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Evolutionary Psychology and Evolutionary Anthropology

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

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

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

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

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

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

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

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

56 The take-home lesson is not that understanding the human mind starts with understanding
57 our mode of locomotion, but rather that the evolution of bipedality, a well-documented
58 progression, reveals i) the importance of phylogenetic history in understanding extant traits; ii)
59 the jury-rigged nature of many adaptations; iii) the degree to which optimality can be
60 constrained; iv) the fact that most adaptations are not isolated responses to discrete challenges,
61 but rather the confluence of numerous evolutionary trends (opposing and synergistic), many of
62 which are independent of ultimate function; v) the importance of phylogenetically-appropriate
63 comparative studies; and vi) the manner in which adaptations can spawn higher-order
64 adaptations. Though none of these observations are new to EP, in practice they are frequently
65 overlooked, as evolutionary psychologists often adopt optimality assumptions, focusing on
66 selective pressures that pertain to the postulated ultimate function of the trait to the exclusion of
67 constraints and affordances that play a strong role in shaping its final form. Relative to
68 evolutionary anthropologists (see, for example, Nunn, 2011), scholars from other disciplines who

69 employ the EP paradigm are also more prone to either underestimate the importance of
70 comparative studies, or employ comparative evidence distant from the human phylogenetic tree
71 that (at best) reflects analogies rather homologies. This is illustrated by the fact that, particularly
72 in the U.S., EP and comparative psychology proper remain, in practice but not in principle,
73 distinct in both disciplinary and conceptual senses. Inattention to the points mentioned above
74 unnecessarily limits the scope, richness, and complexity of inquiry into evolved psychology.

75 Emotions provide one opportunity to apply to the study of mind the phylogenetic and
76 comparative perspectives that are central to paleoanthropology in particular and EA in general
77 (Fessler & Gervais, 2010). For example, ethological, cross-cultural, and cross-species analyses
78 suggest that the uniquely human emotions *shame* and *pride* are derived from ancestral pan-
79 primate emotions that regulate dominance and subordination in hierarchical interactions
80 (Weisfeld, 1999; Fessler, 1999; Fessler, 2007). Moreover, the co-existence of both the ancestral
81 and the derived forms of these emotions in contemporary humans reveals the importance of
82 serial homology in the study of mind, the process whereby traits are duplicated, with both the
83 duplicate and the original retained in the same organism, and one or both then available for
84 cooptation into a derived trait (Clark, 2010a; Clark, 2010b). The need for such biologically-
85 informed phylogenetic analyses of psychological adaptations is further illustrated by the case of
86 *disgust*. Disgust has multiple forms, operating in such distinct domains as pathogen avoidance,
87 sexuality, and morality (cf. Haidt, McCauley, & Rozin, 1994; Fessler & Navarrete, 2003; Tybur
88 et al., 2013). Although progress has been made in understanding how, over the course of human
89 evolution, a single emotion came to address such diverse adaptive challenges (see, for example,
90 Kelly, 2011), nevertheless, much remains to be done. Also of relevance here, one form of
91 disgust, pathogen disgust, functions in part as a third-order adaptation, as disease-avoidance

92 responses are up-regulated in a manner that compensates for the increases in vulnerability to
93 pathogens that accompany pregnancy and preparation for implantation – changes that are
94 themselves a second-order adaptation addressing the conflict between maternal immune defenses
95 and the parasitic behavior of the half-foreign conceptus (Fessler, Eng, & Navarrete, 2005; Jones
96 et al., 2005; Fleischman & Fessler, 2011). In sum, the model provided by paleoanthropologists’
97 studies of morphological evolution provides a rich source of insights regarding analogous aspects
98 of psychological evolution.

99 By its nature, paleoanthropology is concerned with the relationship between particular
100 traits evident in a given species and particular features of the environment. Although
101 paleoanthropologists (and evolutionary biologists more broadly) productively explore such
102 relationships without employing the concept of the environment of evolutionary adaptedness
103 (EEA), this notion is not inherently inconsistent with said enterprise. Evolutionary psychologists
104 who have advanced the concept of the EEA have been careful to stress that it is not a particular
105 time or place, but rather a set of selective pressures relevant to explaining a given trait (Tooby &
106 Cosmides, 1990; Symons, 1995). This articulates well with paleoanthropology given the role the
107 latter can play in reconstructing the EEA for a given human trait. Notably, despite the
108 aforementioned efforts by promoters of the EEA concept, there is a strong temptation for
109 evolutionary psychologists to conceptualize it as a unified set of circumstances. Consider, for
110 example, how Kanazawa introduces the concept: “This environment – African savanna where
111 humans lived in small bands of fifty or so related individuals as hunter-gatherers – is called the
112 environment of evolutionary adaptedness (EEA),” (2004, p.42). Such reification is a critical
113 error, as, far from being unified, there are actually many EEAs, depending upon which trait is at
114 issue (Buss et al., 1998). For example, periovulatory reductions in caloric intake, arguably the

