population against evolutionary change in fluctuating environments. It includes Waddington's (1942) concept of developmental canalization, population polymorphisms, facultative adaptations (Chisholm, 1993, 1999), and physiological and developmental plasticity. All these are of the essence of the framework offered here. Robustness is also consistent with long periods of stasis in the fossil record due to stabilizing selection (Eldredge & Gould, 1972). We know that humans during our evolution were exposed to fluctuating environments and adapted with cultural artifacts that may have buffered against genetic change—the variability selection

7

hypothesis (Potts, 1998; Potts et al., 2020). However, cultural adaptations may have selected for rapid brain evolution, partly due to niche construction (Stiner & Kuhn, 2016).

Five Views of the Four Levels

Ernst Mayr's View of Causality

Tinbergen followed Mayr's distinction between ultimate (evolutionary, adaptative) and proximate (mechanistic, physiological) causality (Mayr, 1961). In a long career, Mayr saw this distinction as fundamental to biology and its autonomy as a science not reducible to physics and chemistry (Mayr, 1988, 1996, 2001). Science generally was seeing limits to reductionism in chaos, emergence, and complexity (Anderson, 1972; Holland, 2014; Ruelle, 1991). Mayr's levels resemble Tinbergen's. He asks, "Why did the warbler on my summer place in New Hampshire start his migration on the night of the 25th of August? I can list four equally legitimate causes." (Mayr, 1961:1502): (1) *An ecological cause* (the warbler would starve wintering in place); (2) *A genetic cause* (the warbler's evolved genes respond to certain stimuli with migration); (3) *An intrinsic physiological cause* (photoperiodicity, tied to decreasing day length); and (4) *An extrinsic physiological cause* (northerly winds brought cold air that day). 3 and 4 are "immediate" or "*proximate* causes of migration"; 1 and 2, "*ultimate* causes" (1961:1503). The latter are nested in the former and ultimately caused by them; the genetic cause is the *result* of the ecological or evolutionary cause.

Failure to distinguish the levels leads to arguing at cross-purposes. A critic of evolutionary approaches relates that when she was teaching undergraduates, she shared students with evolutionist E. O. Wilson (Ruti, 2015). The students would say that sex is reproduction. She responded: "So, when you're having your 3 AM hookup at Winthrop House, are you trying to produce a baby?' 'Why do you think so many American women spend much of their lives on the pill, despite the unpleasant side effects?' 'You don't seriously think that two gay men getting it on are hoping that a child will follow, do you?'' She ends with a one-sentence paragraph: "I rest my case." (Ruti, 2015:90) There is no case; she conflates levels of explanation— the emotional or neurohormonal causes of the 3 AM hookup no more preclude an evolutionary explanation than the warbler's photoperiodicity does. Natural selection could not anticipate the pill, but women take it because they want sex, and that desire results from eons of RS. Gay men use evolved mechanisms to enhance their lives; natural selection did not preclude their inclinations, either because it doesn't erase human variation or because their ancestors achieved fitness in other ways.

Even within biology, students have a poor grasp of the levels despite studying Tinbergen's framework (Pinxten et al., 2016); scientific articles citing it show confusion (Barbosa & da Rocha, 2018). Is it perverse to confront this confusion with an increase from four to nine levels of explanation? No, it is clarifying, as a synthesis of (1) Tinbergen's, Mayr's, and other frameworks; (2) the new range and power of behavioral science; and (3) a simple graphic that I have been teaching with for half a century (Fig. 1).

"On Aims and Methods of Ethology"

Tinbergen had four goals: (1) honoring Konrad Lorenz's sixtieth birthday; (2) defining ethology as "the biology of behavior"; (3) reviewing aims and methods; and (4) a history—the naturalists who founded the science, his own generation's field and laboratory experiments, and a future including genetics, brain science, and human applications. Huxley, he wrote,

likes to speak of "three major problems of biology": ... causation, ... survival value, and ... evolution — to which I ... add a fourth ... ontogeny. There is of course, overlap ... yet I believe with Huxley that it is useful both to distinguish between them and to insist that a comprehensive, coherent science of Ethology has to give equal attention to each ... and to their integration. (Tinbergen 1963:411)

By *causation* he means *short-term causation* (1963:430). He cites Huxley on the courtship habits of the great crested grebe (*Podiceps cristatus*) and the redthroated diver (*Colymbus stellatus* Pontopp) (Huxley, 1914, 1923, 1968), but Huxley explicitly develops these "three aspects of biological fact" in *Evolution: The Modern Synthesis* (Huxley, 1942:40–42). Tinbergen's headings are Huxley's—"Causation," "Survival Value," and "Evolution"—adding "Ontogeny." The value of Tinbergen's levels has often been affirmed (Bateson & Laland, 2013a, 2013b; Burkhardt, 2014; Dawkins, 2014; Nesse, 2013; Sherman, 1988; Taborsky, 2014), as has the ultimateproximate distinction (MacDougall-Shackleton, 2011; Nesse, 2019b; Scholl & Pigliucci, 2015). They are applied to many problems he could not foresee: melatonin synthesis and binding in seasonal breeding (ViviD & Bentley, 2018), gonadotropin inhibiting hormone effects on behavior (Calisi, 2014), the "lemur syndrome"





Fig. 1 Nine levels in the explanation of behavior

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(Kappeler & Fichtel, 2015), insect sociogenomics (Kapheim, 2019), and mirror neurons (Heyes, 2014).

Reconciling Tinbergen, Huxley, and Mayr

The words *cause, causation*, and *causality*, like the question *Why?*, have been used variously. Huxley's *causation* matches Tinbergen's proximate mechanisms, whereas Mayr applies the word to all four of his levels—the "kinds of causes" in his subtitle (Mayr, 1961); for Sherman, "there are multiple types of 'correct' answers to any question about causality" (Sherman, 1988). I follow Mayr and Sherman in equating levels of analysis with levels of causality. Tinbergen and Huxley use "Causation" for two kinds of proximate causes—physiology and eliciting stimuli—whereas Mayr distinguishes the "intrinsic physiological cause" (3) from the "extrinsic physiological cause" (1) equals Tinbergen's and Huxley's "survival value," while his "genetic cause" (2) has elements of Tinbergen's "evolution" (the genome *results* from evolution) and "ontogeny" (the "genetic cause" guides development). These differences led me to parse the levels more finely, grouping them in broad categories.

Recent Retrospectives and Controversies

Bateson and Laland, commemorating Tinbergen, applied the levels to birdsong (Bateson & Laland, 2013b: Fig. 1), labeling them as (A) Mechanism (neural circuitry); (B) Current utility (how song helps the bird *now*); (C) Development (what ontogenetic conditions are necessary and sufficient); and (D) Evolution (taxonomy, as in a phyletic tree of orioles). Their section headings are "What is it for?" "How did it develop?" "How did it evolve?" and "How does it work?" Bateson and Laland match the last three questions to Tinbergen's headings "Ontogeny," "Evolution," and "Causation," but they reject his term "Survival Value," preferring "current utility' to 'adaptive significance', because . . . the current and original function of a character can differ, and because it makes no assumption about the processes that generated the functionality" (Bateson & Laland 2013b:713), noting the roles of exaptation, cultural evolution, and genetic drift.

But exaptation leads to adaptation (Gould & Vrba, 1982; Reeve & Sherman, 1993), and cultural evolution is as adaptive as genetic evolution (Boyd et al., 2011; Durham, 1991; Stiner & Kuhn, 2016). Genetic drift, neutral evolution, transposable elements, lateral gene transfer, and varieties of mutation provide directionality only by chance; selection is the signal in their noise—even in molecular evolution, the first subject of neutral theory (Kern & Hahn, 2018). We now infer selection from extant and fossil genomes (Grealy et al., 2017; Gross, 2019; Theofanopoulou et al., 2017). Nesse (2013) critiques Bateson and Laland, applying Tinbergen's levels in the light of ultimate and proximate causes (Nesse, 2019b): "gene-culture evolution, levels of selection, and epigenetics . . . are certainly worth discussion" but may "obscure Tinbergen's accomplishment" (Nesse 2013:681). For Nesse, "current utility" admits lay claims (noses are for holding up eyeglasses); with Tinbergen, he

denies that "survival value must necessarily be guesswork" (Tinbergen, 1963:418, quoted by Nesse, 2013:682).

"Survival Value"

Tinbergen's experiments on black-headed gulls (*Larus ridibundus* L.) show it is not (Tinbergen et al., 1962): "My colleagues and I demonstrated that gulls' eggs, laid out well scattered over the hunting area of Carrion Crows and Herring Gulls, were found more readily when they had an empty egg shell at 4 inches distance" (Tinbergen, 1963:422). Removing empty shells frustrates these predators. This strengthened the inference that shell removal, part of the gull parents' natural repertoire, is an adaptation. Could it have been an exaptation of functionally different ancestral behavior—gathering nesting material, or courtship feeding? It wouldn't matter, because selection *adapted* its function. Could protocultural transmission be involved in the development of the behavior? Perhaps, and that could be studied, but it would not negate the behavior's adaptive value. Similar reasoning applies to epigenetics, gene-culture coevolution, and levels of selection, all grist for natural selection's mill.

