



Obstacles and catalysts of cooperation in humans, bonobos, and chimpanzees: behavioural reaction norms can help explain variation in sex roles, inequality, war and peace

Adrian V. Jaeggi^{a,*}, Klaree J. Boose^b, Frances J. White^b and Michael Gurven^a

^a Department of Anthropology, University of California Santa Barbara, Humanities and Social Sciences Building (HSSB) 2001, Santa Barbara, CA 93106-3210, USA

^b Department of Anthropology, University of Oregon, 308 Condon Hall, 1321 Kincaid Street, Eugene, OR 97403, USA

*Corresponding author, current address: Department of Anthropology, Emory University, 1557 Dickey Drive, Atlanta, GA 30322, USA, e-mail address: adrian.jaeggi@emory.edu

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Abstract

Our closest living relatives, bonobos and chimpanzees, along with small-scale human societies figure prominently in debates about human nature. Here we emphasize and explain behavioural variation within and among these three species. In the logic of behavioural ecology, individuals have been selected to adjust their behaviour along evolved reaction norms that maximize fitness given current socio-ecological conditions. We discuss variation in three behavioural contexts: relationships between the sexes, hierarchy and inequality, and intergroup interactions. In each context, behavioural variation can be related to two broad socio-ecological conditions: (i) the defensibility of contested resources, and (ii) differences in bargaining power. When defensibility of resources and differences in bargaining power are great, interactions are rife with conflict; when they are minimal, interactions are more harmonious. These socio-ecological conditions therefore constitute key catalysts and obstacles of cooperation. We conclude that human nature should be seen as consisting of evolved reaction norms.

Keywords

cooperation, division of labour, human nature, inequality, peace, sexual conflict, violence, war.

1. Introduction: explaining behavioural variation

Are humans inherently selfish and aggressive or are they cooperative and peaceful? Figuring prominently in the long-standing debate surrounding this question are our closest living relatives, bonobos and chimpanzees, as well as ‘traditional’ human societies such as hunter-gatherers (Knauff, 1991; de Waal, 1996; Keeley, 1996; Pinker, 2011; Boehm, 2012; Fry, 2013). While chimpanzees typically serve as a model for a violent human nature and bonobos for a peaceful one (Wrangham & Peterson, 1996; Stanford, 1998; de Waal, 2005), notions of the ‘typical’ hunter-gatherers have changed over time (Kelly, 2013) and have been used to make either case (e.g., Pinker, 2011; Fry, 2013). Our goal in this paper is to emphasize and explain the substantial variation both within and between these three species using a behavioural-ecological approach, which links behavioural variation to environmental differences. From this perspective, behaviour is context-dependent, as individuals flexibly adjust their strategies to the perceived fitness costs and benefits in their current environment. We consider three broad behavioural domains: relationships between the sexes, hierarchies and inequality, and intergroup interactions. In elaborating the behavioural-ecological perspective on behavioural variation, we aim to provide a more nuanced answer to the opening question.

Behavioural ecology is the study of behaviour as shaped by natural selection, based on the assumption that all organisms (including humans) have been selected to adopt behavioural strategies that on average maximize their inclusive fitness, subject to constraints (Winterhalder & Smith, 2000; Krebs & Davies, 2009; Nettle et al., 2013). Behaviour may not always be fitness-maximizing; deviations from optimality can occur through mechanistic or cognitive constraints or learning biases (McNamara & Houston, 2009; Fawcett et al., 2012), or mismatches between current and ancestral environments, in which the cues that trigger behavioural strategies were more reliably indicative of fitness benefits (Tooby & Cosmides, 1990). Furthermore, multiple stable equilibria may exist for behavioural strategies and a population’s current behavioural profile is therefore partly shaped by its phylogenetic and cultural history (Richerson & Boyd, 2004; Chapman & Rothman, 2009). Behavioural ecology thus provides a useful first approximation to understand behavioural variation, but may not always be sufficient (Borgerhoff Mulder, 2013).