115 product of an adaptive mechanism that solves the time-allocation conflict between foraging and
116 mate-seeking in favor of the latter, are found across a wide range of mammals, including humans
117 (Fessler, 2003). The key features of the EEA for this adaptation are the combination of food
118 resources that require time and attention to procure and a social/spatial distribution of
119 prospective mates wherein finding and attracting a valuable partner requires time and attention.
120 These features occur in the environments of many mammals, likely including a long succession
121 of hominid species. Hence, while humans' hunting and gathering on the African savanna during
122 the Middle Paleolithic maintained the EEA for this trait, it by no means uniquely defined it.

123 A careful reading of the EA literature is often fundamental to the proper reconstruction of
124 the EEA for a given trait, a goal that, in turn, influences assessments of both function and
125 phylogeny. Consider again the case of disgust. Disgust was clearly originally focused on the
126 mouth, as oral incorporation of contaminated matter is a primary disgust elicitor, and both oral
127 rejection and nausea/emesis remain characteristic responses to a broad range of elicitors, whether
128 ingestible or not (Rozin & Fallon, 1987). Seeking to explain how an emotion so centered on oral
129 incorporation has as one of its principal domains of operation the avoidance of contact – oral or
130 otherwise – with cues of the presence of pathogens, Kelly (2011) posits that meat-eating played a
131 central role in the evolution of disgust. Building on prior work on the ultimate functions of
132 dietary preferences and avoidances, Kelly reasons that, while a rich source of nourishment, meat
133 is also a primary source of pathogens. He argues that two separate mechanisms, one regulating
134 oral incorporation, the other focused on cues of the presence of other pathogens (e.g.,
135 ectoparasites, etc.), became “entangled,” meaning that they fused into a single adaptation in
136 humans. This occurred, Kelly asserts, because our ancestors adopted meat-eating too quickly for
137 more conventional physiological defenses to evolve in time. While the centrality of meat-eating

138 in Kelly's explanation is both cogent and consonant with other evidence regarding the unique
139 salience that meat holds for humans as both a resource and a threat, nevertheless, his account
140 runs afoul of a realistic reconstruction of the EEA for the postulated adaptation.
141 Paleoanthropology provides abundant evidence that meat-eating evolved over a period of at least
142 3 million years (McPherron et al., 2010), hence Kelly's need-for-speed explanation cannot be
143 correct – the EEA for this trait was not merely human meat consumption, but rather meat
144 consumption practiced by a succession of hominid species (Clark & Fessler, n.d.). This matters
145 because if we abandon this aspect of Kelly's account, we must direct our attention to other facets
146 of the EEA for this trait, prominent among which are the longstanding sociality of hominids and
147 the corresponding progressive increases in encephalization, a feature that reduces the costs of
148 brain-based (i.e., psychological) adaptations relative to physiological adaptations (Clark &
149 Fessler, n.d.) – a pattern of likely importance in explaining many aspects of human evolved
150 psychology.

151 As the above case illustrates, paleoanthropology provides vital time depth in the
152 reconstruction of EEAs. Nevertheless, the richness of the portraits of the past that
153 paleoanthropology can provide is necessarily limited given that past behavior cannot be
154 observed, but rather must be inferred. Paleoanthropology thus provides one of two pillars
155 needed to operationalize the concept of the EEA for many features of mind, the second being
156 anthropologists' observations of contemporary small-scale societies that provide points of
157 reference with which to approximate ancestral humans' ecological and social conditions.
158 Traditionally, the study of small-scale societies was the heart and soul of anthropology, with
159 cultural anthropologists playing the central role. Over the course of the last four decades,
160 cultural anthropologists have increasingly focused on large societies, while sometimes also

161 eschewing the objective methods – and scientific objectives – most likely to produce findings of
162 relevance to EP. However, even as cultural anthropology has retreated some from the
163 investigation of small-scale societies, evolutionary anthropologists have increasingly taken such
164 groups as their central objects of study. Anthropologists – evolutionary or otherwise – thus
165 generate a rich corpus of material offering many positive affordances for EP. When exploring a
166 particular EP hypothesis, operationalizing the concept of the EEA can be greatly enhanced
167 through the use of observations of life in small-scale societies in general, and extant hunter-
168 gatherer groups in particular. The importance of this is illustrated by two topics of extensive
169 debate in the current literature, (1) the evolution of cooperation, and (2) the relationship between
170 disease avoidance and social attitudes.