But actually this behavior does not have *survival* value for gull parents; it improves their RS. Tinbergen wrote before a wave of new theories transformed behavioral ecology, influencing ethology, psychology, and anthropology (Alcock, 2001): kin selection/inclusive fitness (Dawkins, 1979; Hamilton, 1964), replicator selection or "selfish genes" (Dawkins, 1978; Williams, 1966), parental investment and sexual selection (Emlen & Oring, 1977; Hrdy, 1974, 1984; Mayr, 1972; Trivers, 1972), reciprocal altruism (Trivers, 1971), and game-theoretic approaches to cooperation (Axelrod & Hamilton, 1981) and evolutionarily stable strategies (Maynard Smith, 1982). This body of *Neo-Darwinian* theory holds that natural selection maximizes RS, including the collateral RS of genes of kin.

Challenges to sexual (Gowaty et al., 2012) and kin selection (Nowak et al., 2010) have been answered, both for the former (Janicke et al., 2016; Wilson et al., 2014) and the latter (Abbot et al., 2011; Ferriere & Michod, 2011; Herre & Wcislo, 2011; Rousset & Lion, 2011; Strassmann et al., 2011). Both ideas have had immense heuristic value, but they don't explain everything; combinations with other approaches include multilevel selection (Nowak, 2006; Sober & Wilson, 2011), cooperation among non-kin (Clutton-Brock, 2002; Silk, 2007), and multiplying relatedness by reproductive value (Hasegawa & Kutsukake, 2019). However, since even group selection, to be effective, must ultimately increase relative group RS, we may say that RS, not survival, is maximized by adaptation through natural selection. As the males in some praying mantids might have taught us, the purpose of survival is reproduction.

There is a tendency to conflate natural selection with population genetics (Love, 2017; Müller, 2017). TMS did aim to explain selection in population-genetics terms, which works up to a point (Lewontin, 1974). But Darwin knew nothing of genes; his theory was mainly about individual competition and adaptation regarding traits, not genes or gene pools. Post-TMS, mathematical modeling of selection for two-gene traits proved difficult, and for three genes, formidable. This is why Neo-Darwinian

theory's 1960 s renaissance made two end runs around population-genetic models: (1) returning to Darwin's emphasis on traits that enhanced survival and RS of individuals (Williams, 1966) and (2) modeling certain behaviors (e.g., altruism) *as if* they were single-gene traits and asking how that gene might spread in a population (Hamilton, 1964). One result of this "as if" modeling was inclusive fitness theory, which has motivated thousands of studies. Population genetics has yet to bridge the gap between the two-gene case and broadly multigenic behavioral traits. The "as-if," "gene-for-altruism" models worked partly because simplification often does, but also because the models did not *require* a single gene for altruism, only one gene among many that promote it.

Some Notes on Terminology

Adaptive Value

We might want to replace "survival value" with "reproductive value," but the latter has another, vital meaning (Fisher, 1930; Hasegawa & Kutsukake, 2019). My *adaptive value* is Mayr's *ecological cause*, Sherman's *functional consequences*, Bateson and Laland's *current utility*. By *adaptive value* I mean *positive for fitness*, defined as *relative* RS (Lewontin, 1974; Williams, 1966). It is what Darwin meant by adaptation.

Ultimate and Proximate Causation

Mayr thought this distinction unique to biology (Mayr, 1982, 1988, 1993, 1996, 1997, 1999). We do not refer to an ultimate cause of the periodic table, or of Newton's, Maxwell's, or Einstein's laws, except in theology. But the Krebs cycle and the mammalian four-chambered heart have final causes in adaptive value. There is an ultimate "why" for the four-chambered heart: it worked better, was selected for, and evolved. The white-crowned sparrow song has a similar ultimate cause. Critics note that the boundary is somewhat arbitrary (Dewsbury, 1994; Laland et al., 2011); this objection has been answered (Alcock & Sherman, 1994; Bock, 2017), and a "lean version" of the distinction proposed (Scholl & Pigliucci, 2015), allowing for ontogenetic processes not selected for. Mayr the taxonomist, for whom all kinds were ambiguous, knew his most ambitious distinction was "tentative" and "immediately results in certain difficulties, such as the necessity of splitting genetics. . . . Ecology is hard to place" since "most ecological problems involve both proximate and ultimate causes" (Mayr 1997:119-20). But as Darwin said of natural selection, "The ultimate result is that each creature tends to become more and more improved in relation to its conditions" (Darwin, 1958:102).

There is nothing absolute about Mayr's or Darwin's "ultimate." Alcock and Sherman (1994), answering Dewsbury (1994), show that cultural evolution and organismal constraints on evolution *are* ultimate causes and note, "the vast majority of behavioral hypotheses and questions can be assigned unambiguously to either the proximate or ultimate category" (Alcock & Sherman 1994:59). Laland et al. (2011) claim that phenotypic plasticity and reciprocal causation cannot fit Mayr's scheme, and that "many instances of co-evolution, habitat selection, social evolution, frequency-dependent selection, and maternal effects. . contrast with Mayr's paradigm in that acquired characteristics" may be "sources of selection and/or novel variation" (2011:1512). They build a straw man: "Mayr, by separating proximate from ultimate causation, legitimised screening off ontogenetic processes by evolutionary biologists. Ontogeny was someone else's problem" (Laland et al., 2013:730). But Mayr wrote,

Why does a mammal not develop the neck region directly instead of round-about through the gill arch stage? The answer is that the development of the phenotype is not strictly, exclusively, and directly controlled by the genes but by the interaction between the genotype of the developing cells and their cellular environment. At any stage of ontogeny, the next stage of development is controlled by both the genetic program of the genotype and by a "somatic program" consisting of the embryo at this stage. . . . The gill arch system is the somatic program for the subsequent development of the avian and mammalian neck region. . . . In spite of the new term "somatic program," this interpretation is more than one hundred years old. (Mayr, 1997:171–72)

Thus in morphology as well as behavior—although he did not call it "evodevo"-Mayr was keenly aware of complex and reciprocal ontogenetic causation. That he did not think it demanded a rethinking of Standard Evolutionary Theory (SET) or TMS does not mean he ignored it, nor that his ultimate-proximate distinction was simplistic (Scholl & Pigliucci, 2015). His "somatic program" relates to Waddington's (1942) canalization, a set of genetically coded pathways that development tends to return to in the face of environmental perturbation, and to *robustness*, an organism's stability under environmental variation (Meyers & Bull, 2002); all are constraints on evolution as well as on development (Maynard Smith et al., 1985). Natural selection can only alter phenotypes by altering developmental pathways (Gould, 1977), yet these are often constrained and conserved—a point Darwin made in the "Development and Embryology" section of The Origin (1958:377-86); citing Von Baer, he wrote, "generally the embryos of the most distinct species belonging to the same class are closely similar" (1958:378). He also knew that organisms must survive every stage of life, so some developmental plans produce early stages very different from adults, by natural selection; forms are constrained yet subject to selection.

Ontogeny can't be reduced to physics and chemistry, but it must work with them, in addition to working around and through phylogenetic inertia. Gravity constrains shape and movement; ion flow, nerve conduction; and fluid dynamics, cardiovascular function. Chaos and self-organization cause unpredictable protoforms for genetic canalization to limit and guide (Collinet & Lecuit, 2021; Wolpert, 1992; Zhu & Zernicka-Goetz, 2020). Neither natural selection nor its genomic result is all-powerful in ontogeny.

Love (2017) considers *developmental form challenges* to SET, notably Sean Carroll's (2008) and Gerd Müller's (2007). The two differ markedly, although both ask

for a revision of TMS, Müller wanting an "extension" (at the margins?) and Carroll an "expansion" (internal reorganization?). Carroll sees developmental form—something like Mayr's somatic program— not adaptation, as life's most interesting feature and what he aims to explain. A decade after Mayr contemplated the gill arch in mammal embryos, Carroll fielded a theory of the somatic program in which *cis*regulatory elements and mosaic pleiotropy are the genetic substrate of both stability and change; it is a theory of form more than of evolution, although it belongs in the broad framework of evolutionary biology. Carroll's modern genetics of form gives substance not only to Mayr's somatic program but also to Waddington's (1942) presumptive genes underlying canalization. Müller's work focuses on the ecological niche and reciprocal causation and should also be part of TMS (Müller, 2017), but it does not require changing it much, as I now show.