Importantly, different social and ecological conditions favour different strategies; if individuals routinely experienced a range of socio-ecological conditions over evolutionary time with varying pay-offs to different behavioural strategies, then natural selection should produce mechanisms that flexibly shift behaviour along a continuum given reliable cues of shifts in expected pay-offs, i.e., behavioural reaction norms (Dingemanse et al., 2010; Figure 1). By incorporating behavioural reaction norms as causes of adaptive variation, behavioural ecology can be a useful framework for understanding behavioural variation across a wide range of conditions, including among human populations (Winterhalder & Smith, 2000; Kelly, 2013). Cultural differences, in this view, are often tied to current socio-ecological conditions,

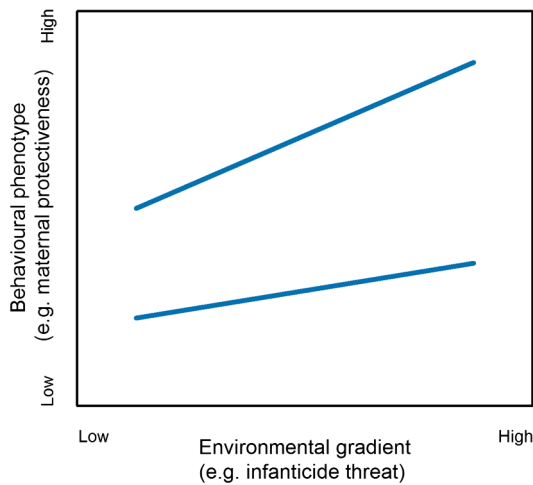


Figure 1. Behavioural reaction norms express how individuals respond to variation in the environment (x -axis) by adaptive changes in behavioural strategy (y -axis) (Dingemanse et al., 2010). Individuals or species can differ in their average behaviour (elevation of the reaction norm) and/or their behavioural plasticity (slope) (Jaeggi et al., 2010a); here, two hypothetical individuals or species are shown that differ in both (see Dingemanse et al., 2010 for discussion of this and other examples). Ultimately, species differences in elevation or slope should correspond to differences in the fitness benefits of the behavioural strategy and the expected range of environmental variation as calibrated by ancestral environments. Proximally, shifts along these behavioural reaction norms could, e.g., be mediated by neuroendocrine mechanisms, through changes in baseline hormone levels (elevation) or acute reactivity (slope) (Trumble et al., 2015). For simplicity we here adopt linear reaction norms though other shapes are plausible. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1568539x>.

with social norms of behaviour functioning as heuristics for successful strategies.

In the evolution of behaviour, the targets of selection are thus not single, obligate types of behaviours but behavioural reaction norms and the mechanisms that underlie them (McNamara & Houston, 2009; Dingemanse et al., 2010; Trumble et al., 2015). Describing human nature therefore requires linking behavioural variation to socio-ecological conditions that tend to promote certain behaviours (and prevent others) because they were reliably associated with fitness benefits in ancestral environments. This leads to a more nuanced view of human nature as consisting of “context-dependent universals” (Chapais, 2014), and can have important implications for addressing problems in crime, conservation, or public health (Penn & Myserud, 2007; Gibson & Lawson, 2014, 2015); some examples include biasing care to biological children over stepchildren (Daly & Wilson, 1998), overharvesting of resources given efficient technology (Alvard, 1998), or the (lack of) adoption of conservation practices (Tucker, 2007) or health-promoting behaviour (Pepper & Nettle, 2014) depending on rates of future discounting as calibrated by environmental risk. Such findings do not generate normative conclusions, such as which behaviours ought to be promoted or prevented, but they can provide useful information about how to best promote or prevent certain behaviours for normative fields like ethics (Kitcher, 2014) or social policy (Gibson & Lawson, 2015).