171 First, viewed in comparison with the vast majority of other species, humans are
172 remarkable for the degree to which they cooperate in large groups of unrelated individuals, a
173 feature that must play a central role in explaining human history (Chudek & Henrich, this
174 volume; Norenzayan, this volume). Considerable disagreement surrounds the processes whereby
175 the capacity for such cooperation arose, with postulated positions ranging from various forms of
176 biological group selection (e.g., Sober & Wilson, 1999; Wilson, 2012), to combinations of
177 biological and cultural group selection (e.g., Bowles, 2006), to gene-culture coevolution (e.g.,
178 Boyd & Richerson, 2009; Chudek, Zhao, & Henrich, 2013), to the scaling up of mechanisms and
179 processes operating in dyadic interactions due to evolutionarily novel increases in the scope of
180 social life in contemporary societies (e.g., Burnham & Johnson, 2005; Hagen & Hammerstein,
181 2006). Recent work synthesizing diverse studies of extant hunter-gatherers indicates that such
182 societies characteristically involve co-residence among many unrelated individuals (Hill et al.,
183 2011) combined with high rates of contact with members of other bands (Hill et al., 2014) –

184 including ephemeral interactions (Chudek et al., 2013). Taken together, the resulting portrait of
185 the likely social dimensions of the EEA calls into question the thesis that the evolved
186 psychological mechanisms governing human cooperation at larger scales derive principally from
187 kin selection and reciprocal altruism, as such a position is more consistent with an EEA
188 characterized by high degrees of relatedness within groups, more restrictive social networks, and
189 a paucity of short-term interactions (reviewed in Brown & Richerson, 2014).

190 Second, findings from EA underscore the importance of the extensive variation in
191 ecologies and social structures likely characteristic of our species throughout its history and
192 beyond (Foley, 1995). It is vital to understand that, for many traits of interest, the relevant
193 features of the environment have been variable. This is because, depending on the nature of that
194 variation, it is likely that one of two classes of adaptations will have evolved, namely either i)
195 adaptations that facultatively adjust their output in light of local environmental cues, or ii)
196 adaptations for cultural acquisition. Illustrating this, one rapidly-expanding area of research
197 concerns the relationship between pathogen prevalence and social attitudes. In a series of
198 influential papers, Fincher, Thornhill, Schaller, Murray, and colleagues have argued that
199 pathogen prevalence predicts the extent of individualism versus collectivism (Fincher et al.,
200 2008) and conformism (Murray, Trudeau, & Schaller, 2011) across cultures; ingroup homophily
201 and outgroup avoidance (Fincher & Thornhill, 2012) and resulting speciation in cultural
202 evolution (Fincher & Thornhill, 2008); cross-national differences in personality (Schaller &
203 Murray, 2008; Thornhill et al., 2010); and a wide range of related social phenomena (Thornhill
204 & Fincher, 2014). The core thesis, termed the parasite-stress theory (PST), holds that the mind
205 contains adaptations that regulate social behavior to optimize disease avoidance (see Schaller,
206 this volume). The PST then argues that, in the relevant EEA, members of outgroups constituted

207 a key source of unfamiliar – and thus dangerous – pathogens. However, the extent of the threat
208 posed by pathogens varied across the ecologies inhabited by ancestral populations. As a
209 consequence, selection produced psychological mechanisms that adjust the degree to which
210 individuals preferentially assort with members of the ingroup, and avoid and are hostile to
211 members of the outgroup, as a function of cues indicative of the density and virulence of
212 socially-transmitted pathogens in the local ecology. Aggregated across the members of a
213 society, the outputs of these mechanisms then produce a wide variety of socio-cultural
214 concomitants, including phenomena as diverse as political orientation and religiosity.

