

# Evolutionary Psychology and Evolutionary Anthropology

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# 1 **Introduction**

2           Evolutionary psychology (EP) is a paradigm, not a discipline, and from its inception, has  
3 both drawn on, and influenced, practitioners in a variety of academic fields. Many chapters in  
4 this volume testify to the contributions evolutionary anthropology (EA) has made to EP. Here,  
5 rather than catalogue past interplays, we underscore the positive affordances of EA for the  
6 practice of EP and vice versa.

7           The student of EP interested in learning what EA has to offer encounters an assortment of  
8 approaches and findings, including:

- 9       • The biology and behavior of extinct hominids, and their relationship to the origins of H.  
10       sapiens
- 11       • The study of extinct primates and their relationships to contemporary species
- 12       • The evolution of technology, both in prior hominids and in humans
- 13       • Human biology and the biology of extant primates
- 14       • The study of behavior, cognition, and affect in other species as a window onto the  
15       evolution of analogous or homologous human capabilities
- 16       • Human evolution and population history through the lens of genetics
- 17       • Behavior, mind, reproduction, and health in extant societies, importantly including small-  
18       scale societies

19       Given the range of topics addressed by EA, we cannot provide a full accounting of the interface,  
20 or potential for interface, with EP within a single chapter. We ourselves work on but a small  
21 subset of these topics, limiting our ability to comment on the full scope of EA. We will instead  
22 focus on what we consider some of the most exciting and promising areas in this regard, an  
23 accounting that overtly reflects our own interests. Seeking to outline opportunities to advance

24 the study of human behavior, we present examples of how some existing approaches are  
25 challenged by the intersection of the EP perspective and the knowledge base and methods of EA.

26

### 27 **Some lessons from paleoanthropology**

28 We begin with the study of hominid evolution through fossil remains and archeological  
29 materials. While specific paleoanthropological discoveries will often be relevant to particular EP  
30 enterprises, for the purposes of advancing EP in general, several overarching implications  
31 transcend such specifics.

32 Skeletal features are well preserved in the fossil record, and skeletal adaptations present  
33 ideal case studies of the transformation of traits that is the hallmark of natural selection. For  
34 example, paleoanthropologists have documented in detail the modifications of the hip, pelvis,  
35 knee, and spine that occurred in the course of the evolution of bipedality (e.g., Lovejoy, 2005).  
36 Our species' particular form of locomotion may raise discrete questions for the evolutionary  
37 psychologist, such as, for example, the correspondence between the frequency of oscillation that  
38 infants find soothing (Vrugt & Pederson, 1973) and the cadence of human walking (MacDougall  
39 & Moore, 2005); the absence of motion sickness in young infants (Gordon & Shupak, 1999),  
40 who must be carried; and the nature of locomotory experience required for the development of  
41 visual cliff responses in infants (Witherington et al., 2005). However, as interesting as such  
42 topics may be for the specialist, they hinge only on the fact that humans are bipedal, and do not  
43 depend on the specifics of how bipedality evolved. In contrast, the latter is relevant for all  
44 evolutionary psychologists, be they interested in locomotion or not, because it reveals the  
45 importance of path dependence in natural selection, the kludgy nature of the adaptations that  
46 natural selection constructs, and the conflicts that can arise between multiple adaptations, along

47 with the higher-order adaptations that can evolve as a consequence. For example, the S-curve in  
48 the human spine reflects the determinative influence of the original function of the spine as a  
49 suspensory beam in a quadrupedal mammal, in contrast to its current function as a load-bearing  
50 pillar: whereas the original design functioned efficiently in a horizontal position, the transition to  
51 bipedality required the introduction of bends in the spine to position weight over the pelvis  
52 (Lovejoy, 2005). The resulting configuration makes humans prone to lower-back injury,  
53 illustrating how path dependence can both set the stage for kludgy designs and constrain their  
54 optimality. Moreover, the combination of bipedality and pressures favoring large brain size in  
55 humans exacerbates a conflict between the biomechanics of locomotion (favoring a narrow  
56 pelvis) and the need to accommodate a large infant skull during parturition. This increases the  
57 importance of higher-order adaptations such as relaxin, a hormone that loosens ligaments during  
58 pregnancy, allowing the pelvic bones to separate.

59         The take-home lesson is not that understanding the human mind starts with understanding  
60 our mode of locomotion, but rather that the evolution of bipedality, a well-documented  
61 progression, reveals i) the importance of phylogenetic history in understanding extant traits; ii)  
62 the jury-rigged nature of many adaptations; iii) the degree to which optimality can be  
63 constrained; iv) the fact that most adaptations are not isolated responses to discrete challenges,  
64 but rather the confluence of numerous evolutionary trends (opposing and synergistic), many of  
65 which are independent of ultimate function; v) the importance of phylogenetically-appropriate  
66 comparative studies; and vi) the manner in which adaptations can spawn higher-order  
67 adaptations. Though none of these observations are new to EP, in practice they are frequently  
68 overlooked, as evolutionary psychologists often adopt optimality assumptions, focusing on  
69 selective pressures that pertain to the postulated ultimate function of the trait to the exclusion of

70 constraints and affordances that play a strong role in shaping its final form. Relative to  
71 evolutionary anthropologists (see, for example, Nunn, 2011), scholars from other disciplines who  
72 employ the EP paradigm are also more prone to either underestimate the importance of  
73 comparative studies, or employ comparative evidence distant from the human phylogenetic tree  
74 that (at best) reflects analogies rather homologies. This is illustrated by the fact that, particularly  
75 in the U.S., EP and comparative psychology proper remain, in practice but not in principle,  
76 distinct in both disciplinary and conceptual senses. Inattention to the points mentioned above  
77 unnecessarily limits the scope, richness, and complexity of inquiry into evolved psychology.