For a behavioural ecologist then, the best approach to understanding the “obstacles and catalysts of peaceful behaviour” (the theme of this Special Issue) is to identify the socio-ecological conditions that predictably instigate conflict or foster cooperation among individuals or groups. For the purpose of this article, we equate “peaceful behaviour” with cooperation loosely defined, i.e., situations in which the interests of individuals or groups are aligned because of mutual gains (cf., peace defined as “mutually harmonious interactions”, Verbeek, 2008, p. 1501) as opposed to conflict, when interests are not aligned. Here we apply this approach to three broad behavioural domains: (1) Relationships between the sexes, (2) hierarchies and inequality; and (3) intergroup interactions. Throughout these three sections we briefly summarize the relevant theoretical background (Section 2) and review evidence explaining variation among our two closest living relatives, bonobos and chimpanzees (Section 3), as well as among pre-industrialized human societies that best exemplify the link between ecological factors and adaptive

strategies (Section 4). We describe evidence consistent with behavioural reaction norms, especially how greater defensibility of resources is associated with greater conflict in all species and contexts (Dyson-Hudson & Smith, 1978; van Schaik, 1989; Boone, 1992; Sterck et al., 1997; Kaplan et al., 2009), as are greater differences in bargaining power (Summers, 2005; Gurven et al., 2009; Barclay, 2013). However, we also note that some of the proposed connections between socio-ecology and behaviour are tentative and require more research.

2. Relationships between the sexes

2.1. Theoretical background: sexual selection theory

Sexual selection theory attempts to explain the evolution of sex roles, parental investment, and mating systems and their variation across species as individuals of each sex attempt to maximize their potential reproductive success (Trivers, 1972; Emlen & Oring, 1977; Clutton-Brock & Vincent, 1991; Kokko & Jennions, 2008). The modal mammalian pattern is for females to provide virtually all parental care and to be choosy about who to mate with, while males invest their time and energy into competing for and controlling access to fertile females, oftentimes evolving specialized weaponry to do so. While theorists have explained these ‘classical’ sex roles in different ways (Kokko & Jennions, 2008), variation in sex roles within and among species can stem from differences in the monopolizability of mates and their relative bargaining power. If fertile females are scarce and defensible, as indicated by a skewed operational sex ratio (OSR, the ratio of males to fertile females), males should compete more heavily for mating access resulting in more sexual coercion and constrained female choice; females might therefore benefit from levelling the OSR if they can. If females gain additional bargaining power, e.g., through coalitions, they can exercise even more choice and select for more tolerant and investing males, potentially resulting in less sexual conflict. When both sexes invest in offspring, the sex in greater demand has more bargaining power and can therefore invest less, as indicated by effects of adult sex ratios or mate quality among birds (Liker et al., 2014).

2.2. Explaining variation in intersexual relations among chimpanzees and bonobos

The reproductive rates of female apes are limited by the amount of energy (food) available to them (Emery Thompson et al., 2012), such that

females typically avoid feeding competition by reducing their time spent in association with others (Wrangham, 1980; van Schaik, 1989). Furthermore, mating itself has costs (Daly, 1980) such as the energetic burden of producing exaggerated sexual swellings, increased feeding competition from males (Williams et al., 2002; Wrangham, 2002), sexually transmitted disease (Nunn et al., 2000), and physical coercion and injuries inflicted by males (Muller et al., 2007). It has therefore been suggested that for female chimpanzees and bonobos, the ability to (i) level the OSR and reduce male-male competition through increased sexual activity, and to (ii) increase their bargaining power and mate choice through increased association with coalition partners directly depends on food availability (Stumpf, 2007; Furuichi, 2011; Hare et al., 2012).

Indeed, in areas with low food availability, chimpanzee females cannot afford to be very social, but instead must spend considerable time alone or with their dependent offspring (Stumpf, 2007). Seasonality (Doran et al., 2002), population density (Mitani, 2006a), and habitat structure (Pruetz, 2006) have all been found to vary the amount of fruit available for chimpanzee communities, with greater habitat productivity associated with higher rates of female affiliation (Mitani et al., 2002). As such, the proportion of time females spend alone varies greatly across chimpanzee populations (Table 1). Bonobo habitats are characterized by larger and less variable food patches (mostly large fruiting trees) (White & Wrangham, 1988), less seasonal variation in fruit availability (Malenky, 1990; Chapman et al., 1994), and more terrestrial herbaceous vegetation (Hare et al., 2012). Bonobo females can therefore afford to remain social throughout the year (White, 1996), spending only 2–3% of their time alone (Table 1).