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

221 First, the PST assumes an EEA for the proposed mechanism in which 1) interactions
222 between neighboring groups were rare, and 2) such groups were sufficiently geographically and
223 ecological disparate as to allow distinct pathogens to evolve independently in each group, such
224 that, upon contact, members of one group would lack a history of prior exposure – and thus
225 immunity – to the given strain. As discussed above, studies of extant hunter-gatherers indicate
226 high rates of contact between bands. The PST concerns relations between groups that possess
227 distinct, bounded cultural identities (termed *ethnies* in anthropology); as such, at first glance,
228 inter-band interactions might seem irrelevant, as, in most cases, the two bands will belong to the
229 same ethnies. However, from an epidemiological perspective, frequent inter-band contact unites

230 all members of a given hunter-gatherer ethnies into a single group, as infectious disease
231 contracted by members of one band will rapidly spread to other bands. The archeological record
232 provides extensive evidence of long-distance trade during the Paleolithic (see Blades, 2001;
233 Chalmin et al., 2007; d’Errico et al., 2009), indicating that both intra-ethnies and inter-ethnies
234 contact occurred with some frequency. Viewed with regard to the interests of the various
235 members of a group, the costs and benefits of inter-group contact are unevenly distributed.
236 Individuals who elect to interact with members of another group (be they of the same ethnies or a
237 different one) stand to reap the benefits of trade, as well as expanded access to territorial
238 resources, mating opportunities, knowledge transfer, etc. Such individuals are also at risk of
239 both disease transfer and aggression or exploitation. Notably, while both the benefits of inter-
240 group interaction and the risks of aggression and exploitation are primarily limited to those
241 individuals who elect to interact with outsiders, the same is not true of the risk of disease
242 transfer. In a world with minimal hygiene, little knowledge of disease transmission, extensive
243 food-sharing, and intimate physical proximity, if one individual in a band contracts a
244 transmissible illness, all members of the band become exposed; and, if bands interact regularly
245 and band composition is fluid, then the same holds true for the entire ethnies. This creates an
246 evolutionarily unsustainable dynamic from the perspective of the PST. For highly transmissible
247 diseases (precisely the type assumed by the PST), if individual A interacts with outgroups and
248 thereby both reaps fitness gains and suffers pathogen-inflicted costs, while individual B avoids
249 outgroups but suffers the same pathogen-inflicted costs due to intra-group disease transmission
250 from A, then A’s fitness will be higher than B’s fitness. Thus, following the dictum that
251 reconstructions of the EEA for a given trait should leverage the findings of EA regarding present
252 and past behavior, it appears that the portrait of the world of our ancestors that can be compiled

253 using ethnographic and archeological sources is inconsistent with that EEA required for the
254 evolution of an adaptation that would facultatively adjust attitudes toward ingroups and
255 outgroups as a function of pathogen prevalence.

256 Reconstructions of EEAs should employ all relevant material. Historical and
257 archeological evidence indicates that infectious disease decimated the New World in the initial
258 stages of colonialism. Does this speak to the EEA required by the PST? No. Extensive direct
259 contact between previously widely separated groups only occurred following the evolutionarily
260 recent development of transoceanic sailing technology. Paleolithic pedestrian hunter-gatherer
261 groups, inhabiting similar ecologies to those of their neighbors and linked to them through trade,
262 would have co-evolved with endemic pathogens, precluding the devastation recorded during
263 historical times (R. Thornton, personal communication). Indeed, in many areas, the
264 depopulation of Native American tribes due to European diseases is thought to have predated
265 direct contact with Europeans (Thornton, Miller, & Warren, 1991), revealing the population-
266 level networks that preclude both substantial intergroup variation in pathogen types and the
267 utility of ethnocentrism and xenophobia as prophylactic measures.

268 Many evolutionary psychologists assume that the human mind has changed little since
269 the Paleolithic (e.g, Tooby & Cosmides, 1989). While this is a reasonable heuristic, a heuristic is
270 not an inviolate rule, and EA presents evidence of rapid genetic evolution since the
271 domestication of plants and animals (Hawks et al., 2007), including genes relevant to pathogen
272 defense (see Laland, Odling-Smee, & Myles, 2010). Might life in the Neolithic therefore fit the
273 PST's requirements for an EEA? On the one hand, agriculture, animal domestication, and
274 increases in population density led to new diseases and large-scale epidemics (Barrett et al.,
275 1998), while network size probably shrank due to lesser reliance on far-flung partners for risk

276 management. However, trade increased dramatically (e.g., Hirth, 1978; Robb & Farr, 2005;
277 Bradley & Edmonds, 2005). Combined with the greater transmissibility and virulence
278 characteristic of pathogens that evolve to exploit high-density hosts (Ewald, 1994), the elevation
279 of trade – and the increase in the profits to be reaped thereby – would have enhanced the fitness
280 advantages of those who interacted with outgroups relative to those who eschewed doing so.
281 Hence, while we encourage investigators to entertain the possibility of relatively recent EEAs for
282 some traits, in this case, neither the Paleolithic nor the Neolithic provide the requisite features of
283 an EEA for the adaptation postulated by the PST.

