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Original Article

The kiss of death: three tests of the relationship between disease threat and ritualized physical contact within traditional cultures

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ABSTRACT

The direct adaptive impact of rituals and other forms of behavior dictated or shaped by culture may be one factor influencing their persistence or lack thereof over time. Given that physical contact is a common means through which transmissible disease is spread, we explored the possibility that levels of normative physical contact would be negatively associated with levels of infectious disease prevalence. We tested this prediction across three domains of such behavior – greetings, romantic kissing, and mortuary rituals – by compiling ethnographic information on normative behavior in traditional cultures and comparing it with epidemiological estimates of pathogen prevalence. We find small but significant negative correlations between pathogen prevalence and both greetings and romantic kissing. Ancillary analyses suggest that these relationships are driven by human-transmitted pathogens. The relationship between pathogen prevalence and mortuary rituals is non-significant. Causal mechanisms that may account for these results, as well as implications and limitations, are discussed.

> *"Greeting and farewell are expressed by joining the middle fingers of the right hand and jerking them together "till they snap and crack again"; when doing this with a superior, a woman may bow, and both sexes will lower a load or a weapon before a superior as a sign of respect. The Azande do not kiss."*
>
> [Baxter & Butt, 1953, p. 152.]

1. Introduction

Culturally shaped social behaviors, including both formal rituals and quotidian normative actions, vary extensively between cultures. Among mid-century Apache, traditional cultural norms dictated that one greet an acquaintance with a warm embrace (Opler, 1941); among the Otavalo Quichua of the same period, on the other hand, it was customary to greet acquaintances without any contact whatsoever (Parsons, 1945). Similar variation is apparent in regard to romantic behaviors: whereas romantic sexual kissing is described as an integral part of dyadic sociosexual relationships in ethnographic accounts of traditional Assiniboine, Basque, and Chipewyan cultures, among the Akan, Banyoro, and Cherokee it was reportedly nonexistent (Jankowiak, Volsche, & Garcia, 2015). What shapes such variation? Here, we investigate whether cultural variation in these types of behaviors – specifically social greetings, romantic kissing, and mortuary rituals – is due, at least in part, to variation in the prevalence of infectious disease.

1.1. Disease threat, adaptive behavior, and cultural variation

Throughout human history, infectious disease has posed one of the largest threats to survival and welfare, historically accounting for more deaths than any other factor (Inhorn & Brown, 1990; Wolfe, Dunavan, & Diamond, 2007). The adaptive utility of disease avoidance and management has led to the evolution of many sophisticated physiological, behavioral, and cultural defense mechanisms. The most well-known of these defenses are the mechanisms that comprise the immune system. Although this system is generally effective, it is also costly: fighting infections that are already present comes at a substantial metabolic cost. Raising body temperature by just 1 degree Celsius – as during fever – requires a 13% increase in metabolism (Dantzer, Kent, Bluthe, & Kelley, 1991). Relying on immune reactions that are mounted in response to substantial infection is also extremely risky, as some infections can prove fatal. Those that are not fatal in themselves may put individuals at greater risk of predation or reduce their chances of reproduction. Consequently, contingent on their costs, adaptations favoring

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proactive behaviors that prevent or reduce initial contact with infectious pathogens would have conferred a reproductive advantage, and would have almost certainly been selected for in human evolution. A substantial body of evidence on cognitive and affective mechanisms that facilitate proactive prophylactic behaviors suggests that this is indeed the case (e.g., Fleischman & Fessler, 2011; Murray & Schaller, 2016).

Recent studies have also demonstrated associations between regional variation in disease threat and an array of behaviors, attitudes, and cultural practices. Higher disease threat is associated with higher levels of intergroup violence (Letendre, Fincher, & Thornhill, 2010), greater social conservatism and political authoritarianism (Murray, Schaller, & Suedfeld, 2013; Terrizzi, Shook, & McDaniel, 2013; Thornhill, Fincher, & Aran, 2009), higher levels of behavioral and attitudinal conformity (Murray, Trudeau, & Schaller, 2011; Cashdan & Steele, 2013), higher collectivism (Fincher, Thornhill, Murray, & Schaller, 2008), more socially cautious personality traits, such as lower extraversion and lower openness to experience (Schaller & Murray, 2008), and more restrictive sexual attitudes and behaviors (Schaller & Murray, 2008). The idea that behavioral tendencies may vary cross-culturally as a result of local disease risk has been formalized as parasite stress theory (see Thornhill & Fincher, 2014).

Each of these relationships is logically underpinned by a cost/benefit framework. Consider one specific cultural practice, the prevalence of spices in food preparation. The use of spices in cooking confers disease-relevant benefits, as spices are natural antibiotics (Billing & Sherman, 1998), and consuming spices is linked to lower risk of disease-related mortality (Lv et al., 2015). However, using spices also comes with costs: spices offer little nutritive value, yet they consume labor, arable land, and resources that could otherwise be dedicated to more calorically dense crops. The antipathogen benefits of spices are more likely to outweigh their costs when the threat of disease is especially high within the local ecology, which suggests that cultural norms dictating the use of spices are most likely to develop and persist in regions characterized by especially high disease threat. This is exactly what Sherman and Billing (1999) found: in regions of higher disease prevalence, cultural norms dictate the more frequent use of spices in local cuisine.