Differences in food availability affect the OSR as females in good condition are better able to pay the energetic costs of mating, allowing them to cycle more frequently and for longer durations (Stumpf, 2007). As a result, female bonobos and some chimpanzees (especially at Tai) spend a larger portion of their adult lives with sexual swellings, effectively reducing the OSR and thereby decreasing male mating competition (Furuichi, 2011). The ratio of males to females with maximal sexual swellings thus ranges from 2–3 among bonobos and Tai chimpanzees to 12 at Gombe (Table 1), changing the ability of males to monopolize fertile females and potentially explaining divergent patterns of female choice across populations (Stumpf & Boesch, 2006; Muller et al., 2011; Figure 2).

Table 1.
Variation in socio-ecology among long-term chimpanzee and bonobo study sites.

Species	Study site	Mean party size ^a	% time females alone ^a	Adult sex ratio (σ/φ) ^a	Oestrous sex ratio ^{a,b}	Hierarchy steepness ^c	Intergroup death rate ^d
Chimpanzee <i>Pan troglodytes</i> <i>verus</i>	Tai	8.3	4	0.25	1.6	South: 0.83 (σ^2 : 0.82, φ : 0.55) ^e North: σ^2 : 0.39 ^g –0.72 (DCI = 0.71) ^h	South: 0.05 North: 0–<0.05 ^f Middle: 0 East: 0 0
	Bossou Gombe	4 4.5	10 65	0.43 0.74	12.3	φ : 0.07 (DCI = 0.97) ^h	Kasakela: 0.5–0.7 Kahama: 0.25 Mitumba: 0.15–0.25
<i>Pan troglodytes</i> <i>schweinfurthii</i>	Mahale	6.1	31.8	0.28	4.2	M-Group σ^2 : 0.22–0.57 ^g	M-Group: 0.1–0.5 K-Group: 0–0.05
	Kanyawara	5.1	70 ^j	0.7		σ^2 : 0.39 ^g	0.05
	Ngogo Budongo	10.3 5.7	20 ^j	0.6 ^j 0.29–0.42 ^k		σ^2 : 0.4–0.7 ^g	1.55–1.65 0.8–0.85

Table 1.
(Continued.)

Species	Study site	Mean party size ^a	% time females alone ^a	Adult sex ratio (σ'/ϱ) ^a	Oestrous sex ratio ^{a,b}	Hierarchy steepness ^c	Intergroup death rate ^d
Bonobo <i>Pan paniscus</i>	Wamba	15	2	0.33	2.8	0	0
	Lomako	7.1	3	0.83		0.03–0.18 (DCI = 1) ^h	Bakumba: 0 Eyengo: 0–<0.05
	LuiKotale	9 ^h		0.31–0.45 ^h		σ' : 0.9–0.99 (DCI = 0.94) ^l	0

^a Source is Stumpf (2007), unless otherwise indicated.

^b Males/maximally tumescent females. Note that this is not the same as the OSR (but should correlate with it), which was calculated at 60.7 for Kanyawara, and 40.1 for combined data from Bossou, Gombe, Kanyawara, Mahale and Tai (Coxworth et al., 2015).

^c A measure derived from dyadic fighting abilities ranging from 0 (egalitarian) to 1 (despotic) (de Vries et al., 2006). It should be noted that this measure underestimates steepness when relationships are unknown (Klass & Cords, 2011), which is often the case here, and the directional consistency index (DCI) is given as an alternative where available (Koenig & Borries, 2006).

^d Wilson et al. (2014), unless otherwise indicated.

^e Gomes & Boesch (2011).

^f Second number includes suspected deaths.

^g Kaburu & Newton-Fisher (2015).

^h Own calculations based on Boesch & Boesch-Achermann (2000) for Tai, Murray (2007) for Gombe, White & Wood (2007) for Lomako (based on very few observations so likely underestimating steepness) and Surbeck et al. (2015) for LuiKotale (mean party size only included parties with males). ASR includes adult males, parous females, and up to five nulliparous immigrant females. When subadult males (>10 years) are included, the ratio is 0.56–0.82.