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

298 How then can we account for the evidence amassed by proponents of the PST, which
299 almost certainly reflects an important pattern of cultural differences? These correlations may
300 reflect factors unrelated to the postulated adaptation, such as the effectiveness of government
301 institutions (Hruschka & Henrich, 2013b), and the broad impact of differing life history
302 trajectories (Hackman & Hruschka, 2013b). Research and debate continues (see Hruschka &
303 Henrich, 2013a; Hackman & Hruschka, 2013a; Cashdan & Steele, 2013; Thornhill & Fincher,
304 2014; van Leeuwen et al., in press; Pollet et al., in press), hence the jury is still out on these
305 questions. However, one possibility neglected in these debates is that the correlations at issue
306 may reflect the interaction of individual-level evolved disease-avoidance adaptations and group-
307 level cultural evolution.

308 In addition to our remarkable cooperativeness, humans are unique in our reliance on
309 socially-transmitted information in addressing adaptive challenges. While a variety of
310 adaptations likely undergird this capacity, one class in particular is relevant here. Whenever a
311 critical challenge is present in all environments historically inhabited by humans, but differs in
312 key attributes across environments, we can expect natural selection to have crafted domain-
313 specific culture-acquisition mechanisms (Fessler, 2006; Fessler & Machery, 2012). Consider,
314 for example, Barrett's work (this volume) concerning dangerous animals. All environments
315 occupied by humans contain dangerous animals. Some features, such as a sinuous legless body,
316 prominent teeth, or large size reliably predict the hazard posed by an animal in most
317 environments, hence natural selection can build sensitivity to such cues into mechanisms that
318 address this challenge. However, many dangerous animals lack these features (e.g., scorpions).
319 Cultural evolution involves the cumulative accretion and refinement of locally-relevant
320 information (Chudek & Henrich, this volume). Dangerous animals pose an important threat,

321 hence all cultures can be relied upon to contain information about avoiding or addressing
322 endemic dangerous species. Natural selection has exploited this reliable feature of culture by
323 crafting mechanisms that motivate and support early, rapid acquisition of cultural information
324 regarding dangerous animals. Importantly, for the same reasons, selection can be expected to
325 have crafted culture-acquisition mechanisms in many other domains as well. Hence, paralleling
326 Barrett's work, similar considerations apply to the question of disease avoidance.

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

341 While paralleling biological evolution in a number of respects, cultural evolution
342 importantly differs in that it does not necessarily maximize individual fitness, instead operating
343 to maximize the spread of a given set of ideas, often by increasing the size of a corresponding

344 culture-bearing group; this process is sometimes parallel to, and sometimes orthogonal to (or
345 even opposed to), individual fitness maximization (see Chudek & Henrich, this volume).
346 Relations with other groups are often a central determinant of the size of a cultural group: *ceteris*
347 *paribus*, belief systems that motivate their holders to direct their cooperative efforts toward
348 ingroup members, and their exploitative efforts toward outgroup members, will outcompete
349 belief systems that are less ethnocentric in this regard (Bowles & Gintis, 2011, Ch. 8).
350 Behavioral avoidance and a desire to expel targeted individuals are adaptive responses to
351 individuals posing a risk of disease transmission. Cultural evolution can therefore achieve
352 group-functional (but possibly individually costly) ingroup favoritism and outgroup hostility by
353 depicting outgroup members as posing a disease risk (witness outgroup derogations such as
354 ‘cockroaches,’ ‘rats,’ ‘scum,’ or ‘vermin’).