1.2. Ritualized physical contact across cultures

Physical contact, universal among humans, is crucial to human interaction (Field, 2014), and plays a key role in many types of affiliative relationships. A large body of research indicates the importance and benefits of physical contact in affiliative interaction (see Thayer, 1986), whether with children (Main & Stadtman, 1981), romantic partners (Ditzen et al., 2007), or strangers (Crusco & Wetzel, 1984). Physical contact reduces stress, makes people feel more secure, and increases cooperation and trust (Ditzen et al., 2007; Joule & Guéguen, 2007; Levav & Argo, 2010). Some of these effects may be mediated by increased levels of oxytocin and reduced cortisol (Ditzen et al., 2007; Uvnäs-Moberg, 1997, 1998). In the industrialized world, physical contact has been shown to affect monetary transactions: physical contact makes people spend more time and money in shops, tip more in restaurants, and take greater financial risks (Crusco & Wetzel, 1984; Hornik, 1992; Levav & Argo, 2010). Contact in industrialized societies also increases monetary generosity among American strangers (Morhenn, Park, Piper, & Zak, 2008), and makes French women more likely to give each other cigarettes (Joule & Guéguen, 2007). Here we consider three specific forms of contextual ritualized physical contact.

1.2.1. Greetings

All known cultures have multiple forms of greeting, and there is considerable variation in the forms of greeting used in different societies. There is also evidence from industrialized societies that physical contact during greetings may amplify the benefits of a prosocial presentation of self to the other party. Behavioral and neurophysiological measures indicate that shaking hands increases the positive social impact of approach behavior (Dolcos, Sung, Argo, Flor-Henry, & Dolcos, 2012). Among Americans, handshaking makes people cooperate more in negotiations (Schroeder, Risen, Gino, & Norton, 2014) and mediates the positive effects of extraversion on job interview success (Stewart, Dustin, Barrick, & Darnold, 2008).

1.2.2. Romantic sexual kissing

Romantic kissing has a long history; written references date back at least to the Vedas, which are among the oldest sacred texts in the world. Kirshenbaum (2011) claimed that kissing is a near universal; however, this conclusion was based on a very broad definition of kissing, which included various non-romantic contexts and greatly differing levels of physical context. Kissing seems to have several potential beneficial functions, including assessing the genetic fitness (Thornhill & Gangestad, 1999) and compatibility (Wedekind, Seebeck, Bettens, & Paepke, 1995) of partners, strengthening pre-existing relationships (Wlodarski & Dunbar, 2013), and exchanging commensal microbiota (Montiel-Castro, González-Cervantes, Bravo-Ruiseco, & Pacheco-López, 2013). Despite the purported benefits of kissing, all of its forms do not appear to be universal. Jankowiak et al. (2015) recently conducted the first rigorous study of romantic-sexual kissing across 168 cultures worldwide (mostly drawn from the Human Relations Area Files), finding that, contrary to popular belief, it was reported to be absent in the majority (54%) of the cultures examined.

1.2.3. Mortuary rituals

Mortuary rituals are thought to be among the oldest human cultural traditions and are common to all known human cultures. White, Marin, and Fessler (in press) examined 57 geographically disparate cultures and found that most had rituals in which mourners were able to see and touch the corpse. They also observed diversity in the procedural details of these practices, but relative uniformity in terms of the level of contact: 93% of funerals involved family having visual exposure to the corpse, and 89.5% involved physical contact.

While there has long been evidence that engagement in funerary rituals may be associated with better outcomes for family members (e.g., Rosenblatt, Walsh, & Jackson, 1976), it has not been clear why so many mortuary rituals involve visual and physical contact with the dead. White et al. (in press) propose that having such contact with a deceased loved one assists the bereaved in altering their mental representations of the beloved (a postulated component of bereavement) by providing cues that the individual is indeed dead, and thus no longer an agent with whom a relationship can be maintained. This provides a plausible functional reason for the widespread presence of contact in funerary rituals.

1.3. Cultural rituals and pathogen prevalence

While each of these culturally dictated behaviors has specific benefits, they also share a significant cost: the possibility of exposure to novel infectious pathogens. Direct, non-intimate physical contact is a major means through which a large proportion of infectious diseases are spread (e.g., Salathé et al., 2010; Taylor, Latham, & Mark, 2001). Handshakes during greetings play a role in the transmission of infectious diseases (Hill & Mathews, 1926; Hamburger, 1947; Mathews, 1928) to the point that many medical professionals have recently called for a ban on them in healthcare settings (Sklansky, Nadkarni, & Ramirez-Avila, 2014). What is more, the probability of pathogen transfer increases with the greater strength and longer duration of contact; essentially, a more involved handshake is riskier than a fleeting one (Mela & Whitworth, 2014). Romantic or intimate kissing also provides ample opportunity for exposure to novel pathogens: the average ten-second open mouth kiss transfers approximately 80 million bacteria (Kort et al., 2014). Contact with human cadavers also poses certain

blood-borne and gastrointestinal pathogen-transmission risks (e.g., Morgan, 2004). Cultural variation in these practices may thus be influenced, at least in part, by the local prevalence of infectious disease.