The Baldwin Effect and Reciprocal Causation

It is ironic to charge someone who often said, "Behavior is the pacemaker of evolution" (Mayr 1988:408), with ignoring niche construction; he knew it as "the Baldwin effect," named for the author who in *American Naturalist* in 1896 called it "a new factor in evolution" (Baldwin, 1896). Huxley and G. G. Simpson, two of Mayr's TMS co-architects, endorsed it (Huxley, 1942; Simpson, 1953). By "organic selection,' the reappearance, in subsequent generations, of the variations first secured in ontogenesis is accounted for without the inheritance of acquired characteristics" (Baldwin 1896:448–49). Or as Mayr put it,

In animals, almost invariably, a change in behavior is the crucial factor initiating evolutionary innovation. As has been stated so often, behavior is the pacemaker of evolution... When an arboreal bird becomes more terrestrial, as did the mockingbird-like ancestor of the thrashers (*Toxostoma*), this shift set up a selection pressure on strengthening and elongating the legs and strengthening the bill used for digging ... the bill is particularly plastic and apt to respond to shifts in behavior." (Mayr 1988:408)

We might now say that the thrasher's ancestor, through ontogenetic behavioral plasticity, constructed a niche that led to Darwinian evolution—the ultimate cause of the thrasher's terrestrial adaptations. This reciprocal causation does not preclude the ultimate-proximate distinction, nor do gene-culture coevolution, cooperation, or epigenetic inheritance; all are subject to natural selection.

Baldwin cited "the great series of adaptations secured by conscious agency, which we may throw together as 'psycho-genetic.' The processes involved here are all classed broadly under the term 'intelligent,' i.e., imitation, gregarious influences, maternal instruction, the lessons of pleasure and pain, and of experience generally, and reasoning from means to ends, etc." (Baldwin, 1896:443–44). Here are the outlines of the "Extended Evolutionary Synthesis" (EES), a proposed replacement for TMS (Laland et al., 2015)—except that for Baldwin, "intelligence, and the imitation which copies it, will set the direction of the development of the complex instincts even on the Neo-Darwinian theory; and in this sense we may say that consciousness

is a 'factor'" (Baldwin 1896:448). Simpson (1953) named *the Baldwin effect* within TMS: "It is simply one way in which natural selection may affect populations, and clearly it is not a factor either contradictory or additional to natural selection" (Simpson 1953:115). It applies in field studies (Badyaev, 2009; Tanabe and Masuda, 2012), the fossil record (Lister, 2014), and mathematical models (Bailey et al., 2018; Sznajder et al., 2012). EES misjudges the breadth and flexibility of TMS (Futuyma, 2017; Stoltzfus, 2017), which includes reciprocal causation (Dickins & Barton, 2013; Svensson, 2018) and accommodates Müller's developmental ecology (Müller, 2017). We might say that TMS is highly adaptable, and rumors of its extinction are greatly exaggerated.

On "The Innate" and its Ethological Designations

Tinbergen (1963) challenges Lorenz on the innate. Conceding that sticklebacks (*Gasterosteus aculeatus*) deprived of exposure to their fathers' red underbellies still respond as adults to that stimulus with attack, and that young pigeons' (*Columba livia*) "practice" of incomplete flying movements does not contribute to the development of flying, he says, "It is not helpful and even wrong to apply to both behavior patterns the term 'innate', because . . . only one out of various environmental effects was excluded" (1963;424), and, "application of the adjective 'innate' to behavior *characters* [emphasis his] . . . on the basis of eliminations of different kinds is heuristically harmful" (1963:425). This seems to preclude calling *any* behavior innate.

Extreme deprivation stunts development, but *relevant* deprivations are different. The "Hawk/Goose Story," based on experiments Tinbergen and Lorenz did *together* in the 1930s, is instructive. Tinbergen *then* took a *more* innatist view than Lorenz. Experiments by Schleidt and colleagues (2011) resolved the matter: turkey chicks may innately tend to crouch or flee at the shape of an overflying hawk, but the same cutout shape passed over them as a hawk (short neck, long tail) rather than a goose (long neck, short tail) can cause fearful behavior either way, depending on which flight-direction is common; habituation of fear depends on exposure. This should give us pause in calling a stimulus innately frightening. Tinbergen also cites Eibl-Eibesfeldt's experiments showing that components of squirrels' nut-cracking behavior are innate, but practice makes it efficient. He uses Lorenz's term *Instinkt-Dressur-Verschränkung*—roughly "instinct-training-entanglement," noting that birdsong might be mistaken for instinct but often requires ontogenetic exposure, imitation, and practice.

The English term "fixed action pattern" (FAP) is a poor translation of the German *Erbkoordination*—""inherited' or 'legacy' coordination"; the word "fixed" provokes needless criticism. Lorenz and Tinbergen sometimes used the adjective *Angeborene* (inborn) to modify *Auslösemechanismus* ("releasing mechanism"), but they often just used the latter. The English terms FAP and IRM (innate releasing mechanism) rigidify both. But we may claim a softer version of them, and of instinct; as Lorenz wrote, to refer to some behavior patterns as innate is "less inexact than the statement that a steam locomotive or the Eiffel Tower are built entirely of metal" (Lorenz, 1965:27). Tinbergen concedes it is "easy to see why the control in certain behaviour

patterns is largely internal" since "a young Gannet, which has to jump off a high cliff, would be poorly off if he had to acquire . . . flight the way we acquire . . . writing. Similarly, the selective responsiveness to rival males in territorial species might well have to be unconditioned so that it can function at once when a male starts its first breeding cycle" (1963:426). Also, "insight into the internal control of growth of neural machinery is provided by the fascinating work of Sperry" (1963:426), and we may grasp "the genetic control of species-specific behaviour . . . now being studied with all the methods available in genetics. . . . Individuals and populations differ as much in their hereditary behaviour 'blueprints' as in their hereditary structural blueprints. The genetic variation on which natural selection can act is there" (1963:428).

American comparative psychology, long focused on rats, pigeons, and humans, reacted to ethology's concept of species-specific innate behavior in welcoming (Beach, 1950) and critical ways (Lehrman, 1953). The idea of biological preparedness for and constraints on learning resolved fruitless disputes (Garcia et al., 1972, 1989; Hinde & Stevenson-Hinde, 1973; Seligman & Hager, 1972). As Gottlieb wrote, "genetic activity by itself does not produce finished traits" (Gottlieb, 1991:5), but it canalizes development (Waddington, 1942). He proposed experiential canalization, to explain how the young of hole-nesting wood ducks (Aix sponsa) and ground-nesting mallards (Anas platyrynchos) respond to their mothers' speciesspecific calls upon hatching. It seems "instinctive" (Gottlieb, 2002:1289), but in experiments, "ducklings have to hear their own (or siblings') vocalizations to show the species-specific responsiveness to their respective maternal calls" (Gottlieb, 1991:6). In the end, "natural selection operates to preserve adaptive phenotypes . . . [and] favors animals that have had a particular developmental history, including, but not restricted to, their genes" as shown by "normally occurring embryonic sensory stimulation in the development of instinctive perception" (Gottlieb, 2002:1287). Here, "instinctive perception," like Lorenz's "instinct-training entanglement" in motor patterns, need not be completely genetic to be instinctual, if genetic preparedness meets needed input from the species' normal expectable environment (NEE). Selection cannot create an ontogenetic program independent of experience that is always there.

Four Levels?

We already have more than four levels (Table 1). Mayr splits *intrinsic* from *extrinsic physiological causes* as types of *immediate causation*, and uses *genetic cause* to include what others call *evolution* or *phylogeny*. For Tinbergen, genetics is one of "two parts" of "evolution dynamics," the other being "the influence of selection" (1963:428). His "ontogeny" is "change of behaviour machinery during development" (1963:424), but he separates the *innate* from the *environmentally induced*. The genome is the prime mover of the "change of behaviour machinery," just as it is the end result of phylogeny selected for in definable ecologies. We have (so far) three ultimate causes (phylogeny, natural selection, genomics), two ontogenetic ones, and three proximate ones. I'll try to organize these and justify one more: three *ultimate*, three *intermediate*, three *proximate*. My 963-page treatise (including ~ 200)

Table 1 Correspondences	among different authors'	levels of explanation			
Tinbergen	Huxley	Mayr	Sherman	Bateson/Laland	Nesse
Evolution	Evolution	Genetic cause	Evolutionary origins	Evolution	Phylogeny
Survival value	Survival value	Ecological cause	Functional consequences	Current utility	Adaptive significance
Ontogeny	N/A	N/A	Ontogenetic processes	Development	Ontogeny
Short-term causation	Causation	Intrinsic physiology	Mechanisms	Mechanism	Mechanism
		Extrinsic physiology			

pp. of references) on the evolution of the development—evo-devo—of human behavior (Konner, 2010) treats in ways impossible here the evolution of brain development, the Baldwin effect, reciprocal causation, gene-culture co-evolution, cultural evolution, non-genetic inheritance, maternal and grandparental effects, epigenetic inheritance, and other subtleties that some hold require us to rethink evolution. They do not, but are extensions, most long known, of what Baldwin in 1896 called Neo-Darwinian theory.

Nine Levels of Causation of Behavior

Applying Tinbergen's levels, a jay rising from a holly bush up to a longleaf pine branch flies because (1) it's a bird; (2) flight gave it an advantage in its environment of evolutionary adaptedness (EEA); (3) ontogeny gave it light bones, wings, feathers, a motor neuron circuit oscillator for flight, practice, and a sympathetic nervous system attuned to threats, shaped by nutrition, exercise, and experience; and (4) a fox triggered a physiological flight response. We can break these down further, into nine levels in three categories of causes (Fig. 1).