355 Earlier, we stressed the importance of attending to tradeoffs. Disease avoidance is not
356 free. It entails time, energy, and attention costs, and comes at the expense of dietary efficiency
357 and social exchange. We have already seen that mechanisms governing this behavior are
358 sensitive to changes in individual vulnerability, and the same considerations of efficiency make it
359 likely that, as is presumed by the PST, these mechanisms are calibrated in light of the incidence
360 of disease (see Schaller, this volume). If so, and if the upregulation of these mechanisms
361 involves increased attention to, and importance placed on, socially-transmitted information
362 regarding disease, then individuals occupying environments with high pathogen prevalence will
363 be particularly vulnerable to those factually inaccurate messages concerning disease threats
364 posed by outgroup members that promote xenophobia and ethnocentrism. In turn, this will
365 produce the patterns of correlations documented by PST proponents. Although the correlations
366 alone do not provide adjudicate between the original PST and our alternative formulation,

367 experimental avenues for doing so exist. To exploit the power of cultural information in
368 navigating adaptive challenges, individuals must be credulous, as the rationale for cultural
369 practices is often unknown or opaque (Legare & Watson, this volume), while the costs of
370 individual trial-and-error learning will sometimes be high, especially when the information
371 concerns hazards (Boyd & Richerson, 2006; Boyd & Richerson, 2009). However, credulity
372 entails the risk of falling victim to both manipulative actors and, as our proposal presumes,
373 inaccurate information (Kurzban, 2007). Accordingly, we can expect selection to have crafted
374 mechanisms that adjust credulity in light of expected benefits and costs (Fessler, Pisor, &
375 Navarrete, 2014). Cues of the prevalence of a given class of hazards should therefore shift the
376 balance toward greater credulity in that domain. Specifically, our proposal predicts that
377 individuals living in (or, perhaps, who were raised in) high-pathogen environments should evince
378 elevated credulity toward cultural information relevant to disease avoidance. This is a testable
379 prediction.

380 Whether our proposal is correct or not, this discussion serves to illustrate a number of
381 important points central to the intersection of EP and EA. The first of these concerns the
382 distinction between evoked culture and transmitted culture. Although classically defined in
383 anthropology as information acquired through learning from one's group, the term 'culture' is
384 often used simply to refer to behavioral and psychological features that are shared within a group
385 but differ across groups – whether or not there is evidence that such patterns stem from socially-
386 transmitted information. Tooby and Cosmides (1992) noted that such commonalities need not be
387 the product of such information, but can instead result from the output of shared adaptations
388 responding to the same environmental input, a pattern that they termed *evoked culture*, in
389 contrast to *transmitted culture*. Hence, the PST argues that patterned differences across groups

390 that correlate with differences in pathogen prevalence constitute evoked culture, being the
391 aggregate of the output of each individual's biologically-evolved disease-avoidance mechanisms.
392 In contrast, the alternative explanation that we have proposed assumes that such patterned
393 differences constitute transmitted culture, as individuals acquire the given beliefs and attitudes
394 by learning them from other members of their group. Note, however, that, in both models, both
395 biologically-evolved psychological adaptations and processes of cultural evolution must be
396 adduced.

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

410 Viewed more broadly, in both proposals, psychological adaptations create attractors
411 (Sperber, 1996) such that some ideas are more likely to be attended to, acquired, retained, and
412 transmitted than other ideas, thereby influencing which possibilities succeed and which fail in the

413 marketplace of ideas (see Chudek & Henrich, this volume). Thus, as this case illustrates, as
414 tempting as it is to interpret the dichotomy between evoked and transmitted culture in terms of
415 nature versus nurture, doing so is a grave misstep – there are likely few cases in which evoked
416 culture alone can explain humans’ rich beliefs and practices, while even what seem the purest
417 cases of transmitted culture will necessarily involve an underlying set of evolved adaptations.
418 Moreover, while we have argued in the above case that the relevant adaptations focus on
419 information acquisition, the set of likely possibilities is far larger than this, as cultural evolution
420 often exploits or bootstraps evoked preferences and ideas produced by a variety of adaptations.
421 For example, military history reveals increasing refinement of procedures for recruitment,
422 training, and deployment of troops, techniques that harness the evolved mechanisms that
423 generate small-group affiliation in the service of fielding effective armies of millions (Richerson
424 & Boyd, 1999); likewise, incest taboos and, more broadly, marriage rules (key components of
425 the social structures of small-scale societies) extrapolate sentiments generated by evolved
426 inbreeding-avoidance mechanisms; and so on.