78

79 *Applying phylogenetic and comparative perspectives to emotions*

80       Emotions provide one opportunity to apply to the study of mind the phylogenetic and  
81 comparative perspectives that are central to paleoanthropology in particular and EA in general  
82 (Fessler & Gervais, 2010). For example, ethological, cross-cultural, and cross-species analyses  
83 suggest that the uniquely human emotions *shame* and *pride* are derived from ancestral pan-  
84 primate emotions that regulate dominance and subordination in hierarchical interactions  
85 (Weisfeld, 1999; Fessler, 1999; Fessler, 2007). Moreover, the co-existence of both the ancestral  
86 and the derived forms of these emotions in contemporary humans reveals the importance of  
87 serial homology in the study of mind, the process whereby traits are duplicated, with both the  
88 duplicate and the original retained in the same organism, and one or both then available for  
89 cooptation into a derived trait (Clark, 2010a; Clark, 2010b). The need for such biologically-  
90 informed phylogenetic analyses of psychological adaptations is further illustrated by the case of  
91 *disgust*. Disgust has multiple forms, operating in such distinct domains as pathogen avoidance,  
92 sexuality, and morality (cf. Haidt, McCauley, & Rozin, 1994; Fessler & Navarrete, 2003; Tybur

93 et al., 2013). Although progress has been made in understanding how, over the course of human  
94 evolution, a single emotion came to address such diverse adaptive challenges (see, for example,  
95 Kelly, 2011), nevertheless, much remains to be done. Also of relevance here, one form of  
96 disgust, pathogen disgust, functions in part as a third-order adaptation, as disease-avoidance  
97 responses are up-regulated in a manner that compensates for the increases in vulnerability to  
98 pathogens that accompany pregnancy and preparation for implantation – changes that are  
99 themselves a second-order adaptation addressing the conflict between maternal immune defenses  
100 and the parasitic behavior of the half-foreign conceptus (Fessler, Eng, & Navarrete, 2005; Jones  
101 et al., 2005; Fleischman & Fessler, 2011). In sum, the model provided by paleoanthropologists’  
102 studies of morphological evolution provides a rich source of insights regarding analogous aspects  
103 of psychological evolution.

104

### 105 **Understanding EEAs**

106 By its nature, paleoanthropology is concerned with the relationship between particular  
107 traits evident in a given species and particular features of the environment. Although  
108 paleoanthropologists (and evolutionary biologists more broadly) productively explore such  
109 relationships without employing the concept of the environment of evolutionary adaptedness  
110 (EEA), this notion is not inherently inconsistent with said enterprise. Evolutionary psychologists  
111 who have advanced the concept of the EEA have been careful to stress that it is not a particular  
112 time or place, but rather a set of selective pressures relevant to explaining a given trait (Tooby &  
113 Cosmides, 1990; Symons, 1995). This articulates well with paleoanthropology given the role the  
114 latter can play in reconstructing the EEA for a given human trait. Notably, despite the  
115 aforementioned efforts by promoters of the EEA concept, there is a strong temptation for

116 evolutionary psychologists to conceptualize it as a unified set of circumstances. Consider, for  
117 example, how Kanazawa introduces the concept: “This environment – African savanna where  
118 humans lived in small bands of fifty or so related individuals as hunter-gatherers – is called the  
119 environment of evolutionary adaptedness (EEA),” (2004, p.42). Such reification is a critical  
120 error, as, far from being unified, there are actually many EEAs, depending upon which trait is at  
121 issue (Buss et al., 1998). For example, periovulatory reductions in caloric intake, arguably the  
122 product of an adaptive mechanism that solves the time-allocation conflict between foraging and  
123 mate-seeking in favor of the latter, are found across a wide range of mammals, including humans  
124 (Fessler, 2003). The key features of the EEA for this adaptation are the combination of food  
125 resources that require time and attention to procure and a social/spatial distribution of  
126 prospective mates wherein finding and attracting a valuable partner requires time and attention.  
127 These features occur in the environments of many mammals, likely including a long succession  
128 of hominid species. Hence, while humans’ hunting and gathering on the African savanna during  
129 the Middle Paleolithic maintained the EEA for this trait, it by no means uniquely defined it.

130

### 131 *Reconstructing the EEA for disgust – the question of time depth*

132 A careful reading of the EA literature is often fundamental to the proper reconstruction of  
133 the EEA for a given trait, a goal that, in turn, influences assessments of both function and  
134 phylogeny. Consider again the case of disgust. Disgust was clearly originally focused on the  
135 mouth, as oral incorporation of contaminated matter is a primary disgust elicitor, and both oral  
136 rejection and nausea/emesis remain characteristic responses to a broad range of elicitors, whether  
137 ingestible or not (Rozin & Fallon, 1987). Seeking to explain how an emotion so centered on oral  
138 incorporation has as one of its principal domains of operation the avoidance of contact – oral or

139 otherwise – with cues of the presence of pathogens, Kelly (2011) posits that meat-eating played a  
140 central role in the evolution of disgust. Building on prior work on the ultimate functions of  
141 dietary preferences and avoidances, Kelly reasons that, while a rich source of nourishment, meat  
142 is also a primary source of pathogens. He argues that two separate mechanisms, one regulating  
143 oral incorporation, the other focused on cues of the presence of other pathogens (e.g.,  
144 ectoparasites, etc.), became “entangled,” meaning that they fused into a single adaptation in  
145 humans. This occurred, Kelly asserts, because our ancestors adopted meat-eating too quickly for  
146 more conventional physiological defenses to evolve in time. While the centrality of meat-eating  
147 in Kelly’s explanation is both cogent and consonant with other evidence regarding the unique  
148 salience that meat holds for humans as both a resource and a threat, nevertheless, his account  
149 runs afoul of a realistic reconstruction of the EEA for the postulated adaptation.