1.4. Overview of the present study

If, i) via one or more possible pathways (see Discussion), the development and persistence of cultural practices is shaped by the fitness consequences thereof for adherents, and ii) cultural norms involving physical contact entail pathogen-related costs, then the observed prevalence of such practices should be inversely related to recorded pathogen prevalence. We tested this prediction by investigating three cross-culturally variable forms of culturally shaped physical contact: 1) rituals commencing social interactions (greetings), 2) behaviors commencing romantic interactions (sexual kissing), and 3) rituals involving deceased individuals (mortuary or funerary rituals). We predicted that each of these forms of contact would be negatively associated with pathogen prevalence. Rather than using modern nation states as the units of analysis (as has been the predominant practice in previous cross-cultural investigations of related topics), we investigated these relationships in relatively smaller-scale societies. As documented at the time of initial extensive ethnographic description (i.e., the Otavalo Quichua of 1945, rather than the indigenous peoples of Peguche Canton in 2015), these societies have the inferential advantages of i) being less likely to have undergone large-scale immigration or cultural changes within very recent history (and as such may better reflect the nature of changes across human cultural history), and ii) representing more independent units of analysis relative to modern nation states.

2. Method

Our samples for each of the three tests reported below were drawn predominantly from cultures included within the electronic Human Relations Area Files (eHRAF; www.ehrafworldcultures.yale.edu), a database comprised of over a million pages of ethnographic information on hundreds of cultures across the globe, documenting an array of cultural practices, norms, and social systems. This information is indexed in paragraph units in line with the *Outline of Cultural Materials* (OCM) classification system.

2.1. Assessment of physical contact during greetings

In order to identify greeting practices within eHRAF, we performed a search using the subject Etiquette (OCM code 576) and the keyword "greeting*" (the asterisk returned results for both "greeting" and "greetings"). This search returned 837 paragraphs from 407 different documents describing 186 cultures.

A total of four coders who were blind to the purpose of the study coded the level of physical contact among people during culturally normative greetings. Physical contact was coded on a six-point scale, with higher scores indicating higher chance of bacterial transmission: 0 = no contact (e.g., bow, air salutation); 1 = light contact (e.g., hand to shoulder or head); 2 = medium contact (e.g., hand or forearm grasp); 3 = full contact (e.g., hug or other body embrace); 4 = light kiss (e.g., to cheek or head); 5 = full kiss or other form of salivary transmission (e.g., mouth-to-mouth kiss; a "spit shake"). Coders also indicated between whom the greetings were performed (between friends or family, between strangers, or between authority figures and subordinates). In the event that the records contained information from multiple paragraphs on a greeting within the same dyad in the same culture and the level of contact described was different between the paragraphs, the numerical estimates were averaged. When two coders' estimates differed, their scores were averaged as well. Each coder read and rated approximately half of the total number of paragraphs (two coders rated paragraphs for the Americas, Asia, and East Africa, while the other two coders rated Europe, Middle East, all other parts of Africa, and Oceania). In slightly more than half of the coded instances, the two coders agreed precisely in their assessments of the level of contact. For the full sample, the intraclass correlation between the two coders' sets of ratings was moderate, $r = .64$. Importantly, however, for only 11 of the societies examined did each of the two coders' averaged estimates of contact in a society differ from one another by more than a single point; excluding these 11 cases from the analyses does not meaningfully change the pattern of results. Many of the paragraphs and phrases returned from the search provided no tractable information about greeting rituals themselves (e.g., "greetings are exchanged among neighbors", etc.). The majority of relevant paragraphs described greetings between close friends and family; these greeting scores were available for 123 cultures. For 55 cultures there was information given about contact when meeting strangers, and for 47 cultures there was information given for contact between individuals who differed patently in social status in some way. The intercorrelations for level of contact between each of these different greeting dyads were all positive, r's = .31–.47. In total, information was evaluated for 137 cultures' physical contact during greetings.

2.2. Assessment of presence of romantic sexual kissing

Using information from 128 cultures from the general eHRAF sample and a further 27 from the Standard Cross Cultural Sample, Jankowiak et al. (2015) conducted an ethnographic analysis to determine the existence and prevalence of romantic kissing across cultures. Jankowiak et al. searched for the keywords "kiss" or "kissing." The data were coded simply as 1 = present, 2 = not present. They defined romantic kissing as intentional, prolonged lip-to-lip contact, although descriptions of the Oceanic or Malay kiss (face rubbing) were included if there was explicit reference to its being used in a romantic-sexual context. "Not present" coding was determined if one of two criteria were met: 1) The ethnographer explicitly stated that they never witnessed romantic kissing or that it was considered taboo or disgusting in that culture, or 2) The ethnographer discussed other types of kissing (such as between family members) but did not mention romantic couples kissing.