ⁱ Wrangham et al. (1996).

^j Wakefield (2008).

^k Crockford et al. (2013), 0.5–0.74 when subadults are included.

^l Surbeck et al. (2011).

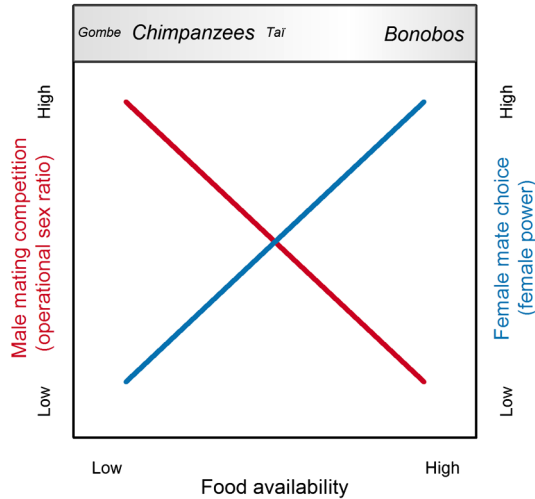


Figure 2. Proposed variation in mating patterns and sexual selection among chimpanzees and bonobos as a function of food availability. Primary effects of higher food availability (less seasonality, larger patches) are to increase female sociality by alleviating feeding competition and thereby increasing female power through coalitions, as well as to increase female sexual activity (by alleviating the costs of mating and reproduction) and thereby levelling the operational sex ratio. Secondary effects then are increased female mate choice (blue line) and decreased male mating competition (red line). Shaded areas at the top indicate the suggested chimpanzee and bonobo ranges, with Gombe and Tai as extreme examples. For simplicity, the two species are represented as having identical, linear reaction norms. See Section 2.2 for details and Table 1 for data on female sociality and sex ratios. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1568539x>.

Recent reformulations of sexual selection theory (Kokko & Jennions, 2008) argue for a greater role of the adult sex ratio (ASR), wherein males in more female-biased populations invest less time in a given female; for chimpanzees and bonobos this ‘investment’ could mostly be in the form of mate-guarding (Coxworth et al., 2015), which can be highly coercive even outside of the oestrous period (Muller et al., 2011). Indeed, there is a strong positive correlation between ASR and the oestrous sex ratio ($r = 0.8$, $N = 4$, Table 1), with the chimpanzee extremes of 0.25 (Tai) and 0.7 (Kanyawara) perhaps reflecting different male mate-guarding strategies (Stumpf & Boesch, 2006; Muller et al., 2011). Of course, mate-guarding can also be less coercive and instead take the form of investment in a long-term relationship, which can have reproductive consequences (Langergraber et al., 2013). At

this point, more research on ASR and mating strategies in *Pan* seems warranted.

Food availability and the resulting levels of sociality also affect females' social leverage and mate choice. When females are largely solitary, mating patterns are dominated by male-male competition and male coercion (Muller et al., 2009, 2011), whereas males may shift their mating strategies to investment in particular relationships when females are more social and can exercise choice (Gomes & Boesch, 2009; Langergraber et al., 2013; Kaburu & Newton-Fisher, 2015). Among bonobos, females are better able to form coalitions against males, which has been described as female power (White & Wood, 2007), and females tend to occupy the highest ranks in the hierarchy in captivity and in the wild (Stevens et al., 2008; Surbeck & Hohmann, 2013; see Section 3.2). While male bonobos may still compete with one another for mating access, especially during a female's peak sexual swelling period, male bonobos rarely aggress against (sexually active) females (White & Wood, 2007; Surbeck & Hohmann, 2013) and male aggression against females is rarely followed by mating. Infrequent male sexual coercion is typically mild and directed at young, newly immigrated females (F.J. White, unpublished data). Under these conditions, female mate choice in bonobos is less constrained and so avoiding to mate with coercive males may explain the stark difference in male temperament between the two species (Hare et al., 2012), and the fact that some females are dominant to males even in the absence of coalition partners (Surbeck & Hohmann, 2013).