150 Paleoanthropology provides abundant evidence that meat-eating evolved over a period of at least  
151 3 million years (McPherron et al., 2010), hence Kelly’s need-for-speed explanation cannot be  
152 correct – the EEA for this trait was not merely human meat consumption, but rather meat  
153 consumption practiced by a succession of hominid species (Clark & Fessler, n.d.). This matters  
154 because if we abandon this aspect of Kelly’s account, we must direct our attention to other facets  
155 of the EEA for this trait, prominent among which are the longstanding sociality of hominids and  
156 the corresponding progressive increases in encephalization, a feature that reduces the costs of  
157 brain-based (i.e., psychological) adaptations relative to physiological adaptations (Clark &  
158 Fessler, n.d.) – a pattern of likely importance in explaining many aspects of human evolved  
159 psychology.

160

161 *The importance of contemporary small-scale societies in EEA reconstruction*



162           As the above case illustrates, paleoanthropology provides vital time depth in the  
163 reconstruction of EEAs. Nevertheless, the richness of the portraits of the past that  
164 paleoanthropology can provide is necessarily limited given that past behavior cannot be  
165 observed, but rather must be inferred. Paleoanthropology thus provides one of two pillars  
166 needed to operationalize the concept of the EEA for many features of mind, the second being  
167 anthropologists' observations of contemporary small-scale societies that provide points of  
168 reference with which to approximate ancestral humans' ecological and social conditions.  
169 Traditionally, the study of small-scale societies was the heart and soul of anthropology, with  
170 cultural anthropologists playing the central role. Over the course of the last four decades,  
171 cultural anthropologists have increasingly focused on large societies, while sometimes also  
172 eschewing the objective methods – and scientific objectives – most likely to produce findings of  
173 relevance to EP. However, even as cultural anthropology has retreated some from the  
174 investigation of small-scale societies, evolutionary anthropologists have increasingly taken such  
175 groups as their central objects of study. Anthropologists – evolutionary or otherwise – thus  
176 generate a rich corpus of material offering many positive affordances for EP. When exploring a  
177 particular EP hypothesis, operationalizing the concept of the EEA can be greatly enhanced  
178 through the use of observations of life in small-scale societies in general, and extant hunter-  
179 gatherer groups in particular. The importance of this is illustrated by two topics of extensive  
180 debate in the current literature, (1) the evolution of cooperation, and (2) the relationship between  
181 disease avoidance and social attitudes.

182

183 **Case study: The evolution of cooperation**

184 First, viewed in comparison with the vast majority of other species, humans are  
185 remarkable for the degree to which they cooperate in large groups of unrelated individuals, a  
186 feature that must play a central role in explaining human history (Chudek & Henrich, this  
187 volume; Norenzyan, this volume). Considerable disagreement surrounds the processes whereby  
188 the capacity for such cooperation arose, with postulated positions ranging from various forms of  
189 biological group selection (e.g., Sober & Wilson, 1999; Wilson, 2012), to combinations of  
190 biological and cultural group selection (e.g., Bowles, 2006), to gene-culture coevolution (e.g.,  
191 Boyd & Richerson, 2009; Chudek, Zhao, & Henrich, 2013), to the scaling up of mechanisms and  
192 processes operating in dyadic interactions due to evolutionarily novel increases in the scope of  
193 social life in contemporary societies (e.g., Burnham & Johnson, 2005; Hagen & Hammerstein,  
194 2006). Recent work synthesizing diverse studies of extant hunter-gatherers indicates that such  
195 societies characteristically involve co-residence among many unrelated individuals (Hill et al.,  
196 2011) combined with high rates of contact with members of other bands (Hill et al., 2014) –  
197 including ephemeral interactions (Chudek et al., 2013). Taken together, the resulting portrait of  
198 the likely social dimensions of the EEA calls into question the thesis that the evolved  
199 psychological mechanisms governing human cooperation at larger scales derive principally from  
200 kin selection and reciprocal altruism, as such a position is more consistent with an EEA  
201 characterized by high degrees of relatedness within groups, more restrictive social networks, and  
202 a paucity of short-term interactions (reviewed in Brown & Richerson, 2014).

203

#### 204 **Case study: The Parasite-Stress Theory**

205 Second, findings from EA underscore the importance of the extensive variation in  
206 ecologies and social structures likely characteristic of our species throughout its history and

207 beyond (Foley, 1995). It is vital to understand that, for many traits of interest, the relevant  
208 features of the environment have been variable. This is because, depending on the nature of that  
209 variation, it is likely that one of two classes of adaptations will have evolved, namely either i)  
210 adaptations that facultatively adjust their output in light of local environmental cues, or ii)  
211 adaptations for cultural acquisition. Illustrating this, one rapidly-expanding area of research  
212 concerns the relationship between pathogen prevalence and social attitudes. In a series of  
213 influential papers, Fincher, Thornhill, Schaller, Murray, and colleagues have argued that  
214 pathogen prevalence predicts the extent of individualism versus collectivism (Fincher et al.,  
215 2008) and conformism (Murray, Trudeau, & Schaller, 2011) across cultures; ingroup homophily  
216 and outgroup avoidance (Fincher & Thornhill, 2012) and resulting speciation in cultural  
217 evolution (Fincher & Thornhill, 2008); cross-national differences in personality (Schaller &  
218 Murray, 2008; Thornhill et al., 2010); and a wide range of related social phenomena (Thornhill  
219 & Fincher, 2014). The core thesis, termed the parasite-stress theory (PST), holds that the mind  
220 contains adaptations that regulate social behavior to optimize disease avoidance (see Schaller,  
221 this volume). The PST then argues that, in the relevant EEA, members of outgroups constituted  
222 a key source of unfamiliar – and thus dangerous – pathogens. However, the extent of the threat  
223 posed by pathogens varied across the ecologies inhabited by ancestral populations. As a  
224 consequence, selection produced psychological mechanisms that adjust the degree to which  
225 individuals preferentially assort with members of the ingroup, and avoid and are hostile to  
226 members of the outgroup, as a function of cues indicative of the density and virulence of  
227 socially-transmitted pathogens in the local ecology. Aggregated across the members of a  
228 society, the outputs of these mechanisms then produce a wide variety of socio-cultural  
229 concomitants, including phenomena as diverse as political orientation and religiosity.