Jankowiak and colleagues also obtained unpublished responses from 34 ethnographers (mostly taken from Ember and Ember's Encyclopedia of Sex and Gender, 2004) to the question: "Did you observe or hear of people kissing on the mouth in a sexual, intimate setting?" These unpublished reports led to the addition of 13 further cultures, giving 168 in total.

2.3. Assessment of contact during mortuary rituals

Using data from the Human Relations Area Files, we analyzed cross-cultural differences in the amount of contact with the deceased reported in 57 cultures worldwide. For this test, we used data originally obtained and reported by White et al. (in press). These authors used the *Probability Sample Files* (PSF), a dataset containing information from 60 cultures chosen to be representative of global variation. To minimize Galton's error – the assumption of independence of non-independent data points – the societies included in the PSF were selected in such a manner as to control for cultural contact and historic relatedness among societies. We use an identical definition of mortuary ritual to that presented in previous work: "a conventional action following the death of an individual, conducted prior to, or during, initial corpse disposal" (White et al., in press, p. 5). This definition excludes secondary burial or other secondary treatment of the corpse. Accounts were only included if they occurred after 1901 (as some earlier reports are likely unreliable), and accounts of mortuary rituals for very high-status individuals (e.g., royalty, chiefs) were excluded, as these can be presumed to differ substantially from common practices. Finally, only cases that were described in detail by ethnographers, rather than mentioned briefly or in passing, were included. Following these criteria, 51 of the 60 cultures

were deemed to have sufficient information available and were therefore included in the current analysis.

White and colleagues instructed trained research assistants who were blind to any hypotheses to assess whether the family made physical contact with the corpse during the funerary ritual. Physical contact was quantified on a scale of 1–5 (*1 – very low Intimacy, 3 – moderate intimacy, 5 – very high intimacy*). The initial compilation of ethnographic material from the eHRAF was conducted by 10 research assistants and then coded as described by 10 different assistants. In the first phase, White et al. randomly assigned each assistant to compile information from 6 cultures, recording only the most detailed description for each culture. Another 10 assistants were then tasked with coding these descriptions (again, 6 cultures per assistant). Inter-rater reliability was then assessed by having two further assistants evaluate material from all of the cultures using the same methods. Reliability was high (Cronbach's alpha = 0.82) and any disagreements between the original coders and the two later coders were resolved through subsequent discussion.

2.4. Assessment of historical disease prevalence

Cashdan, Steele, and Murray (2014) provide numerical estimates of the relative historical pathogen prevalence across 186 societies contained within the Standard Cross-Cultural Sample. These numerical estimates are based upon the historical prevalence of ten disease-causing pathogens reported in epidemiological atlases published in the mid twentieth century (e.g., Rodenwaldt & Bader, 1952–1961). The pathogens included in this index (and the diseases they cause) are dengue (dengue fever), filariae (filariasis), malaria-causing plasmodia, rickettsia (typhus), trypanosomes (trypanosomiasis), *Yersinia pestis* (plague), leishmanias (leishmaniasis), schistosomes (schistosomiasis), disease-causing spirochetes, and mycobacterium leprae (leprosy) (interquartile range = 1880–1939). The prevalence of most of these pathogens was coded on a four-point scale (1 = absent; 4 = present at severe levels). This index is internally reliable, Cronbach's alpha = .81. Construction of these numerical estimates used source materials and methods adapted from Low (1990), and Murray and Schaller (2010). There are many cultures in the eHRAF that are not included in the SCCS. To generate an approximate historical disease prevalence score for these cultures, we imputed the score of the geographically closest SCCS culture.

2.5. Assessment of human-transmitted vs. non-human transmitted disease prevalence

Parasite stress theory suggests that human-transmitted pathogens should have relatively greater implications for human behavior and culture than non-human-transmitted pathogens, and country-level research provides some support for this hypothesis (e.g. Fincher & Thornhill, 2012; Thornhill, Fincher, Murray & Schaller, 2010). The available source materials that form the basis of estimates of historical pathogen prevalence in SCCS societies do not reliably distinguish between human-transmitted and non-human-transmitted pathogen prevalence. However, in their supplementary materials, Fincher and Thornhill (2012) provide numerical estimates of *contemporary* human-transmitted, non-human-transmitted, and total pathogen prevalence for each of 226 countries worldwide (available from http://www.journals.cambridge.org/bbs2012002). Fincher and Thornhill obtained these values from the Global Infectious Disease & Epidemiology Online Network (GIDEON, www.gideononline.com) – a frequently updated database of contemporary infectious disease prevalence.