427 Consonant with the complexity described above, neither cross-cultural variation nor
428 cross-cultural uniformity is uniquely indicative of the processes generating observed patterns.
429 Variation can reflect divergent pathways of cultural evolution acting in different societies, or it
430 can reflect diverse evoked cultures produced by divergent physical or social ecologies.
431 Uniformity can reflect uniform functioning of panhuman adaptations across different ecologies,
432 or it can reflect convergent cultural evolution. In exploring these possibilities, the question of
433 the relevant EEA again becomes central. Is it likely that variation in the relevant features of the
434 environment characterized the EEA required for a postulated adaptation? If so, then selection
435 may well have crafted mechanisms for facultative adjustment, in which case evoked culture may

436 play a central role in cross-cultural variation. For example, due to differing ecologies and
437 degrees of inter-group competition, the environments occupied by ancestral populations will
438 have varied in rates of extrinsic mortality and the reliability of resources. Such variation is
439 directly linked to fitness, and therefore likely favored adaptations that calibrate future
440 orientation, risk-taking, mating strategy, parental investment, cooperativeness, and aggression in
441 light of local circumstances. This topic has been productively explored in EP, often by
442 evolutionary anthropologists (see Kaplan & Gangestad, this volume; Mace, this volume). When
443 viewed at the level of societies, the resulting evoked cultures may drive much observed variation
444 along these and related dimensions. In contrast, the Neolithic Revolution brought about forms of
445 social organization and related adaptive challenges that were largely unprecedented. These
446 radical departures make it likely that corresponding axes of cultural variation reflect a greater
447 proportion of transmitted relative to evoked culture. For example, although hunter-gatherer
448 groups vary in the degree to which individuals must defend resources against theft, or the degree
449 to which present labor yields returns far in the future, these considerations loom vastly larger in
450 pastoralist versus agriculturalist societies. The correspondence between these modes of
451 subsistence and locally-functional values and social orientations (Edgerton & Goldschmidt,
452 1971) is therefore best explained principally in terms of cultural evolution (albeit plausibly
453 bootstrapping evolved mechanisms). Likewise, cultural evolution likely applies in the case of
454 adjacent regions in which people pursue either rice or wheat agriculture: these crops entail
455 different levels of interdependence, and reliance upon each is matched by corresponding
456 differences in social orientation (Talhelm et al., 2014). Lastly, phylogeny is again important,
457 albeit here in terms of the histories of the cultures at issue, as cultural phylogenetic inertia
458 (driven by the self-reinforcing nature of institutions and values) can create differences between

459 groups that persist after the respective selective pressures have vanished (e.g., differences
460 between formerly pastoralist and formerly agriculturalist U.S. subcultures – Nisbett & Cohen,
461 1996).

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

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

476 Central to EA research exploring gene-culture coevolution (see Chudek & Henrich, this
477 volume) is a focus on the question of when it pays to imitate successful individuals versus
478 imitate the majority, as the consequences of these choices ramify across diverse social
479 phenomena. Though defined in behavioral terms, these are psychological processes, hence EP
480 can illuminate them. Although investigators have begun to explore cues operating in such
481 imitation (e.g., Chudek et al., 2012; Chudek & Henrich, this volume), the underlying

482 psychological mechanisms remain largely unexplored. Earlier, we stressed the importance of
483 emotions as evolved drivers of behavior, yet the psychology of cultural imitation remains largely
484 divorced from the psychology of affect. Likewise, we emphasized the importance of
485 understanding adaptations as kludgy mechanisms colored by their phylogeny, yet, beyond
486 laudable efforts to compare learning biases across humans and apes (Haun, Rekers, &
487 Tomasello, 2012), no research addresses how the structure of learning mechanisms reflects their
488 evolution. Lastly, the nature and ramifications of domain-specific culture-acquisition
489 mechanisms remain largely overlooked. There are thus many ways in which EP can further
490 gene-culture coevolutionary EA.

491 The late introduction of EP into work on gene-culture coevolution reflects the centrality
492 of population-level models in the latter field. In contrast, EP shares with human behavioral
493 ecology (HBE) a focus on individual behavior. However, HBE differs from EP in that it
494 generally eschews exploration of mechanisms (psychological or otherwise) in favor of outcome
495 measurements used to test optimality predictions. Far from engendering harmony, the shared
496 focus on individual behavior instead witnessed acrimonious debates between proponents of HBE
497 and advocates of EP (Smith, Borgerhoff Mulder, & Hill, 2001). Central to these was the
498 criticism by the latter that HBE's assumption that behavior maximizes fitness – termed the
499 behavioral gambit – is unreasonable in highly variable contemporary environments. The
500 behavioral gambit is problematic, advocates of EP argued, given the combination of the domain-
501 specific nature of adaptations and the slow rate of their evolution relative to the rapidity of recent
502 socio-ecological change (i.e., the problem of evolutionary disequilibrium, or adaptive lag).
503 Proponents of HBE, in return, criticized practitioners of EP for underestimating both the range of
504 environmental variation characteristic of our species' history and the attendant adaptive plasticity

505 to be expected of behavior. Advocates of EP pointed to the apparently maladaptive nature of
506 much contemporary behavior; supporters of HBE countered that fitness outcomes cannot be
507 merely presumed. And so on.