230           The PST elegantly deploys the notion of adaptations that, by virtue of having ecological  
231 variation as a central feature of the relevant EEA, incorporate facultative adjustment to local  
232 circumstances. While the authors are to be applauded for their sophisticated thesis, and while  
233 their rapidly-growing corpus of findings demonstrates that there are important phenomena to be  
234 explained here, when examined in terms of a more complete reconstruction of the EEA for the  
235 postulated adaptation, there are many reasons to doubt the theory, at least in its strictest form.

236           First, the PST assumes an EEA for the proposed mechanism in which 1) interactions  
237 between neighboring groups were rare, and 2) such groups were sufficiently geographically and  
238 ecological disparate as to allow distinct pathogens to evolve independently in each group, such  
239 that, upon contact, members of one group would lack a history of prior exposure – and thus  
240 immunity – to the given strain. As discussed above, studies of extant hunter-gatherers indicate  
241 high rates of contact between bands. The PST concerns relations between groups that possess  
242 distinct, bounded cultural identities (termed *ethnies* in anthropology); as such, at first glance,  
243 inter-band interactions might seem irrelevant, as, in most cases, the two bands will belong to the  
244 same ethnies. However, from an epidemiological perspective, frequent inter-band contact unites  
245 all members of a given hunter-gatherer ethnies into a single group, as infectious disease  
246 contracted by members of one band will rapidly spread to other bands. The archeological record  
247 provides extensive evidence of long-distance trade during the Paleolithic (see Blades, 2001;  
248 Chalmin et al., 2007; d’Errico et al., 2009), indicating that both intra-ethnies and inter-ethnies  
249 contact occurred with some frequency. Viewed with regard to the interests of the various  
250 members of a group, the costs and benefits of inter-group contact are unevenly distributed.  
251 Individuals who elect to interact with members of another group (be they of the same ethnies or a  
252 different one) stand to reap the benefits of trade, as well as expanded access to territorial

253 resources, mating opportunities, knowledge transfer, etc. Such individuals are also at risk of  
254 both disease transfer and aggression or exploitation. Notably, while both the benefits of inter-  
255 group interaction and the risks of aggression and exploitation are primarily limited to those  
256 individuals who elect to interact with outsiders, the same is not true of the risk of disease  
257 transfer. In a world with minimal hygiene, little knowledge of disease transmission, extensive  
258 food-sharing, and intimate physical proximity, if one individual in a band contracts a  
259 transmissible illness, all members of the band become exposed; and, if bands interact regularly  
260 and band composition is fluid, then the same holds true for the entire ethnies. This creates an  
261 evolutionarily unsustainable dynamic from the perspective of the PST. For highly transmissible  
262 diseases (precisely the type assumed by the PST), if individual A interacts with outgroups and  
263 thereby both reaps fitness gains and suffers pathogen-inflicted costs, while individual B avoids  
264 outgroups but suffers the same pathogen-inflicted costs due to intra-group disease transmission  
265 from A, then A's fitness will be higher than B's fitness. Thus, following the dictum that  
266 reconstructions of the EEA for a given trait should leverage the findings of EA regarding present  
267 and past behavior, it appears that the portrait of the world of our ancestors that can be compiled  
268 using ethnographic and archeological sources is inconsistent with that EEA required for the  
269 evolution of an adaptation that would facultatively adjust attitudes toward ingroups and  
270 outgroups as a function of pathogen prevalence.

271           Reconstructions of EEAs should employ all relevant material. Historical and  
272 archeological evidence indicates that infectious disease decimated the New World in the initial  
273 stages of colonialism. Does this speak to the EEA required by the PST? No. Extensive direct  
274 contact between previously widely separated groups only occurred following the evolutionarily  
275 recent development of transoceanic sailing technology. Paleolithic pedestrian hunter-gatherer

276 groups, inhabiting similar ecologies to those of their neighbors and linked to them through trade,  
277 would have co-evolved with endemic pathogens, precluding the devastation recorded during  
278 historical times (R. Thornton, personal communication). Indeed, in many areas, the  
279 depopulation of Native American tribes due to European diseases is thought to have predated  
280 direct contact with Europeans (Thornton, Miller, & Warren, 1991), revealing the population-  
281 level networks that preclude both substantial intergroup variation in pathogen types and the  
282 utility of ethnocentrism and xenophobia as prophylactic measures.

283         Many evolutionary psychologists assume that the human mind has changed little since  
284 the Paleolithic (e.g, Tooby & Cosmides, 1989). While this is a reasonable heuristic, a heuristic is  
285 not an inviolate rule, and EA presents evidence of rapid genetic evolution since the  
286 domestication of plants and animals (Hawks et al., 2007), including genes relevant to pathogen  
287 defense (see Laland, Odling-Smee, & Myles, 2010). Might life in the Neolithic therefore fit the  
288 PST's requirements for an EEA? On the one hand, agriculture, animal domestication, and  
289 increases in population density led to new diseases and large-scale epidemics (Barrett et al.,  
290 1998), while network size probably shrank due to lesser reliance on far-flung partners for risk  
291 management. However, trade increased dramatically (e.g., Hirth, 1978; Robb & Farr, 2005;  
292 Bradley & Edmonds, 2005). Combined with the greater transmissibility and virulence  
293 characteristic of pathogens that evolve to exploit high-density hosts (Ewald, 1994), the elevation  
294 of trade – and the increase in the profits to be reaped thereby – would have enhanced the fitness  
295 advantages of those who interacted with outgroups relative to those who eschewed doing so.  
296 Hence, while we encourage investigators to entertain the possibility of relatively recent EEAs for  
297 some traits, in this case, neither the Paleolithic nor the Neolithic provide the requisite features of  
298 an EEA for the adaptation postulated by the PST.