Levels 1 and 2 are Tinbergen's; his Level 3 would include 3 through 6 in this model, which breaks out the ontogenetic causes; and his Level 4 encompasses 7, 8, and 9 here. Mayr's Genetic Cause *expresses* his Evolutionary Cause (a culmination of Level 1 and 2 here), and he splits the *immediate* cause in two. But in Mayr's case of the warbler migration, his *intrinsic physiological cause* would be Level 7 here because it involves hormonal changes over weeks as day length falls. That environmental change would be at Level 6, while the cold air mass moving in *that day* (Level 9) triggers a Level 8 short-term circuit in the warbler's brain in the context of the hormonal changes. The levels depicted in the figure are ordered and summarized in Table 2.

The nine levels are grouped into three "kinds of causes" (Mayr's phrase): ultimate or remote; intermediate or developmental; and proximate/immediate or mechanistic. Giving ontogeny its own status as an *intermediate kind of cause* recognizes (1) Tinbergen's insight in adding it to Huxley's levels; (2) the importance of evo-devo *within* the basic Darwinian framework; (3) reciprocal causation in ontogeny influencing the phenotype; and (4) a "lean" version of Mayr's ultimate/proximate distinction, using ontogeny to explain some traits not specifically selected for (Scholl & Pigliucci, 2015).

Levels 1–3: Ultimate, Remote, Evolutionary Causation

 Phylogeny. An organism's taxon limits change under selection, a constraint expressed through ontogeny—genomic coherence, canalized development, morphological commitments, etc. (Maynard Smith et al., 1985). Selection may have to cross troughs in the adaptive landscape on the way to new adaptive peaks (Levins, 1964), consistent with robustness (Meyers & Bull, 2002) and stabilizing selection

3 Types of Causation	9 Levels of Explanation		
Ultimate/Remote	1 Phylogeny	2 Adaptive value	3 Genome
e a materiale	History over	Ecology/demography	Result of selection
	eons type of	natural & sexual	on phylogeny
	animal	selection one to	cause of/
	taxon	many generations	constraints on
	constraints	many generations	ontogeny
	on selection		ontogeny
	Data: fossil	Data: field	Data: Genomics
	DNA	arnarimants PS	breeding/twin
	aladistia/	DNA selection	studios
	comparative	signals	studies
Intermediate/	4 Embruoganasis/	5 Sensitive Period	6 Ongoing/Pouting
Onto constia/	4. Embryogenesis/	S. Sensuive I entou	0. Ongoing/Routine
David a manufal	Maturation	Effects	External Effects
Developmental	Unfolding	Principaged high	Environmental
	ganomia	impact	influences
	genom	impuci	operating
	intrinsio	environmeni offoots usually	throughout life:
	abanga	ejjecis, usualiy	ataooo looming
	through the	difficult to	illness, rearning,
			uness, nurnion,
	Ine course	reverse	cuiture, etc.
	Data:	Data: phase-	Data: pnase-
	embryology	specific	general
	experiments,	interventions/	interventions/
	deprivations	aeprivations	deprivations
Proximate/	/. Hormones/	8. Neural circuits/	9. Elicitors/Releasers
Immediate/	Metabolism	Neurotransmitters	
Mechanistic	Slower short-	Faster short-term	Most immediate
	term	physiology,	extrinsic cause,
	physiology,	milliseconds to	trigger of
	minutes to	seconds, most	behavior,
	weeks,	immediate	seconds to
	readying	intrinsic cause	minutes
	neural		
	circuits		
	<u>Data</u> :	Data: neuroimaging,	Data: stimulus-
	hormone/glucose	neuropharmacology	response
	etc. flux		experiments

 Table 2
 Levels of explanation organized (after Nesse 2013)

Nine levels of explanation arrayed in a 3×3 table, corresponding to three broad kinds of causation, each kind comprising three levels of explanation. Numbering corresponds to Fig. 1. Intrinsic (inside-the-organism) levels are shown in normal type and green, outside-the-organism levels in italics and *blue*

(Eldredge & Gould, 1972; Gould & Eldredge, 1993; Simpson, 1944). Phylogeny reflects the taxon's environments over eons, stored in the developmental plan.

Adaptive Value. Because the organism's fitness (RS) was optimized for its EEAs, studying it *in* them is useful (Lee, 2018). Relevant research includes behavioral ecology (Codding & Bird, 2015; Krebs & Davies, 1997), demography (Howell, 1979, 1986, 2010), life-history theory (Charnov, 1993; Chisholm, 1993, 1999; Sibly & Brown, 2007), field experiments, genomics (Dong et al., 2016; Pruefer et al., 2012), gene-culture coevolution (Boyd et al., 2011; Durham, 1991), recent selection in current genomes (Karmin et al., 2015), age-specific survival (Endler, 1986), sexual choice (Dakin & Montgomerie, 2011), brood or family size (Exposito-Granados et al., 2016), and transgenerational RS (Arnold, 2011; Berg et al., 2014; Richardson et al., 2007; Shama & Wegner, 2014).

3. Genome. The individual's genome is in a spectrum of variation for its species and sex, and its transcriptome is age-specific. It results from phylogenetic and ecological causes, and it causes all further possibilities (not all outcomes) in the life cycle. It is the bottleneck that funnels phylogenetic into developmental constraints (Bakken et al., 2016; Silver, 2016). It can be seen as an ultimate cause (Mayr), or part of ontogeny (Tinbergen); where to place it on the ultimateproximate (here, ultimate-intermediate) boundary is somewhat arbitrary. Also, genomes are not fixed. Synergies of parental genes and changes in meiosis mean the zygote's genome is partly unpredictable. Transposable elements (jumping genes) and somatic mutations in neural lineages make monozygotic twins diverge genetically (Lodato et al., 2015; Mustafin, 2019). Genomic imprinting (Wang et al., 2017), trophic effects of use (Changeux & Danchin, 1976; Kano & Hashimoto, 2009; Purves & Lichtman, 1985), and formal chaos (Goodwin, 1994; Kauffman, 1993) cause more divergence. Yet what Tinbergen called "the genetic control of species-specific behavior" is real, and "classifications based on behaviour taxonomy have, on the whole, corresponded very closely to the already existing classifications . . . a striking justification of treating behaviour patterns as 'organs'" (1963:428).

Levels 4–6: Intermediate, Ontogenetic, Developmental Causation

4. Embryonic/maturational processes. Given the species' NEE or ontogenetic niche (West & King, 1987; West-Eberhard, 2003), the genome not only starts ontogeny but guides it (Klingler et al., 2021); birth (hatching, pupation) is important, but genes guide throughout life, often similarly pre- and postnatally, in neurogenesis, programmed cell death, guided migration, overproduction of neurons and synapses, pruning back of cells and connections, myelination, and other processes. Activity, trophic effects, and experience play a role (Changeux & Danchin, 1976; Kano & Hashimoto, 2009; Purves & Lichtman, 1985), but genes guide maturation (Bakken et al., 2016). Genetic control does not wane in proportion to time since conception, despite large environmental influences. Genes control much of pubertal change; Huntington's and Alzheimer's diseases prove genetic influences in mid- and late-life; identical twins often show convergence in adulthood; heritability estimates increase as children and adolescents outgrow developmental "noise" and parental controls, seeking their own niches. Developmental convergence in monozygotic more than dizygotic twins is true for general cognition (Davis et al., 2009; Plomin et al., 2016), oral language (Tosto et al., 2017), body mass index (Haworth et al., 2008), religiosity (Koenig et al., 2005), and delinquency (Harden & Mann, 2015). Complex traits are multigenic, and genomewide association studies with single-nucleotide polymorphisms can't explain high heritabilities (Cheesman et al., 2017), making twin and adoption studies more necessary (Sniekers et al., 2017). The claim that it makes no sense to parse genetic (G) from environmental (E) contributions because $G \times E$ interactions and common-parlance "interaction" dominate development is flawed (Rutter, 2006; Rutter et al., 2006). It is not meaningless to say that width contributes less to the volume of a skyscraper than to a same-volume one-story factory, nor that genes contribute more to height than to piano playing.