508 While outcome measurement remains the central pillar of HBE, behavioral ecologists
509 increasingly recognize the importance of attending to mechanisms, as i) doing so illuminates
510 trade-offs and other constraints on optimality ignored by the behavioral gambit (Monaghan,
511 2014), and ii) cultural evolution can account for the particular form of a local configuration (via
512 cultural phylogeny), account for behavior that may be maladaptive at the individual level but
513 adaptive at the group level (Brown, 2013), and, given the possibility of adaptive lag in cultural
514 evolution itself, account for behaviors that may be maladaptive at both the individual and group
515 levels (Mace, 2014).

516 Against the above backdrop, Nettle and colleagues (2013) recently advocated employing
517 the behavioral gambit in HBE until it fails in a given case, and only then resorting to the
518 examination of mechanisms. While their prescription for HBE is defensible, it unnecessarily
519 limits the range of phenomena that HBE addresses. HBE presents polished methods and
520 strategies for assessing real-world behavior and its somatic correlates, tools that can be
521 productively deployed in exploring many of the challenges facing societies today.
522 Contemporary epidemics of addictions to alcohol, tobacco, and drugs of abuse, or the spread of
523 obesity, osteoarthritis, or cardiovascular disease – to name but a few – are fitness-reducing
524 behaviors that cry out for the careful methods of HBE. Happily, some of these same
525 investigators are beginning to explore such problems from a decidedly EP angle (cf. Pepper &
526 Nettle, 2014), investigating, for example, how evolutionarily novel environments present cues to
527 evolved mechanisms that calibrate future discounting in light of mortality risk (Nettle, Coyne, &

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

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

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

545 Second, of relevance to the above, an important scholarly resource that is arguably both
546 the most accessible to, and the most under-utilized by, evolutionary psychologists is the
547 Electronic Human Relations Area Files (eHRAF), a collection of digitized ethnographies
548 spanning the full range of human societies. This remarkable archive allows for comparisons not
549 only relevant to attempts to reconstruct EEAs (e.g., Wrangham & Glowacki, 2012), but, in
550 addition, efforts to test for cultural patterns predicted to arise from postulated psychological

551 adaptations (e.g., Fessler et al., 2014), examine hypotheses concerning large-scale phenomena
552 (e.g., Kline & Boyd, 2010), and pursue similar goals that go far beyond questions of EEAs.

553 Third, while the eHRAF provides a valuable avenue for testing a broad range of
554 hypotheses, because the information contained therein was collected for a wide variety of
555 reasons, investigators will often find that there is no substitute for direct measurement of
556 behavior. Importantly, as we hope to have conveyed, rapid, evolutionarily recent culture-based
557 changes in lifestyle constitute both a challenge and an opportunity for the evolutionary
558 psychologist. Small-scale societies in which state regulation of behavior is minimal, kinship and
559 longstanding social ties are central pillars of the social structure, economic activities are
560 intimately linked to subsistence, access to healthcare – including contraception – is limited, and
561 life is less awash in the sea of global electronic media, provide important points of contrast for
562 studies conducted in large-scale technologically sophisticated societies. Increasingly,
563 evolutionary anthropologists working in small-scale societies are incorporating the EP paradigm
564 into their work, seeking to test hypotheses – such as the facultative calibration of sexual and
565 emotional jealousy in light of paternal investment (Buss et al., 1992) – that predict patterned
566 differences or similarities across divergent cultures (e.g., Scelza, 2014). Often, such work is
567 collaborative, incorporating the complementary expertise of scholars from multiple disciplines
568 (e.g., Bryant & Barrett, 2007). Indeed, as is evident in the composition of this edition of the
569 Handbook of Evolutionary Psychology, cross-disciplinary collaborations and exchanges are
570 increasingly generating a fertile syncretic paradigm in the evolutionary behavioral sciences. The
571 future of the relationship between evolutionary psychology and evolutionary anthropology is
572 thus a bright one indeed.

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