In order to perform ancillary tests, we therefore applied Fincher and Thornhill's pathogen prevalence values to our current sample by imputing the pathogen prevalence scores (human-transmitted, non-human-transmitted, total) of the country within which the SCCS culture is predominantly based. This methodology suffers at least two significant shortcomings. First, these imputed values are country-level estimates, and thus provide only an oblique measure of local pathogen prevalence in the mostly small-scale societies in our sample. Second, these values reflect contemporary estimates of pathogen prevalence and thus are temporally preceded by the outcome variables of interest. With these caveats in mind, these values offer a preliminary avenue whereby we can explore the possible differential impacts of human-transmitted and non-human-transmitted pathogens, and thus complement the other materials that we employ.

3. Results

Given that our principal analyses involved multiple tests of the central hypothesis, we performed a sequential Holm-Bonferonni correction to the *p*-values of these three tests, which corrects most conservatively for the lowest *p*-values within a set of tests (e.g., Abdi, 2010; Holm, 1979).

3.1. Test #1: is historical pathogen prevalence associated with the prevalence of physical contact during greetings?

Preliminary paired-samples *t*-tests revealed that greetings between friends and family ($M = .69$, SD = 1.10) and between status-differential dyads ($M = .84$, SD = 1.23) had significantly more physical contact than greetings between strangers ($M = .43$, SD = .76; p's < .03). We looked at zero-order correlations between historical pathogen prevalence and degree of physical contact during culturally normative greetings. Only 52 of the specific societies in the current sample were also in the Standard Cross-Cultural Sample's disease prevalence estimates provided by Cashdan et al. (2014); accordingly, for the remaining 85 societies we used the score from the geographically closest society instead. Historical pathogen prevalence was weakly but significantly negatively associated with overall levels of physical contact during greetings, $r(137) = -.18$, $p = .03$ (Holm-Bonferroni corrected $p = .06$). Across the three types of dyads, the relationships were similar in magnitude and direction, but, consistent with reductions in statistical power that occur when the sample is subdivided, individually nonsignificant: historical pathogen prevalence correlated nonsignificantly with degree of physical contact during greetings between close friends or family, $r(123) = -.09$, $p = .33$; between strangers $r(55) = -.12$, $p = .40$; and between status-differential dyads, $r(47) = -.21$, $p = .15$.

In order to perform an analysis that further minimizes the potential effects of spatial autocorrelation, the non-specificity of the imputed pathogen prevalence scores, and other issues of nonindependence, we also investigated these relationships within only those 52 cultures for which Cashdan et al. (2014) provided a specific pathogen prevalence score. Within this subsample, historical pathogen prevalence was significantly negatively associated with overall levels of physical contact during greetings, $r(52) = -.30$, $p = .03$. Historical pathogen prevalence correlated nonsignificantly with degree of physical contact during greetings between close friends or family, $r(48) = -.20$, $p = .18$; between strangers $r(21) = -.39$, $p = .08$; and between status-differential dyads, $r(16) = -.31$, $p = .24$. Thus, using these less-attenuated scores produced relationships that were slightly greater in magnitude.

3.2. Test #2: is historical pathogen prevalence associated with the prevalence of romantic kissing?

For 64 of the cultures coded for the presence/absence of kissing, Cashdan et al. (2014) provide scores for historical pathogen prevalence. Of the remaining cultures, we were able to estimate pathogen prevalence based on geographically proximate cultures for a further 49, giving a total of 113 cultures for our analysis.

To assess whether historical pathogen prevalence predicted the presence of romantic kissing we conducted a binary logistic regression comparing standardized SCCS scores and the coded values for presence

of kissing. Historical pathogen prevalence significantly negatively predicted the presence of kissing, $B = -0.79$, $SE = 0.31$, $p = .01$ (Holm–Bonferroni corrected $p = .03$). For interpretive purposes, we assessed the prevalence of romantic kissing in high versus low pathogen prevalence cultures by performing a mean split. This revealed that whereas romantic kissing was present in 63% of the cultures having below-average pathogen prevalence, it was present in just 42% of the cultures having above-average pathogen prevalence.

3.3. Test #3: is historical pathogen prevalence associated with physical contact during mortuary rituals?

As with the previous two tests, we compared the coded values with values for historical pathogen prevalence from Cashdan et al. (2014). In this case 32 of the 51 cultures analyzed were represented in Cashdan et al.'s catalogue. For the remaining 19 cultures, we again used data for the most geographically proximate culture available. Scores for levels of physical contact during mortuary rituals indicated relatively high levels of contact across cultures (M = 3.81, SD = 0.83), and relatively little variation, with 39 of the 51 cultures available for this analysis being ranked as a four ("intimate"). There was no significant correlation with historical pathogen prevalence, $r(51) = 0.19$, $p = 0.19$ (corrected $p = .19$). Although this relationship is similar in magnitude to those of the first two studies, its direction is opposite that of the first two studies.