299 Earlier, we stressed the importance of comparative and phylogenetic analyses.  
300 Commendably, PST advocates have sought to employ these more than is typical in EP, arguing  
301 that the requisite social and epidemiological dynamics have precursors in other animals.  
302 However, here too, details matter. We noted previously that, when evaluating comparative  
303 evidence, investigators must take phylogenetic distance into consideration. Many of the species  
304 cited by proponents of the PST are phylogenetically removed from humans, making parallels  
305 explicable in terms of analogy rather than homology. While analogies can illuminate the  
306 possibility space of adaptations, they do not aid in reconstructing the history of a postulated trait.  
307 PST advocates do note possible precursors in primates, citing Freeland (e.g., 1976), who  
308 provided initial evidence concerning the possible effects of pathogens on primate behavior and  
309 group structure. However, Freeland's hypothesis has not been tested, and the evidence is  
310 equivocal. The closest primate correlate of xenophobia and ethnocentrism is territoriality, yet  
311 territoriality appears to primarily function to protect resources rather than avoid disease, and can  
312 actually *increase* pathogen stress (see Nunn & Altizer, 2006).

313 How then can we account for the evidence amassed by proponents of the PST, which  
314 almost certainly reflects an important pattern of cultural differences? These correlations may  
315 reflect factors unrelated to the postulated adaptation, such as the effectiveness of government  
316 institutions (Hruschka & Henrich, 2013b), and the broad impact of differing life history  
317 trajectories (Hackman & Hruschka, 2013b). Research and debate continues (see Hruschka &  
318 Henrich, 2013a; Hackman & Hruschka, 2013a; Cashdan & Steele, 2013; Thornhill & Fincher,  
319 2014; van Leeuwen et al., in press; Pollet et al., in press), hence the jury is still out on these  
320 questions. However, one possibility neglected in these debates is that the correlations at issue

321 may reflect the interaction of individual-level evolved disease-avoidance adaptations and group-  
322 level cultural evolution.

323

### 324 **Evolved psychology and cultural evolution**

325         In addition to our remarkable cooperativeness, humans are unique in our reliance on  
326 socially-transmitted information in addressing adaptive challenges. While a variety of  
327 adaptations likely undergird this capacity, one class in particular is relevant here. Whenever a  
328 critical challenge is present in all environments historically inhabited by humans, but differs in  
329 key attributes across environments, we can expect natural selection to have crafted domain-  
330 specific culture-acquisition mechanisms (Fessler, 2006; Fessler & Machery, 2012). Consider,  
331 for example, Barrett’s work (this volume) concerning dangerous animals. All environments  
332 occupied by humans contain dangerous animals. Some features, such as a sinuous legless body,  
333 prominent teeth, or large size reliably predict the hazard posed by an animal in most  
334 environments, hence natural selection can build sensitivity to such cues into mechanisms that  
335 address this challenge. However, many dangerous animals lack these features (e.g., scorpions).  
336 Cultural evolution involves the cumulative accretion and refinement of locally-relevant  
337 information (Chudek & Henrich, this volume). Dangerous animals pose an important threat,  
338 hence all cultures can be relied upon to contain information about avoiding or addressing  
339 endemic dangerous species. Natural selection has exploited this reliable feature of culture by  
340 crafting mechanisms that motivate and support early, rapid acquisition of cultural information  
341 regarding dangerous animals. Importantly, for the same reasons, selection can be expected to  
342 have crafted culture-acquisition mechanisms in many other domains as well. Hence, paralleling  
343 Barrett’s work, similar considerations apply to the question of disease avoidance.



344 *Evolved psychology and cultural evolution: The case of disease avoidance*

345           Disgust and related disease-avoidance motivators play a prominent role in some PST  
346 work. These responses are elicited by two distinct classes of stimuli. First, disgust is evoked by  
347 cues that, across all ecologies, have uniformly been associated with the presence of pathogens:  
348 feces, vomit, odors of putrefaction, etc. are reliable indices of disease risk, and thus appear to be  
349 either hardwired, or privileged with regard to learning (Curtis & Biran, 2001). Second, disgust is  
350 also evoked by information the meaning of which is entirely cultural in origin: for example,  
351 whether decayed or fermented items are viewed as disgusting or delectable depends in part on  
352 cultural framing (Rozin & Fallon, 1987); the same is true of the perceived disease risk of  
353 drinking untreated water, having unprotected sex, and so on. This is understandable given the  
354 parochial nature of some avenues for disease transmission, and the inventive countermeasures  
355 that cultures devise using locally-available technologies. Evolved human disease-avoidance  
356 mechanisms thus contain an important culture-acquisition component. Though functional in  
357 many instances, this feature also creates an opportunity for cultural evolution to hijack this  
358 system for other purposes.

359           While paralleling biological evolution in a number of respects, cultural evolution  
360 importantly differs in that it does not necessarily maximize individual fitness, instead operating  
361 to maximize the spread of a given set of ideas, often by increasing the size of a corresponding  
362 culture-bearing group; this process is sometimes parallel to, and sometimes orthogonal to (or  
363 even opposed to), individual fitness maximization (see Chudek & Henrich, this volume).  
364 Relations with other groups are often a central determinant of the size of a cultural group: *ceteris*  
365 *paribus*, belief systems that motivate their holders to direct their cooperative efforts toward  
366 ingroup members, and their exploitative efforts toward outgroup members, will outcompete

367 belief systems that are less ethnocentric in this regard (Bowles & Gintis, 2011, Ch. 8).  
368 Behavioral avoidance and a desire to expel targeted individuals are adaptive responses to  
369 individuals posing a risk of disease transmission. Cultural evolution can therefore achieve  
370 group-functional (but possibly individually costly) ingroup favoritism and outgroup hostility by  
371 depicting outgroup members as posing a disease risk (witness outgroup derogations such as  
372 ‘cockroaches,’ ‘rats,’ ‘scum,’ or ‘vermin’).