- 5. Sensitive period (SP) effects. Sensitive or critical period effects, our second component of Tinbergen's ontogeny, change phenotypes in hard-to-reverse ways—whether maladaptive deprivations or facultative adaptations (normal developmental options); ontogeny detects environmental quality to shape later adaptation (Chisholm, 1999). Of extrinsic causes of development, we can separate routine environmental effects that alter behavior at any age (stress, learning, illness, nutrition, culture, etc.) from those that have a privileged impact in early life. One-week closure of one eye in the first six months in rhesus monkeys prevents axons from that eye from forming synapses on binocularly responsive cells; the open eye monopolizes them, with irreversible loss of depth perception (Hubel et al., 1977; LeVay et al., 1980). Toxic effects (thalidomide, ethanol) profound in embryos can be minor later (Newman, 1986).
- 6. Ongoing/routine environmental effects. Nutrition, stress, and reinforcement contingencies may have SP effects, but they can also work similarly throughout life; in principle, they are reversible, although trauma at any life stage can have lasting effects, and chronic stress can exhaust the hypothalamic-pituitary-adrenal (HPA) axis (Dunlop & Wong, 2019). Plasticity at any age includes habituation, classical conditioning, association learning, avoidance conditioning, instrumental learning, observational learning, and imitation (Domjan, 2015). It depends on changes in synaptic size and density, neurotransmitter-related receptors and enzymes, immediate early genes in stimulated neurons, and other neural processes from sea slugs to humans (Kandel et al., 2014). Explicit, declarative, and episodic memories depend on the hippocampus. Social facilitation occurs in all social species, but observational learning is more restricted (Laland, 2004). Culture bathes the developing human through these processes from conception to senescence (LeVine, 2007).

Levels 7–9: Proximate, Immediate, or Mechanistic Causation

- 7. Longer-term physiology. Hormonal and metabolic effects (energy flow, sleep cycles, muscle fatigue, etc.) work over minutes to weeks; they are intrinsic but respond to external changes. Mayr's warbler responds hormonally to decreasing day length, preparing it for a trigger (cold? social facilitation?) to fly south. In birdsong, *increasing day length and spring warming stimulate the hypothalamopituitary-gonadal (HPG) axis, and rising testosterone (T) augments song centers, with neurogenesis, in some species (Small et al., 2015); T plays multiple roles in different time-frames and brain circuits (Alward et al., 2018).*
- 8. Short-term physiology. Immediate basis of the behavioral output in neural circuits acting over milliseconds to minutes, by ion flux and neurotransmitters, under the influence of neuromodulators; proximate internal causes of behavior. In some songbirds, fully developed, practiced, and seasonally regrown song circuits con-

trol the motor pattern underlying song (Bolhuis & Moorman, 2015; Marler & Slabbekoorn, 2004; Woolley & Sakata, 2019).

 Elicitors or releasers. Events in the stimulus envelope that precipitate the behavior; the releasing mechanism of the ethologists, the conditioned or unconditioned stimulus of the learning psychologists; the immediate external causes of behavior.

Reciprocal Causation in the Nine-Level Model

Where do reciprocal ontogenetic causation and the Baldwin effect (niche construction) fit when all the arrows point in one direction, and the nested causation flows simply from left to right? The scheme is designed for parsimony and testability, but feedback is inherent. The behavioral output *must* change the environment at least in the short term, changing the animal's experience of the world—in ethological terms, its *Umwelt*. The thrasher's ancestor spends more time on the ground, the warbler migrates a bit farther south, a wolf hangs around human hunters. Behavioral outputs occur at all points in the life history; the human fetus's hand-to-mouth activity (Mori & Koniyoshi, 2010), the two-month-old's first social smiles, the teenager's risk-taking, the decision to adopt a baby at age 40 or retire at 60 all change the environment for ontogeny. Across generations the change may set up new selective forces, causing genome-based adaptive changes. Nothing about this, including the conscious human decisions Baldwin highlighted, departs from Neo-Darwinian theory.

Figure 2 shows how the model can accommodate reciprocal causation. In 2A, behavioral output at any life stage alters elicitors and routine environmental effects. The thrasher's ancestor responds to new cues on the ground; in time, differences in nutrition, stress, and so on, shape its further ontogeny, even in adulthood. In 2B, the second generation's environment is changed from the outset by the parents' choices, and new SP effects may result. In 2C, the n^{th} generation has had gene changes due to selection for stronger bills or better walking. In Middle Pleistocene hominins, behavioral choices such as stone-tool making, bringing food to a central processing place, controlling fire, and building camps altered the human ancestral niche (Stiner & Kuhn, 2016). These changes, Baldwin's conscious and intelligent "psycho-genetic" factors—parental influence, gregariousness, planning, etc.—set up selective forces that expanded the brain in one of the fastest changes in the fossil record, which in turn changed the environment, further intensifying selection.

On a shorter time scale, the evolution of lactase persistence in populations that chose dairying as a subsistence mode is another human example of the Baldwin effect, since a lactose-tolerance gene, changing digestive physiology, spread in the wake of a behavioral and cultural choice (Chenling Xu et al., 2017). Note that this was a change in ontogeny since we generally have lactose tolerance until weaning, but its persistence through life involved a genetically guided ontogenetic change.



Fig. 2 Reciprocal causation in the nine-level model

Examples from Ethology, Behavioral Ecology, and Psychobiology

Phylogeny

Lorenz's classics, "*Der Kumpan in die Umwelt des Vogels*" (roughly "The Companion in the Bird's World," 1937) and "Comparative Studies of Motor Patterns of *Anatinae*" (1941) gave wide overviews and therefore deep phylogenies of relationship types and social displays (Lorenz, 1970, 1971a). "Der Kumpan" included parents, infants, mates, social partners, and siblings—relationship types across avian taxa—suggesting a basis in evolved, neurally wired knowledge about the partner's appearance, what it will do, and how to respond. Relationships may be lasting, crucial to survival or reproduction, and stereotyped; experience guides their emergence, but major features are independent of learning. Innate displays of ducks and geese formed a phylogenetic tree consistent with those based on morphology (Lorenz, 1971a), as have facial expressions of higher primates (Preuschoft 1995; van Hooff 1962), stickleback displays (McLennan & Mattern, 2001), birdsong (Mason et al., 2014; Matysiokova et al., 2017), rodent grooming (Malange et al., 2013), and other behaviors (Stuart et al., 2002).

Adaptive Value

Many observations suggest past patterns of selection. Darwin inferred from Galapagos finches an adaptive phyletic radiation, now confirmed (Grant & Grant, 2008). Anolid lizards in different Caribbean lines show parallel adaptive ecological radiations indicating independent convergent selection (Losos, 1995). Field experiments prove the adaptive value of behaviors such as eggshell removal (Tinbergen et al., 1962). Other confirmations: (1) food-caching by male bull-headed shrikes (Lanius bucephalus) changes their song, making them more attractive to females (Nishida & Takagi, 2019); (2) anole lizards in field studies and bank voles in the lab respond to selection by predation with behavioral adaptations (Lapiedra et al., 2018; Maiti et al., 2019); (3) marmots' (Marmota sp.) social organizations and breeding cycles are adapted to environmental harshness (Barash, 1974); (4) polygyny threshold in wild horses (a female choosing an already mated male) varies with distance from permanent fresh water and seasonal rain (Manning & McLoughlin, 2017); and (5) mother baboons' social bonds (Papio cynocephalus) enhance their infants' survival (Silk et al., 2003). Naked mole rats (Heterocephalus glaber) are exceptionally altruistic and xenophobic due to highly inbred colonies, strongly confirming kin selection (Sherman et al., 1991), although their colonyspecific chirping dialects are learned traditions (Barker et al., 2021) Studies of natural selection in real time (Endler, 1986; Grant & Grant, 1989), experimentercontrolled evolution (Kawecki et al., 2012), and new ways to detect selection in extant genomes (Bruger & Marx, 2018; Gross, 2019; Theofanopoulou et al., 2017) prove that historical hypotheses in selection are testable.

Genomics

Birdsong involves protocultural adaptions, but genes matter (Mello & Clayton, 2015; Scharff & Adam, 2013); ten are unique to songbirds (Wirthlin et al., 2014). Cross-breeding zebra (*Taeniopygia guttata*) and owl finches (*T. bichenovii*) produces first-generation hybrids with songs predictable from gene expression in song after exposure to both songs in ontogeny. Tutoring matters, but species of origin predicts results better (Wang et al., 2019; Woolley & Sakata, 2019). Inbred canaries (*Serinus canaria*) have phonetic oddities in otherwise normal songs, and their female mates have smaller broods (de Boer et al., 2016). Genes' influence transcends reciprocal causation, affecting RS.

Embryogenesis/Maturation

Ontogeny itself is causal. The leopard gecko (*Eublepharis macularius*) has temperature-dependent sex determination (TSD), and the size and aggressiveness of both sexes is also temperature dependent (Crews & Groothuis, 2005), as in many reptiles and amphibians (Booth, 2018; Refsnider et al., 2019). Yet such non-genetic factors and reciprocal causation are subject to natural selection's ultimate role in adjusting sex ratios and differential investment by sex to early-life signals (Lambert et al., 2018; Warner & Shine, 2008), as adaptationist life history theory predicts (Chisholm, 1999). Males grow faster to larger sizes than females, but females from male-biased temperatures are larger and more aggressive than those from female-biased ones and differ in brain areas underlying aggressive and sexual behavior. Both sexes have larger and more active hypothalamic preoptic areas (POA) at male-rather than female-biased temperatures, but the reverse is true for the ventromedial hypothalamus (VMH). Bird and mammal mothers manipulate offspring outcomes (Groothuis et al., 2019). Yellow-legged gull (*Larus michaellis*) mothers control T level in egg yolks, which predicts chicks' begging intensity, paternal feeding, and growth (Noguera et al., 2013). In Japanese quail (*Coturnix japonica*), genes influence maternal hormone transfer to the yolk (Okuliarova et al., 2011), affecting mate choice in female offspring (Ledecka et al., 2019). Crews and Groothuis say progress "since Tinbergen . . . has made the nurture-nature debate obsolete" (2005:366), but progress has only refined it.