3.4. Ancillary analyses comparing the effects of human-transmitted vs. non-human-transmitted pathogen prevalence

Finally, we investigated the relationships between Fincher and Thornhill's (2012) estimates of contemporary pathogen prevalence and each of our three outcome variables. Similar to our central analyses, we used zero-order correlational analyses for greeting closeness and mortuary contact, and binary logistic regressions for the presence of romantic kissing. Preliminary analyses revealed that Cashdan et al.'s (2014) historical pathogen prevalence measure correlated substantially with both Fincher and Thornhill's total contemporary pathogen prevalence and human-transmitted pathogen prevalence (r's = .70 and .67, respectively, p's < .001) but negatively and negligibly with non-human-transmitted pathogen prevalence ($r = -.03$, $p = .65$).

Similar to the relationships obtained with regard to historical pathogen prevalence, total contemporary pathogen prevalence was negatively (but marginally significantly) associated with closeness during ritualized greetings, $r(135) = -.16$, $p = .06$, and with presence of romantic kissing, $B = -.30$, $p < .001$, and was nonsignificantly positively associated with contact during mortuary rituals, $r(49) = .16$, $p = .27$. These relationships were largely driven by human-transmitted pathogen prevalence: human-transmitted pathogen prevalence was negatively (but nonsignificantly) associated with contact during greetings, $r(137) = -.13$, $p = .13$, and with presence of romantic kissing, $B = -.42$, $p < .001$, and was negligibly positively associated with contact during mortuary rituals, $r(51) = .12$, $p = .40$. Non-human-transmitted pathogen prevalence was not meaningfully associated with greeting ($r = .07$), kissing ($B = .01$), or mortuary contact ($r = -.10$; all p's > .40).

4. Discussion

Cultures show variation in the amount of physical contact and closeness involved in normative actions associated with greetings, romantic courtship, and mortuary practices. The current study tested the hypothesis that pathogen prevalence would predict the level of physical contact characteristic of these culturally shaped behaviors. We used three analyses of ethnographic records of different types of culturally dictated behavior, drawn primarily from small-scale societies around the world, focusing on the amount of close contact. Results from Tests 1 and 2 offer modest support for the thesis that historical pathogen prevalence partly accounts for cross-cultural variation in contact and closeness in greetings and likelihood of romantic-sexual kissing. Ancillary analyses using the proxy of nation-level contemporary pathogen prevalence reveal that these relationships are most likely driven by human-transmitted, rather than non-human-transmitted, pathogen prevalence. Test 3 finds no meaningful relationship between historical pathogen prevalence and the amount of contact with the deceased during mortuary rituals.

This investigation is the first to directly examine the relationship between pathogen prevalence and physical contact during culturally specific everyday rituals. The results from Tests 1 and 2 are consistent with findings from prior work examining the relationship between pathogen prevalence and cultural, psychological, and attitudinal variation (e.g., Fincher et al., 2008; Letendre et al., 2010; Murray et al., 2011; Thornhill & Fincher, 2014). Most of these previous studies, however, have shared at least two significant limitations. First, they have largely relied upon contemporary nation states as units of analysis, a practice that frequently entails issues of non-independence (ie, Galton's problem), as many nations are linked through histories of colonialism, migration, and extensive trade. Second, the dependent measures for these studies have been largely psychological in nature, assessing attributes (such as attitudes towards conformity or outgroups, or condemnation of purity-related moral transgressions) that often have only indirect implications for behavioral defense against pathogens. In contrast, the present study is the first to establish evidence for the possible influence of local pathogen prevalence on cultural practices directly pertaining to physical contact – practices that have real, demonstrable implications for pathogen transmission.

4.1. Why no relationship for Test #3?

We found no evidence that regional pathogen prevalence predicts reduced physical contact in mortuary rituals. It is possible that the lack of cultural variation in the dependent measure may have prevented an adequate test of the hypothesis. There was very little variation in levels of physical contact between cultures: of cultures that had funeral rituals involving reported physical contact with kin, 76% were categorized as "intimate" (non-invasive) contact. (Because we employed a dataset originally constructed for other purposes, this test only examined the behavior of kin; however, this will not have substantially biased the result, as kin are excluded from mortuary preparations in only 4 of the 57 cultures examined [White et al., in press].) This then begs the question: given our premise that pathogen risk will shape cultural practices, what may explain the prevalence across diverse pathogen ecologies of intimate contact with corpses during mortuary rituals?

Might intimate contact with corpses be less risky than presumed? When death is a consequence of trauma rather than infection, the risks to others of contact with corpses are generally low (Morgan, 2004). However, when death is due to or concurrent with serious infection, particularly in the immediate postmortem period, contact with corpses poses a real risk of disease transmission (Healing, Hoffman, & Young, 1995; Morgan, 2004). Traditional mortuary practices do not appear to differ as a function of whether death was accidental, and, indeed, given the difficulty of identifying underlying infections in the absence of modern medicine, the fitness-maximizing default response is one that minimizes opportunities for pathogen transfer from the corpse regardless of the apparent cause of death.