373         Earlier, we stressed the importance of attending to tradeoffs. Disease avoidance is not  
374 free. It entails time, energy, and attention costs, and comes at the expense of dietary efficiency  
375 and social exchange. We have already seen that mechanisms governing this behavior are  
376 sensitive to changes in individual vulnerability, and the same considerations of efficiency make it  
377 likely that, as is presumed by the PST, these mechanisms are calibrated in light of the incidence  
378 of disease (see Schaller, this volume). If so, and if the upregulation of these mechanisms  
379 involves increased attention to, and importance placed on, socially-transmitted information  
380 regarding disease, then individuals occupying environments with high pathogen prevalence will  
381 be particularly vulnerable to those factually inaccurate messages concerning disease threats  
382 posed by outgroup members that promote xenophobia and ethnocentrism. In turn, this will  
383 produce the patterns of correlations documented by PST proponents. Although the correlations  
384 alone do not provide adjudicate between the original PST and our alternative formulation,  
385 experimental avenues for doing so exist. To exploit the power of cultural information in  
386 navigating adaptive challenges, individuals must be credulous, as the rationale for cultural  
387 practices is often unknown or opaque (Legare & Watson, this volume), while the costs of  
388 individual trial-and-error learning will sometimes be high, especially when the information  
389 concerns hazards (Boyd & Richerson, 2006; Boyd & Richerson, 2009). However, credulity

390 entails the risk of falling victim to both manipulative actors and, as our proposal presumes,  
391 inaccurate information (Kurzban, 2007). Accordingly, we can expect selection to have crafted  
392 mechanisms that adjust credulity in light of expected benefits and costs (Fessler, Pisor, &  
393 Navarrete, 2014). Cues of the prevalence of a given class of hazards should therefore shift the  
394 balance toward greater credulity in that domain. Specifically, our proposal predicts that  
395 individuals living in (or, perhaps, who were raised in) high-pathogen environments should evince  
396 elevated credulity toward cultural information relevant to disease avoidance. This is a testable  
397 prediction.

398         Whether our proposal is correct or not, this discussion serves to illustrate a number of  
399 important points central to the intersection of EP and EA. The first of these concerns the  
400 distinction between evoked culture and transmitted culture. Although classically defined in  
401 anthropology as information acquired through learning from one's group, the term 'culture' is  
402 often used simply to refer to behavioral and psychological features that are shared within a group  
403 but differ across groups – whether or not there is evidence that such patterns stem from socially-  
404 transmitted information. Tooby and Cosmides (1992) noted that such commonalities need not be  
405 the product of such information, but can instead result from the output of shared adaptations  
406 responding to the same environmental input, a pattern that they termed *evoked culture*, in  
407 contrast to *transmitted culture*. Hence, the PST argues that patterned differences across groups  
408 that correlate with differences in pathogen prevalence constitute evoked culture, being the  
409 aggregate of the output of each individual's biologically-evolved disease-avoidance mechanisms.  
410 In contrast, the alternative explanation that we have proposed assumes that such patterned  
411 differences constitute transmitted culture, as individuals acquire the given beliefs and attitudes  
412 by learning them from other members of their group. Note, however, that, in both models, both

413 biologically-evolved psychological adaptations and processes of cultural evolution must be  
414 adduced.

415         In the PST, psychological adaptations generate attitudes toward ingroup versus outgroup  
416 members, traditional versus novel practices, and so on, but such adaptations do not create  
417 specific beliefs or practices; rather, these must be the product of cultural evolution. Religious  
418 fundamentalism, for example, may exhibit common features the world over, and may hold  
419 particular appeal for individuals in high-pathogen environments, but the identities of the deities,  
420 the rituals performed for them, etc. must all necessarily be the product of transmitted culture –  
421 the PST seeks to explain why some beliefs are more attractive than others in a given  
422 environment, but it in no way promotes the (untenable) notion that evolved mechanisms specify  
423 the details of beliefs. Our proposal that cultural evolution promotes within-group solidarity by  
424 exploiting psychological disease-avoidance mechanisms similarly does not presume a tabula rasa  
425 mind, instead arguing that an adaptation that exists specifically for the purpose of acquiring  
426 cultural information in a particular domain can be hijacked such that it operates in ways that do  
427 not serve its ultimate function.

428         Viewed more broadly, in both proposals, psychological adaptations create attractors  
429 (Sperber, 1996) such that some ideas are more likely to be attended to, acquired, retained, and  
430 transmitted than other ideas, thereby influencing which possibilities succeed and which fail in the  
431 marketplace of ideas (see Chudek & Henrich, this volume). Thus, as this case illustrates, as  
432 tempting as it is to interpret the dichotomy between evoked and transmitted culture in terms of  
433 nature versus nurture, doing so is a grave misstep – there are likely few cases in which evoked  
434 culture alone can explain humans’ rich beliefs and practices, while even what seem the purest  
435 cases of transmitted culture will necessarily involve an underlying set of evolved adaptations.

436 Moreover, while we have argued in the above case that the relevant adaptations focus on  
437 information acquisition, the set of likely possibilities is far larger than this, as cultural evolution  
438 often exploits or bootstraps evoked preferences and ideas produced by a variety of adaptations.  
439 For example, military history reveals increasing refinement of procedures for recruitment,  
440 training, and deployment of troops, techniques that harness the evolved mechanisms that  
441 generate small-group affiliation in the service of fielding effective armies of millions (Richerson  
442 & Boyd, 1999); likewise, incest taboos and, more broadly, marriage rules (key components of  
443 the social structures of small-scale societies) extrapolate sentiments generated by evolved  
444 inbreeding-avoidance mechanisms; and so on.