In sum, variation among chimpanzee populations and comparison with bonobos suggest that when food availability increases, females can be more social and more sexually active, thereby decreasing male mating competition and increasing females' ability to form alliances, both of which allow females to exercise more mate choice and potentially select for more tolerant males (Stumpf, 2007; Furuichi, 2011; Hare et al., 2012). Future research, especially on bonobos in resource-poor habitats and chimpanzees in rich ones is needed to illuminate the extent to which observed variation in *Pan* social and mating systems stem from similar reaction norms responding to a continuum of feeding competition and/or species differences resulting from diverging ancestral environments (Figure 2).

2.3. *Explaining variation in intersexual relations among human populations*

In contrast to chimpanzees and bonobos, human mating is characterized by pair-bonding, the institution of marriage, and a sexual division of labour with considerable though variable levels of male parental investment (Bird, 1999; Marlowe, 2005, 2007; Gurven & Hill, 2009; Chapais, 2013; Hooper et al., 2014, 2016). While the evolutionary history of human mating systems is beyond the scope of this article (Hrdy, 2009; Gavrillets, 2012; Isler & van Schaik, 2012; Chapais, 2013; Coxworth et al., 2015), monogamy is best seen as the minimal attainable form of polygyny, resulting from low variance in male quality or fighting ability as well as the complementarity of male and female foraging strategies (Gurven & Hill, 2009; Chapais, 2013; Hooper et al., 2016). Sexual conflict in human mating and marriage can arise over (in)fidelity and (dis)investment in the shared good of childcare (Bird, 1999; Gurven et al., 2009), wherein the partner in greater demand (due to mate quality, or biased sex ratios) has more bargaining power and can therefore invest less in the current reproductive unit. Variation in marriage and mating patterns across small-scale societies has mostly been studied with regard to the stability of marriages, with greater stability interpreted as a proxy for less conflict of interest, and the extent to which marriages are polygynous vs monogamous, with greater polygyny consistent with stronger male–male competition and greater variance in male quality. Greater mate quality can lead to greater bargaining power and therefore the ability to demand more investment and acquire more mates (Figure 3). Polyandrous marriage is very rare cross-culturally, usually associated with resource-poor environments where joint production (often of brothers) is required to provide sufficient resources for a family (Smith, 1998).

Among foragers, male and female contributions to the diet vary with latitude, effective temperature, and primary production (Marlowe, 2005; Kelly, 2013), which affects mating patterns as marriages cross-culturally are more stable when both sexes contribute equally to subsistence but unstable when one sex contributes disproportionately, thereby finding itself in higher demand (Quinlan & Quinlan, 2007). Thus, relationships between the sexes and the associated cultural norms can differ widely across subsistence populations, ranging from patriarchy to gender equality to matriarchy (Woodburn, 1982; Kelly, 2013; Scelza, 2013). Furthermore, in ecological contexts where women are more self-sufficient, polygynous marriages are more common

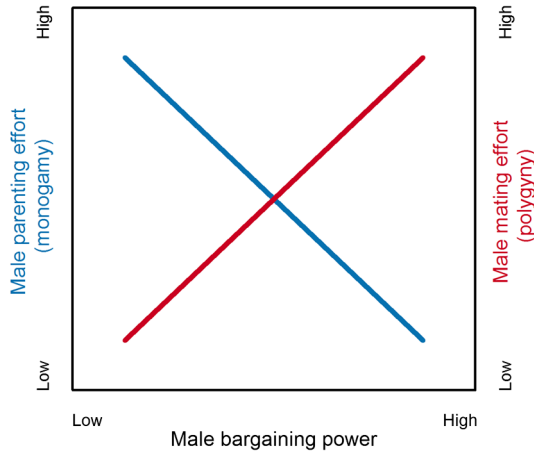


Figure 3. Variation in human marriage, mating and parenting as arising from variation in male bargaining power. As men gain bargaining power (through increased control over the means of production, greater mate quality, a female-biased sex ratio, or more social support), their contribution to existing partnerships decreases (blue line). With lower male parenting effort, monogamous marriage becomes less stable, and male pursuit of additional matings increase, resulting in higher levels of polygyny at the individual and population level (red line). See Section 2.3 for examples and details. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1568539x>.