Rather than reflecting an absence of disease risk, the prevalence of intimate corpse contact by kin during mortuary rituals is likely explicable in terms of a competing selection pressure, namely the benefits of abbreviating bereavement, a debilitating state, by accelerating the cognitive reclassification from relationship partner to non-agent that is thought to be a central component of grief (White et al., in press). If the advantages to kin – and to society at large – of truncating bereavement generally outweigh the costs of pathogen exposure, and if intimate contact with the corpse facilitates this, then such practices will

be relatively ubiquitous, and thus will not reflect local pathogen prevalence; this then may explain our null result in Test 3.

Another feature that distinguishes mortuary practices from greeting and romantic practices – and that may explain the lack of relationship between pathogen prevalence and mortuary practices – is frequency of occurrence. Whereas greeting or romantic-related practices may occur several times a day, mortuary practices for any individual occur far less often over the lifetime. This frequency difference may affect both the actual and perceived relationship between physical contact and contamination threat. Some preliminary evidence suggests that, in many traditional cultures, there is indeed a perceived link between corpse treatment and disease, but that the cultural discourse links proper corpse contact to *lower* disease threat: White, Marin, and Fessler (2016) compared cultural discourse concerning deceased loved-ones across 45 representative cultures extracted from the Human Relations Area Files. They found evidence for the assumption that the recently deceased can cause disease to the living if the corpse was not properly attended to (through ritual burial, for example) in 67% of the cultures sampled. Whether such cultural discourse has adaptive utility, however, remains unclear.

4.2. Limitations and future directions

Correlational investigations such as those presented here cannot reveal the nature and direction of causality. However, in this case, reverse causality is exceptionally unlikely, as there is no logically plausible reason to believe that less physical contact causes higher rates of disease transmission. Slightly more plausible is the possibility that some unmeasured third variable accounts for the modest relationships reported here. Although we cannot rule this possibility out, the patterns that we have found are consistent with a growing body of work documenting the implications of disease prevalence (especially historical disease prevalence) for cultural variation in "cautious" behaviors, attitudes, and cultural practices (e.g., Cashdan & Steele, 2013; Fincher et al., 2008; Murray et al., 2011; Murray, Jones, & Schaller, 2013; Schaller & Murray, 2008). These results are also conceptually consistent with evidence from laboratory experiments that have documented prophylactic behavioral or attitudinal reactions when disease threat is made immediately salient (e.g., Faulkner, Schaller, Park, & Duncan, 2004; Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010; Murray et al., 2013; Murray & Schaller, 2012; Wu & Chang, 2012). There are also consistent relationships between worry about disease and more socially cautious personality traits (Duncan, Schaller, & Park, 2009). The convergence of the present study with other cross-cultural, behavioral, and genetic evidence suggests that a causal effect of historical pathogen prevalence on the amount of physical contact during culturally normative behaviors is the most parsimonious interpretation of the relationships reported here.

A further limitation is that our measurements of both physical contact and historical pathogen prevalence are necessarily crude and noisy. Relative to, for example, prior work that compared attitudinal results at the level of contemporary nation states (e.g., Murray et al., 2011), our comparisons of ethnographic reports of quotidian practices have the advantage of addressing a far broader range of societies, and a larger number of societies that are both less likely to have been subject to substantial changes in the recent past and experientially closer to the challenges of infectious disease. At the same time, however, reliance on qualitative ethnographic descriptions – which frequently include broad-brushstroke generalizations made without reference to the representativeness or lack thereof of the communities observed – necessarily introduces a level of subjectivity and imprecision that does not plague prior work. Nevertheless, this additional measurement error makes the current tests more, rather than less, statistically conservative, as there is every reason to believe that this error is randomly distributed. It is possible that future tests may be able to employ more disattenuated measurements as relevant cross-cultural databases become more exhaustive and precise, allowing for tests that include sufficient controls. With the above caveats in mind, our results provide suggestive preliminary evidence that variation in some culturally shaped practices may be driven by pathogen prevalence. If this interpretation is correct, the risk of transmissible disease may have played an integral part in shaping deeply entrenched aspects of many everyday practices.

Just as this study did not have the inferential luxury of controlling for potential third-variables (unlike contemporarily based cross-national studies), this study also was unable to explore the more ecologically realistic complex causal chains that link historical pathogen prevalence to culturally embedded behavioral norms. Evidence suggests, for example, that higher pathogen prevalence is linked to more collectivist value systems (Fincher et al., 2008; Fincher & Thornhill, 2012). Other work suggests that this pathogen-collectivism relationship partially mediates the cross-national relationship between pathogen prevalence and innovation (Murray, 2014). Future work at the small-scale society level should seek to investigate whether such mediational relationships exist for predicting culturally shaped physical contact as well, and should concurrently seek reliable measures of theoretically-plausible third variables.

4.3. Biological evolution, cultural evolution, or both?

If we accept that pathogen prevalence has a causal effect on some of the behaviors examined here, what remains unanswered is the mechanism by which this cultural variation develops. As we discuss below, there are multiple (and not necessarily mutually incompatible) possibilities.