Sensitive Period Effects

A classic SP effect is imprinting in the first days post-hatching in precocial birds (e.g., goslings, ducklings, and domestic chicks), studies pioneered by Lorenz and made rigorous by others (Bateson, 1966; Horn, 2004; Lorenz, 1965; McCabe, 2019). In the NEE, the SP is terminated by focus on a parent, although the length and exclusivity of the attachment can be experimentally altered (Versace et al., 2019). Chicks are innately disposed toward organic forms (Di Giorgio et al., 2017; Miura & Matsushima, 2016; Rosa-Salva et al., 2019), but imprinting will occur without them. Some forebrain lesions (e.g., the intermediate medial mesopallium, IMM) disrupt imprinting on animate more than inanimate objects; the neural substrate is evolutionarily prepared. The IMM mediates imprinting with increased dendritic spine synapses and N-methyl-D-aspartate (NMDA) receptors, vital in learning (Meparishvili et al., 2015). In the nidopallium (neostriatum), dendritic spines are massively pruned during imprinting, an NMDA-dependent process (Bock & Braun, 1999), which along with increased IMM synaptic area may narrow the hatchling's perceptual focus. Imprinting is biologically prepared rapid learning, essential to juvenile survival and future mating (Irwin & Price, 1999; Yang et al., 2019). In mammals, licking and grooming of rat pups is passed on transgenerationally, depending on epigenetic DNA methylation, not on underlying genes (Champagne, 2016; Curley & Champagne, 2016).

Routine Environmental Effects

Brain plasticity is widespread in animals at all life stages. Rearing rats after weaning in an environment enriched by toys and social partners increases visual cortex weight and thickness, synapse size and number, dendritic branching, spine density on pyramidal cells, and enzyme activity relating to acetylcholine, a forebrain neurotransmitter (Bennett et al., 1996; Diamond et al., 1964); the same effects occur in aged rats (Diamond et al., 1985). In the jewel fish (*Hemichromis bimaculatus*), social vs. isolation rearing changes the number, distribution, and shape of spines on the distal dendritic branches of tectal pyramidal neurons (Coss & Globus, 1978; Globus et al., 1973); repeated social stimulation makes the spine shorter and thicker, affording less resistance to incoming electrical signals (Valverde, 1967). Spine shape changes figure in many learning processes (Brandon & Coss, 1982; Chidambaram et al., 2019; Segal, 2005). However embodied, habituation, classical conditioning, and avoidance and operant learning are ubiquitous (LeDoux, 2003; Leduc et al., 2007; Raderschall et al., 2011; Timberlake and Silva, 1994).

Hormones and Metabolism

Mayr's *intrinsic physiological cause* of the warbler's migration, hormonal change as day length decreases, is increasingly understood (Ramenofsky & Wingfield, 2017; Watts et al., 2018). Corticosterone-dependent "migratory restlessness" predicts departure in some species (Eikenaar et al., 2014), T or thyroid hormones in others (Perez et al., 2016; Robart et al., 2018). Seasonal breeding in many vertebrates (Gorman, 2020) depends on the pineal gland; increase in day-length (perceived directly through the skin in some vertebrates, indirectly through neural circuits in birds and mammals) reduces melatonin, disinhibiting the HPG axis. Rising gonadal hormones in both sexes prime courtship and mating circuits, which respond to cues from mates or rivals, as in the ring dove *Streptopelia risoria* (Burns-Cusato & Cusato, 2013; Lehrman et al., 1961; Mantei et al., 2008). Gelada baboons' (*Theropithecus gelada*) loud alarm calls depend on age, rank, androgens, and fatigue; males assess rivals' calls in deciding to fight, and outcomes affect access to females (Benitez et al., 2016, 2017). In lactating rats the HPG axis regulates maternal aggression and pup defense (Bayerl et al., 2019).

Neural Circuits and Neurotransmitters

Tinbergen's hopes for neuroethology have been realized (Simmons & Moss, 2019). The classic honeybee (Apis mellifera) waggle dance (von Frisch, 1967) involves olfactory cues and pulse vibrations detected by antennae of observing bees (Ai et al., 2019). An identified GABA inhibitory neuron in the dorsal lobe is part of a "stopwatch" system (2019:6) translating duration to distance. When the young bee emerges, "the coarse neural circuitry for vibration processing is already established," but with age and experience, "changes in dendritic density in specific regions" of the neuron suggest a "refinement process" (2019:9). Polarization-sensitive neurons in the brain's central complex signal direction of foraging flights in relation to the sun. Ontogeny (per Tinbergen) reveals a contribution of experience to brain circuitry, yet (per Lorenz) innate wiring counts. In voles (Microtus spp.), socially monogamous species with biparental care have different regional brain expression of receptor genes for oxytocin (OT) in both sexes and arginine vasopressin (AVP) in males, causing species differences in social behavior (Insel, 2010; Numan & Young, 2016; Tickerhoof & Smith, 2017; Walum & Young, 2018). AVP receptor gene expression depends on the highly mutable promoter region, allowing rapid evolution of mating systems in the genus (Donaldson & Young, 2013; Phelps et al., 2017).

Elicitors and Releasers

Short-term triggers are part of Mayr's *extrinsic physiology*, the *Auslösemechanismus* of ethology. Tinbergen notes that male sticklebacks attack dummy rivals with red underbellies without prior exposure, but we now know repeated exposure to such models increases males' courtship and aggression and deepens their own red color (Kim & Velando, 2014). Laughing gull chicks peck at a red spot on parents' bills (the releaser or sign stimulus), causing parental regurgitation and feeding (Tinbergen & Perdeck, 1950). Skeptical experiments confirmed this (ten Cate, 2009; ten Cate et al., 2009), including the role of the redness and size of the dot (Velando et al., 2013). Reciprocal causation fine-tunes genes, serving adaptation.

Examples from Human Ethology and Behavioral Ecology

Tinbergen was glad "that students of human behavior are showing a growing interest in ethological methods" (1963:430); he and Lorenz discussed human behavior in their Nobel Prize speeches (Lorenz, 1974; Tinbergen, 1974). Tinbergen's student Nicholas Blurton Jones pioneered human ethology (Blurton Jones, 1972, 1978, 1986; Blurton Jones & Konner, 1973, 1976), and others followed (Chisholm, 1983; Eibl-Eibesfeldt, 1979; Konner, 1972; McGrew, 1972; Schiefenhövel, 1995, 1996). Human behavioral ecology's stress on adaptive value reshaped anthropology (Betzig, 1989; Betzig et al., 1988; Chagnon, 1988; Hrdy, 1976, 1977a, b, 1981; Irons, 1979; Turke, 1988), psychology (Barkow et al., 1992; Buss, 1984, 1989), and medicine (Eaton & Konner, 1985; Williams & Nesse, 1991), with ongoing impact (Betzig, 2012; Blurton Jones, 2016; Buss, 2018; Caldwell et al., 2019; Chagnon et al., 2017; Chisholm, 1999; Confer et al., 2010; Howell, 2010; Macfarlan et al., 2014; Nesse, 2019a). We focus on parent-offspring relations.

Phylogeny

Since maternal care is well developed in egg-laying mammals such as the platypus (*Ornithorhynchus*), the mammalian mother-offspring relationship (MOR) likely emerged around 178–208 mya (Lopatin, 2019; Luo et al., 2017), further evolving with internal gestation by 150 mya (Lopatin & Averianov, 2017; Luo et al., 2015). From comparative data, Paul MacLean (1985) identified the MOR, infant separation calls, and play as basic mammalian adaptations. The middle-ear bones derived from the reptilian jaw angle by 195 mya (Luo et al., 2001), which along with comparative cochlear physiology (Manley, 2017) suggests that early mammal infant distress calls were in a frequency range inaudible to reptilian predators. Primates intensified and prolonged the MOR, variably adding paternal and other allomaternal care (Konner, 2010, 2016, 2018). The Catarrhine Mother-Infant Complex (CMIC), a suite of behavioral adaptations in Old World monkeys, apes, and humans (parvorder Catarrhini) in our EEAs, includes singleton birth, 24-hr physical contact for weeks to months, proximity until weaning, frequent nursing, gradual transition to a juvenile play group, and variable alloparental care by grandparents, other adults, older siblings, and/or fathers. The CMIC left our hunter-gatherer ancestors with a phylogenetic legacy of prolonged dependency and care despite parent-offspring conflict (Hrdy, 1999; Trivers, 1974). Humans are also secondarily altricial, with exceptionally dependent neonates. It may be that the network of attachments between infants and their caregivers are at the emotional core of "the deep history of culture" (Chisholm, 2021).