445

#### 446 **Interpreting cross-cultural variation and cross-cultural uniformity**

447 Consonant with the complexity described above, neither cross-cultural variation nor  
448 cross-cultural uniformity is uniquely indicative of the processes generating observed patterns.  
449 Variation can reflect divergent pathways of cultural evolution acting in different societies, or it  
450 can reflect diverse evoked cultures produced by divergent physical or social ecologies.  
451 Uniformity can reflect uniform functioning of panhuman adaptations across different ecologies,  
452 or it can reflect convergent cultural evolution. In exploring these possibilities, the question of  
453 the relevant EEA again becomes central. Is it likely that variation in the relevant features of the  
454 environment characterized the EEA required for a postulated adaptation? If so, then selection  
455 may well have crafted mechanisms for facultative adjustment, in which case evoked culture may  
456 play a central role in cross-cultural variation. For example, due to differing ecologies and  
457 degrees of inter-group competition, the environments occupied by ancestral populations will  
458 have varied in rates of extrinsic mortality and the reliability of resources. Such variation is

459 directly linked to fitness, and therefore likely favored adaptations that calibrate future  
460 orientation, risk-taking, mating strategy, parental investment, cooperativeness, and aggression in  
461 light of local circumstances. This topic has been productively explored in EP, often by  
462 evolutionary anthropologists (see Kaplan & Gangestad, this volume; Mace, this volume). When  
463 viewed at the level of societies, the resulting evoked cultures may drive much observed variation  
464 along these and related dimensions. In contrast, the Neolithic Revolution brought about forms of  
465 social organization and related adaptive challenges that were largely unprecedented. These  
466 radical departures make it likely that corresponding axes of cultural variation reflect a greater  
467 proportion of transmitted relative to evoked culture. For example, although hunter-gatherer  
468 groups vary in the degree to which individuals must defend resources against theft, or the degree  
469 to which present labor yields returns far in the future, these considerations loom vastly larger in  
470 pastoralist versus agriculturalist societies. The correspondence between these modes of  
471 subsistence and locally-functional values and social orientations (Edgerton & Goldschmidt,  
472 1971) is therefore best explained principally in terms of cultural evolution (albeit plausibly  
473 bootstrapping evolved mechanisms). Likewise, cultural evolution likely applies in the case of  
474 adjacent regions in which people pursue either rice or wheat agriculture: these crops entail  
475 different levels of interdependence, and reliance upon each is matched by corresponding  
476 differences in social orientation (Talhelm et al., 2014). Lastly, phylogeny is again important,  
477 albeit here in terms of the histories of the cultures at issue, as cultural phylogenetic inertia  
478 (driven by the self-reinforcing nature of institutions and values) can create differences between  
479 groups that persist after the respective selective pressures have vanished (e.g., differences  
480 between formerly pastoralist and formerly agriculturalist U.S. subcultures – Nisbett & Cohen,  
481 1996).

482           As the above examples illustrate, while the complexity of the relationships between  
483 biological and cultural evolution makes the investigator's task more challenging, the range of  
484 possibilities means that there is much to explore in any area of behavior. We view all of these as  
485 within the purview of EP. At a minimum, questions of cultural variation, uniformity, and the  
486 causes thereof must always be considered given the risk that reliance on parochial samples may  
487 lead to erroneous assumptions of universality (Henrich, Heine, & Norenzayan, 2010); indeed,  
488 some of the most compelling EP research has long contained a substantial cross-cultural  
489 component (e.g., Buss, 1989). More broadly, given that we are a highly social species that is  
490 fundamentally reliant on socially-transmitted information, many processes operating outside the  
491 skull fall squarely within the mandate of EP. We are thus encouraged by ventures, such as the  
492 PST, in which non-anthropologists increasingly explore such dynamics.

493

#### 494 **The application of EP in EA**

495           Given the principal audience for this book, the above discussion focuses on how EA can  
496 enhance EP. The chapter would be incomplete, however, without considering how EP can  
497 enhance EA.

498           Central to EA research exploring gene-culture coevolution (see Chudek & Henrich, this  
499 volume) is a focus on the question of when it pays to imitate successful individuals versus  
500 imitate the majority, as the consequences of these choices ramify across diverse social  
501 phenomena. Though defined in behavioral terms, these are psychological processes, hence EP  
502 can illuminate them. Although investigators have begun to explore cues operating in such  
503 imitation (e.g., Chudek et al., 2012; Chudek & Henrich, this volume), the underlying  
504 psychological mechanisms remain largely unexplored. Earlier, we stressed the importance of

505 emotions as evolved drivers of behavior, yet the psychology of cultural imitation remains largely  
506 divorced from the psychology of affect. Likewise, we emphasized the importance of  
507 understanding adaptations as kludgy mechanisms colored by their phylogeny, yet, beyond  
508 laudable efforts to compare learning biases across humans and apes (Haun, Rekers, &  
509 Tomasello, 2012), no research addresses how the structure of learning mechanisms reflects their  
510 evolution. Lastly, the nature and ramifications of domain-specific culture-acquisition  
511 mechanisms remain largely overlooked. There are thus many ways in which EP can further  
512 gene-culture coevolutionary EA.

513         The late introduction of EP into work on gene-culture coevolution reflects the centrality  
514 of population-level models in the latter field. In contrast, EP shares with human behavioral  
515 ecology (HBE) a focus on individual behavior. However, HBE differs from EP in that it  
516 generally eschews exploration of mechanisms (psychological or otherwise) in favor of outcome  
517 measurements used to test optimality predictions. Far from engendering harmony, the shared  
518 focus on individual behavior instead witnessed acrimonious debates between proponents of HBE  
519 and advocates of EP (Smith, Borgerhoff Mulder, & Hill, 2001). Central to these was the  
520 criticism by the latter that HBE's assumption that behavior maximizes fitness – termed the  
521 behavioral gambit – is unreasonable in highly variable contemporary environments. The  
522 behavioral gambit is problematic, advocates of EP argued, given the combination of the domain-  
523 specific nature of adaptations and the slow rate of their evolution relative to the rapidity of recent  
524 socio-ecological change (i.e., the problem of evolutionary disequilibrium, or adaptive lag).  
525 Proponents of HBE, in return, criticized practitioners of EP for underestimating both the range of  
526 environmental variation characteristic of our species' history and the attendant adaptive plasticity  
527 to be expected of behavior. Advocates of EP pointed to the apparently maladaptive nature of



528 much contemporary behavior; supporters of HBE countered that fitness outcomes cannot be  
529 merely presumed. And so on.