First, it is possible that, via underlying psychological traits concerning, for example, contamination sensitivity or affiliative tendencies, the between-society differences that we have observed owe to differences in gene frequencies between cultures. The plausibility of such an account is supported by cross-cultural allele-frequency analyses suggesting that pathogens have been a principal selective force throughout human evolution (Fumagalli et al., 2011), and evidence of relatively rapid evolution of different allele frequencies within populations that differ in the prevalence of specific kinds of pathogens (Williamson et al., 2007). Other recent work suggests that polymorphisms associated with greater vulnerability to disease are also associated with more reserved and cautious personality traits (MacMurray, Comings, & Napolioni, 2014; Napolioni et al., 2014). However, this work is preliminary at best.

Second, it is possible that the patterns that we have documented owe not to selection acting locally to create between-population genetic differences, but rather to a deeper history wherein selection has crafted species-typical adaptations that facultatively adjust specific classes of behavior in response to cues regarding relevant features of the local ecology, creating within-society similarities and between-society differences (that is, what has been termed evoked culture – Tooby & Cosmides, 1992; Gangestad, Haselton, & Buss, 2006) that do not owe to socially transmitted cultural norms. Evidence of the importance of environmental cues in calibrating the immune system to the local pathogen ecology (e.g., Miller et al., 2007) suggest by analogy that relevant facultatively adjusted behavioral adaptations are indeed possible. Here too, the patterns of behaviors observed may reflect underlying cross-cultural psychological differences, albeit in this case reflecting not differences in genotype, but the impact of differing ecological inputs on phenotype. In combination with the previously cited growing corpus of work documenting correlations between relevant attitudinal features and local pathogen prevalence, the plausibility of the proposal that psychological differences, regardless of source, could influence the frequency of the behaviors at issue here is enhanced by anecdotal reports that, upon initial exposure to the practice, members of societies in which romantic kissing was not the norm viewed the activity as disgusting and unclean (see Jankowiak et al., 2015). However, at present, the available evidence does not suffice to determine whether the differences in greeting and kissing behavior explored here reflect underlying psychological

differences, nor does it suffice to determine the proximate causes of any such differences.

Third, it is possible that the patterns that we have observed are exclusively the product of transmitted culture. Cultural evolution parallels biological evolution in a number of respects (Richerson & Boyd, 2008; Sripada & Stich, 2004; Mayfield, 2013); just as genomes evolve in response to ecological pressures, so too do the norms, values, and behavioral prescriptions that define human cultures. Cultural evolution provides a speedy and efficient means through which human populations adapt effectively to their ecological circumstances, while the key features of this process do not require any recognition – whether in terms of overt propositional knowledge or merely affective intuitions – of the functional utility of the practices at issue (Boyd, Richerson, & Henrich, 2011). It is therefore possible that in regions of persistently higher pathogen prevalence, cultural norms that favor prophylaxis and the avoidance of unnecessary contact are more likely to develop and persist. Ceteris paribus, individuals who follow such practices will be healthier and thus more successful, leading others to imitate them; in turn, the average fitness of such groups will rise, leading these practices to spread via intergroup conquest, assimilation, or imitation. These processes will iterate in proportion to the strength of the selection pressure exerted by pathogens: as selective pressure from transmissible disease diminishes with ecological changes over geographical distance, the costs of avoiding the behaviors at issue will diminish, opening the door to their appearance, a process enhanced by any benefits (such as facilitating affiliation or evaluating the biological quality of a prospective mate) that they might provide.

While the first and second explanations presented above are in competition with one another, and the third explanation can stand independent of both the first and second explanations, a fourth possibility is a hybrid account that blends either the first or second explanation with the third. If attitudinal and affective features of individuals vary as a function of pathogen prevalence, due either to i) correlations between pathogen prevalence and genotype, or ii) correlations between pathogen prevalence and facultatively adjusted phenotype, then these features of individual psychology will constitute an attractor (Sperber, 1996) or content bias (Henrich & McElreath, 2003) such that practices that are congruent with these dispositions will be more readily adopted and retained, and thus will be more likely to spread and persist over time (see also Fessler, Clark, & Clint, 2015).

The available evidence does not allow us to adjudicate among the four possibilities listed above, hence additional research is clearly called for. To list but a few possibilities, future investigations might test the first versus the second explanations by taking advantage of patterns of immigration from the developing world to the developed world, examining the stability or lack thereof in relevant features of psychology and behavior among first- and second-generation immigrants who have moved from high-pathogen environments to low-pathogen environments; similarly, the third explanation could be assessed by performing similar tests among immigrant samples that differ in their degree of assimilation. Likewise, the hybrid fourth explanation could be tested by examining correlations between individual psychological differences and the rapidity with which introduced practices – be they romantic kissing or hand-washing with soap – spread in communities previously lacking such norms. In short, should the overarching patterns that we have documented here persist when examined using more fine-grained methods, the study of the relationship between cultural practices and pathogen prevalence may prove to be a productive avenue for exploring key questions regarding the evolutionary processes responsible for cross-cultural differences and similarities.

Author note

The complete datasets to accompany this paper are archived at http://escholarship.org/uc/item/5c33d7jd.

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