Adaptive Value

Hrdy infers from secondary altriciality, difficult human birth, and provisioning of infants and families pre- and post-weaning that cooperative breeding allowed human emergence (Hrdy, 2009, 2016). As partly set out earlier (Kaplan et al., 2000; Lancaster & Lancaster, 1987), it shortened our birth spacing, so we far exceeded other apes in RS. Adoption is common in human cultures, often predictably from inclusive fitness theory (Silk, 1980, 1987a, b)-a generalization of maternal investment-and other adaptationist models (Silk, 1990). Hunter-gatherer cultures, reflecting our EEAs, extend the CMIC with cooperative breeding (Hewlett & Lamb, 2005; Lee, 2018; Meehan and Crittenden, 2016). Hunter-gatherer childhood (HGC) includes prolonged physical contact, indulgent responsiveness, daytime breastfeeding several times an hour, sleeping with the mother, night nursing on demand, weaning around 2.5 years of age, a social context that relieves stress on mothers, less father than mother involvement yet more than in most other cultures, and a gradual shift to a mixed-sex, mixed-age play group (Konner, 2016). Allomaternal care is always present (Konner, 2018; Kruger & Konner, 2010), but may be done by grandmothers (Hawkes, 2003), fathers (Hewlett, 1991; Hill & Hurtado, 2009), both (Marlowe, 1999, 2003, 2005), other allomothers (Morelli & Tronick, 1991, 1992; Tronick et al., 1987), siblings (Blurton Jones, 2016; Ivey Henry et al., 2005), or combinations (Crittenden & Marlowe, 2008). Controversy over whether grandmothers or fathers are more important will likely be resolved pluralistically depending on ecological context (Gurven & Hill, 2009; Hawkes, 1991; Hill & Hurtado, 2009; Kaplan et al., 2000). In the Hadza, sexual selection matters; fathers do more when there are no young women in the camp, but if there are, care defaults to grandmothers (Marlowe, 1999). HGC may not have "current utility" for most humans, but it apparently had adaptive value for our ancestors.

Genomics

Platypus milk protein genes resemble human ones, suggesting lactation for ~ 200 my (Warren et al., 2008). The human genome also encodes biobehavioral aspects of parenting; genes for OT, AVP, prolactin (Prl) and their receptors, and the receptors and enzymes relating to estrogen (E), progesterone (P), and T, which declines in new fathers (Rilling & Mascaro, 2017). These genes are widespread in mammals, as are their physiological and behavioral effects (Bos, 2017; Rilling & Young,

2014); remarkably, some mammalian mothering genes regulate stickleback paternal behavior (Bukhari et al., 2019). We partition human variation (G, E, G×E), but key genetic effects show little variation, and some universals are phylogenetically conserved. As Tinbergen said, their very universality supports genetic influence. But the human brain *must* have genes differentially expressed during development. In our lineage, a Human Accelerated Region, HAR1, is part of an RNA gene expressed in the human cerebral cortex between 9 and 17 gestational weeks, co-expressed with the protein reelin secreted by Cajal-Retzius neurons and essential for normal 6-layered neocortex development (Pollard et al., 2006). Other human-specific gene expression changes have been found in the default mode network (DMN), the prefrontal cortex, cortical dopamine biosynthesis, and other domains involved in intelligence and social cognition (Levchenko et al., 2018; Sousa et al., 2017; Wei et al., 2019). Ontogenetically the human transcriptome supports neoteny, with postnatal expression of many genes expressed only prenatally in nonhuman primates (Bakken et al., 2016; Somel et al., 2009). Uniquely human behavior required human-accelerated evolutionary changes (Mitchell & Silver, 2018; Preuss, 2017).

Embryogenesis/Maturation

Our social development is genetically guided (Konner, 2010). The neurobehavioral status of newborns depends on time since conception, varying little among populations (Brazelton, 1973; Konner, 1972; Prechtl & Beintema, 1964). The cardiovascular system is anatomically reorganized at birth (Adolph, 1968), but the nervous system shows great continuity from late prenatal to early postnatal life (Ouyang et al., 2019; Prechtl, 1984), yielding a postnatal neuroembryology. The neonate is not rewarding socially but can cry and be soothed by feeding, physical contact, and rocking (due to a mature vestibulocochlear system); crying recruits care from mothers and others (Kruger & Konner, 2010). The newborn roots toward something stroking its cheek, latches on, sucks vigorously, makes stripping actions with the tongue, and if sucking a lactating nipple, extracts milk and swallows it without aspirating or neglecting to breathe; this is neurologically complex and instinctual (Geddes et al., 2017; Sakalidis & Geddes, 2016). Over the ensuing "fourth trimester" the infant's social smiles and gaze contact resemble motor milestones in that their emergence is little affected by experience. Crying rises and falls over these three months in a possibly universal crying curve (Barr et al., 1991). Later, children speak one of thousands of languages depending on input, but with similar developmental timing (Gleitman, 2006; Schieffelin & Ochs, 1986), because language circuits are maturational and modular (Lenneberg, 1967; Piattelli-Palmarini, 2017a, 2019; Szalontai & Csiszar, 2013). Language emerges with varied, even impoverished input (Berwick et al., 2013; Piattelli-Palmarini, 2017b); our capacity for language acquisition is instinctual (Pinker, 1994). Social-cognitive milestones such as the false belief task (Callaghan et al., 2005) and the 5-to-7 shift (Sameroff & Haith, 1996) differ little across cultures. Timing of puberty varies, but the behavioral consequences are similar (Kapetanovic et al., 2020).

Sensitive Period Effects

Thalidomide and ethanol have tragic effects specific to embryos, and the SP in the development of binocularly responsive visual cortex cells has led surgeons to try to correct strabismus earlier (Magli et al., 2017). Social deprivation in catarrhines strongly suggests an SP for social input by mothers and playmates in the development of social behavior (Dettmer & Suomi, 2014; Sanchez et al., 2001; Zhang, 2017). Severely socially deprived Romanian orphans adopted into nurturing families before 6 months of age have good behavioral outcomes, but if adopted later they suffer mental health problems resistant to reversal (Scott-Jupp, 2017; Sonuga-Barke et al., 2017), with structural brain differences (Mackes et al., 2020) and HPA axis dysregulation (Kumsta et al., 2017). Other studies of early social deprivation confirm its importance (Garg et al., 2018; Leve et al., 2019; Nelson et al., 2019).

Routine Environmental Effects

For humans, "the natural" includes teaching and learning (Kruger & Tomasello, 1996); our brains are adapted for plasticity (Sherwood & Gomez-Robles, 2017). Caregiver and offspring behavior, instinctual aspects notwithstanding, are culturally shaped. True culture entails symbolic language and teaching; despite fascinating instances of proto-culture in other species from white-crowned sparrows to chimpanzees (Whiten, 2019), fully evolved culture is only human. Yet most learning processes, from habituation to instruction, can occur at all ages, and are largely reversible. The same applies to illness, stress, and other influences, although severe trauma at any age can be difficult to reverse. Human parental behavior, perhaps especially fathering as it is less prepared hormonally, involves learning by imitation, practice, and cultural traditions of coaching and teaching. Even breastfeeding benefits from these, although some aspects, such as milk letdown, are largely innate (Gardner et al., 2015, 2017). Yet OT-dependent milk ejection due to nipple stimulation (the unconditioned stimulus) is soon classically conditioned to crying or other conditioned stimuli (McNeilly et al., 1983; Willis & Mein, 1983). For the infant, after visually-directed reaching matures (~6 mo), rewarding effects of milk or other foods reinforce the instrumental conditioning of reaching and grasping and help shape its emergence in the manner suggested by Lorenz and Tinbergen. While wariness of strangers matures with attachment in most infants by 7–9 mo, exposure to strangers habituates infants, and multiple attachments are experience-dependent (Howes & Spieker, 2008; Jung & Fouts, 2011).

Hormones and Metabolism

Adoptive parents, including same-sex male couples, show that parenting does not require biological motherhood. But adoptions are highly motivated, and natural selection prepared mothers for parenting when motivation is low. Humans draw on deep phylogeny for the gene expression determining hormones of parent-offspring relationships (Bos, 2017; Bridges, 2020; Rilling & Young, 2014; Saltzman & Maestripieri, 2011; Schock et al., 2016). Women undergo gradual changes in hormone levels during pregnancy and equally large but rapid changes at birth. Sex steroids (E, P, estrone, and estriol), mainly from placenta, rise to unprecedented levels—P rising the most—and fall precipitously around birth. Prl surges and stays high during breastfeeding, while OT is promptly released from the posterior pituitary upon nipple stimulation. T rises modestly during pregnancy, and HPA axis activation in labor and postpartum may support alertness and attentiveness (Almanza-Sepulveda et al., 2020). At least 700 genes are preferentially expressed in the postpartum mouse brain, including "potential new key players in the maternal brain" relevant to reward, bonding, addiction, depression, pathways for Prl, OT, AVP, E, P, endogenous opioids, and adult developmental plasticity (Gammie et al., 2016:13). Paternal care too is associated with hormone changes (Feldman et al., 2019; Rilling & Mascaro, 2017). Three to five % of mammal species have biparental care, as do about 14% of primate species, and males live longer in those species (Allman et al., 1998); marmosets and tamarins (Callitrichidae) are examples. Males paired with pregnant females and then doing paternal care in marmosets and humans show increased OT and declining T, correlated with quality and quantity of care; intranasal OT (INOT) enhances fathering (Rilling & Mascaro, 2017). Nulliparous women receiving INOT had greater interest in a "baby schema," activated by particular brain regions, if they had higher T (Holtfrerich et al., 2018). The physiology of alloparental care is under study (Konner, 2018; Rosenbaum & Gettler, 2018).