530         While outcome measurement remains the central pillar of HBE, behavioral ecologists  
531 increasingly recognize the importance of attending to mechanisms, as i) doing so illuminates  
532 trade-offs and other constraints on optimality ignored by the behavioral gambit (Monaghan,  
533 2014), and ii) cultural evolution can account for the particular form of a local configuration (via  
534 cultural phylogeny), account for behavior that may be maladaptive at the individual level but  
535 adaptive at the group level (Brown, 2013), and, given the possibility of adaptive lag in cultural  
536 evolution itself, account for behaviors that may be maladaptive at both the individual and group  
537 levels (Mace, 2014).

538         Against the above backdrop, Nettle and colleagues (2013) recently advocated employing  
539 the behavioral gambit in HBE until it fails in a given case, and only then resorting to the  
540 examination of mechanisms. While their prescription for HBE is defensible, it unnecessarily  
541 limits the range of phenomena that HBE addresses. HBE presents polished methods and  
542 strategies for assessing real-world behavior and its somatic correlates, tools that can be  
543 productively deployed in exploring many of the challenges facing societies today.

544 Contemporary epidemics of addictions to alcohol, tobacco, and drugs of abuse, or the spread of  
545 obesity, osteoarthritis, or cardiovascular disease – to name but a few – are fitness-reducing  
546 behaviors that cry out for the careful methods of HBE. Happily, some of these same  
547 investigators are beginning to explore such problems from a decidedly EP angle (cf. Pepper &  
548 Nettle, 2014), investigating, for example, how evolutionarily novel environments present cues to  
549 evolved mechanisms that calibrate future discounting in light of mortality risk (Nettle, Coyne, &

550 Colléony, 2012). Whether explicitly acknowledged or not, HBE is thus starting to expand its  
551 scope, and its impact, by incorporating EP – a promising trend.

552

### 553 **A roadmap for the use of EA in EP**

554 Having examined ways in which EP can benefit EA, we return to the central thrust of this  
555 chapter, our effort to encourage non-anthropologists who practice EP to take advantage of EA to  
556 enhance their research. Exhortations are most effective when accompanied by roadmaps, hence  
557 we close by discussing tangible steps toward this end.

558 First, consonant with our emphasis on the importance of plausible reconstructions of  
559 EEAs, regardless of discipline, evolutionary psychologists should take full advantage of the rich  
560 literatures in paleoanthropology and comparative psychology (especially primatology), as well as  
561 the ethnographic and behavioral-ecological depictions of contemporary small-scale societies in  
562 general, and of hunter-gatherer societies in particular. Granted, some reliable assumptions about  
563 life in the worlds of our ancestors can indeed be made on the basis of casual observation alone  
564 (e.g., babies were helpless and required care; paternity could not be determined with certainty;  
565 etc.). However, in many cases, the relevant facts cannot be so readily inferred. When this  
566 applies, scientific due diligence in EP should include conscientious efforts to utilize available  
567 literatures to reconstruct the relevant EEAs and plausible phylogenies, a principle that editors  
568 and reviewers – regardless of discipline – should enforce.

569 Second, of relevance to the above, an important scholarly resource that is arguably both  
570 the most accessible to, and the most under-utilized by, evolutionary psychologists is the  
571 Electronic Human Relations Area Files (eHRAF), a collection of digitized ethnographies  
572 spanning the full range of human societies. This remarkable archive allows for comparisons not

573 only relevant to attempts to reconstruct EEAs (e.g., Wrangham & Glowacki, 2012), but, in  
574 addition, efforts to test for cultural patterns predicted to arise from postulated psychological  
575 adaptations (e.g., Fessler et al., 2014), examine hypotheses concerning large-scale phenomena  
576 (e.g., Kline & Boyd, 2010), and pursue similar goals that go far beyond questions of EEAs.

577         Third, while the eHRAF provides a valuable avenue for testing a broad range of  
578 hypotheses, because the information contained therein was collected for a wide variety of  
579 reasons, investigators will often find that there is no substitute for direct measurement of  
580 behavior. Importantly, as we hope to have conveyed, rapid, evolutionarily recent culture-based  
581 changes in lifestyle constitute both a challenge and an opportunity for the evolutionary  
582 psychologist. Small-scale societies in which state regulation of behavior is minimal, kinship and  
583 longstanding social ties are central pillars of the social structure, economic activities are  
584 intimately linked to subsistence, access to healthcare – including contraception – is limited, and  
585 life is less awash in the sea of global electronic media, provide important points of contrast for  
586 studies conducted in large-scale technologically sophisticated societies. Increasingly,  
587 evolutionary anthropologists working in small-scale societies are incorporating the EP paradigm  
588 into their work, seeking to test hypotheses – such as the facultative calibration of sexual and  
589 emotional jealousy in light of paternal investment (Buss et al., 1992) – that predict patterned  
590 differences or similarities across divergent cultures (e.g., Scelza, 2014). Often, such work is  
591 collaborative, incorporating the complementary expertise of scholars from multiple disciplines  
592 (e.g., Bryant & Barrett, 2007). Indeed, as is evident in the composition of this edition of the  
593 Handbook of Evolutionary Psychology, cross-disciplinary collaborations and exchanges are  
594 increasingly generating a fertile syncretic paradigm in the evolutionary behavioral sciences. The

595 future of the relationship between evolutionary psychology and evolutionary anthropology is  
596 thus a bright one indeed.

597

598

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