Neural Circuits and Neurotransmitters

These hormonal changes influence neural circuits in rodents and humans (Bridges, 2020; Feldman et al., 2019; Rilling & Mascaro, 2017). In the rat, maternal behavior centers on the medial preoptic area (MPOA) of the hypothalamus (Numan & Young, 2016; Rilling & Young, 2014). E and P sensitize the MPOA to OT and Prl, while MPOA projections activate OT neurons in the paraventricular nucleus (PVN) and dopamine (DA) neurons in the ventral tegmental area (VTA). The latter project to and release DA in the nucleus accumbens (NAcc), making caregiving rewarding. NAcc disinhibits the ventral pallidum (VP), a processor of emotional behavior, initiating stimulation of the cortex and midbrain movement centers. In parallel, the circuit promotes secretion of Prl from the anterior, and OT from the posterior, pituitary. The system ensures reinforcement of the large part of maternal behavior that is not innate. Imaging implicates similar circuits in humans, with a greater role for cortical systems (Rilling & Mascaro, 2017; Rilling & Young, 2014). The VTA, NAcc, and orbitofrontal cortex (OFC) are activated, proportionate to parental involvement, when mothers or fathers view videos of their children. Infant crying also activates the anterior insula, a visceral cortex vital to empathy—a "gut feeling" in the caregiver. Thus human parenting recruits DA and cortical circuits of empathy:

One . . . is the mirror neuron system, in which the superior temporal sulcus (STS) visually processes face and body movements of others and conveys that

information to the mirror neurons . . . A second system, which includes the anterior insula and the anterior cingulate cortex, helps in simulating internal feeling states of others. A third . . . includes the dorsomedial prefrontal cortex and the temporo-parietal junction . . . involved in understanding the thoughts and beliefs of others. (Rilling & Mascaro, 2017:28)

Studies led by Morten Kringelbach confirm the Kindenschema ("cuteness") pattern identified by Lorenz as key to human responses to infants (Kringelbach et al., 2016; Parsons et al., 2017), tracing "a specific and rapid neural signature for parental instinct" (Kringelbach et al., 2008; Young et al., 2016), including OFC in a network cued to infant faces and voices. "Cortical areas of the 'parental brain' overlap with those of the 'social brain'.... Subcortical (amygdala) and cortical ... regions of the temporal lobe are recruited in the initial processing of affect in the voice. while occipital and temporal regions (including the fusiform gyrus)" perceive facial expressions. These regions then "project to frontal regions" for "higher-order processing" (Young et al., 2017:107). Ancient subcortical areas, including the amygdala, periaqueductal gray (PAG), and VTA, are recruited. Exquisitely time-sensitive studies with magnetoencephalography (MEG) suggest that "specialised processing of infant cues originates in the brainstem, rapidly propagating to sensory cortical regions and the OFC" affecting "sensory processing in temporal lobe regions and preparatory motor responses in cortical motor regions. Within this 'parental brain' network . . . the PAG may act as a rapid route for engaging broader cortical circuitry" and "adaptive physiological responses. The OFC may then perform more refined 'salience detection'. . . . Infant cues provide privileged access to neural mechanisms that ignite motivational states across the whole brain" (Young et al., 2017:108).

Elicitors and Releasers

Both the Kindenschema and infant crying promptly activate specific adult brain circuits initiating care. Human young, like other mammals and birds, have a typical shape: short limbs, large head, flat face, and a relatively large upper face and eyes. With small size and awkwardness, these features release the "cute" response (Lorenz, 1971b:155). It works across species, in children as well as adults (Borgi et al., 2014); Mickey Mouse, first drawn with a rat-like face, increasingly conformed to the Kindenschema and then exaggerated it to a supernormal stimulus (Gould, 1979). Growth dissolves "cuteness," reducing the child's power. But in all human groups, adult smiling in greeting is an inherited coordination (FAP), recognized and responded to in kind (Eibl-Eibesfeldt, 1973, 1989). It is absent at birth but develops by 2-4 mo in all cultures (Konner, 1972, 1991), part of a suite of social adaptations called the two- or three-month revolution (Emde et al., 1976; Rochat, 2009). Social smiling is better predicted from conceptual than postnatal age in preterm infants (Anisfeld, 1982; Crow & Gowers, 1979), shows remarkable cross-cultural consistency (Gewirtz, 1965; Landau, 1977; Wormann et al., 2014), and together with mutual gaze makes parents feel their affection is finally reciprocated (Robson, 1967; Robson & Moss, 1970). It is both a *mostly* inherited coordination and a *mostly* innate releasing mechanism for parental care.

Conclusions

This paper considers Tinbergen's four levels of explanation of behavior in historical context, particularly that of Ernst Mayr's "kinds of causes," but also recent concepts such as robustness, niche construction, and developmental forms. It proposes a more detailed framework, expanding the levels to nine: phylogeny, natural selection, and genomics (ultimate causes); maturation, sensitive period effects, and routine environmental effects (intermediate causes); and hormonal and metabolic processes, neural circuitry, and eliciting stimuli (proximate causes). The proposed classification integrates and supports Tinbergen's multilevel model, while including those of Mayr, Huxley, and others. It also validates and extends Mayr's ultimate/ proximate continuum, adding intermediate causes, in keeping with Tinbergen's emphasis on ontogeny. It requires no modification of Standard Evolutionary Theory or The Modern Synthesis, but expands on much that critics claim was missingnotably, reciprocal causation in ontogeny, developmental form, niche construction (previously known as the Baldwin effect), cultural evolution, and multilevel selection. This framework for the causes of behavior is offered as a respectful extension of Tinbergen's. His vision, articulated about halfway through the history of the field he helped create, has been realized on a grand scale and in countless empirical confirmations, both in the wide array of species that classical ethology was concerned with and in human behavior, which Tinbergen also hoped to explain. The revival and expansion of Neo-Darwinian theory, including sexual and kin selection (inclusive fitness), have made natural selection (Tinbergen's "survival value") more central than ever as the crucial, generative logico-deductive theory within broader frameworks of evolution, and in the different task addressed here, of explaining behavior at all levels of causation. All nine levels are biological, since all entail or result from external causes affecting a biological substrate, whether ultimate (evolutionary), intermediate (ontogenetic), or proximate (mechanistic). When Jane Lancaster founded this journal three decades ago, the title she chose was bold, and the concept is still controversial. But when human behavior is considered in a comprehensive framework against the spectrum of nonhuman species-specific behavior, human nature is readily seen to be real. Ethology is truly now, in the broad sense Tinbergen hoped for, "the biology of behavior," including our own. As such it vindicates, defines, and gives life to the concept of human nature.

Deringer

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Melvin (Mel) Konner is the Samuel Candler Dobbs Professor and teaches anthropology and behavioral biology at Emory University. He went to Brooklyn College (CUNY), and his PhD and MD are from Harvard, where he also taught. He did field research for two years among Ju/'hoansi (!Kung) San (Bushman) hunter-gatherers of the Kalahari in northwestern Botswana. He has also worked in India (teaching Tibetan Buddhist monks and nuns) and the Middle East. His books include *The Tangled Wing: Biological Constraints on the Human Spirit; Becoming a Doctor; Why the Reckless Survive, and Other Secrets of Human Nature; The Evolution of Childhood: Relationships, Emotion, Mind; Women After All: Sex, Evolution, and the End of Male Supremacy; and Believers: Faith in Human Nature. He is a co-author of <i>The Paleolithic Prescription*, an early book about the so-called Paleo diet. He has also written for *Nature, Science, The New England Journal of Medicine, Child Development, The New York Review of Books, The New York Times, Newsweek, The Wall Street Journal,* and other publications. He has testified twice at U.S. Senate hearings related to health care. He is a Fellow of the American Association for the Advancement of Science and a Member of the American Academy of Arts and Sciences. Find him at http://www.melvinkonner.com and on Twitter, @TangledWing.

Authors and Affiliations

Melvin Konner¹

- Melvin Konner antmk@emory.edu
- ¹ Department of Anthropology and Program in Neuroscience and Behavioral Biology, Emory University, Atlanta, GA, USA