(Low, 2003, 2009), presumably because some males can attract and defend more mates when the need to provide for them is reduced, or conversely, because the absence of male productivity as a factor in female mate choice reveals other male qualities with greater variance (Scelza, 2013). Similarly, polygyny is more common in high pathogen environments where fewer men make viable partners (Low, 1990).

Among pastoralists and agriculturalists where the means of production (land, livestock) can be controlled by men, variance in male quality and therefore levels of polygyny also increase (Kaplan et al., 2009). This is consistent with the polygyny threshold model (Borgerhoff Mulder, 1988), wherein women's decisions to marry monogamously or polygynously reflect the relative benefits of receiving a partial share of a rich man's wealth or the full wealth of a poor man. Thus, material wealth becomes an important factor in attracting mates; as such, bride price is an expression of male competition to attract wives, and dowry an expression of female competition to

attract good husbands in societies where monogamous marriage is normative (Gaulin & Boster, 1990).

Variation in marriage, mating, and parenting may also result from variation in sex ratios, which change the relative bargaining power of females and males (Kokko & Jennions, 2008; Liker et al., 2014). Where men are scarce they may find themselves in high demand and can successfully pursue multiple partners, resulting in high variance in male fitness; where women are scarce, men can do better by staying with one mate and investing in their offspring (and/or mate-guarding: Coxworth et al., 2015), resulting in low variance in male fitness (Kokko & Jennions, 2008; Schacht et al., 2014). Indeed, variance in male reproductive success, a measure of the strength of male mating competition in 15 small-scale societies was greater in female-biased populations (Schacht et al., 2014). Female-biased populations therefore tend to have lower rates of marriage and male parental investment, while male-biased populations are characterized by a greater proportion of men being married, more investment, and greater marriage stability (Blurton Jones et al., 2000; Schacht et al., 2014). Lastly, post-marital residence matters as spouses with more co-resident kin have more bargaining power and can bias sexual conflict in their favour (Gurven et al., 2009). Post-marital residence and the resulting availability of co-resident kin also vary with subsistence strategy (Dyble et al., 2015).

In sum, human mating and parenting differs from that of chimpanzees and bonobos through the formation of pair-bonds and varying levels of biparental investment, which then becomes the subject of potential conflict. Variation in male-female relationships is predicted by ecological factors affecting diet and subsistence, sex ratios, and support networks, all of which affect relative bargaining power and therefore contribution to shared investments.

3. Hierarchies and inequality

3.1. Theoretical background: socio-ecological models and reproductive skew theory

Dominance hierarchies represent formalized priorities of access to resources; consequently, high-ranking individuals usually have greater fitness than low-ranking ones (Cowlshaw & Dunbar, 1991; van Noordwijk & van Schaik, 1999; Kutsukake & Nunn, 2006). Yet there is much variation in the strength

of dominance hierarchies and the resulting intragroup relationships within and between species, ranging from egalitarian to despotic groups (Schino & Aureli, 2008). Two theoretical approaches link variation in dominance hierarchies and (in)equality to socio-ecological factors.

Socio-ecological models emphasize the spatial and temporal distribution of resources and their resulting economic defensibility (Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997; Isbell & Young, 2002). Clumped, predictable food patches are expected to lead to stronger female dominance hierarchies, while male dominance hierarchies depend on the temporal and spatial distribution of fertile females (see Sections 2.1 and 2.2). If resources are defensible only by multiple individuals, coalitions and alliances are formed, which can either reinforce or level the hierarchy (Bissonnette et al., 2015). All else equal, greater differences in relative fighting ability, formalized as the steepness of the dominance hierarchy (de Vries et al., 2006), are associated with upward flow of goods and services (food, grooming, mating) towards dominants and downward flow of (coalitionary) aggression against subordinates, whereas weaker hierarchies are associated with more reciprocal exchanges (van Schaik, 1989; Barrett et al., 1999; Schino & Aureli, 2008). In this case, fighting ability equates to bargaining power, and therefore the ability to bias the distribution and flow of commodities.

Reproductive skew theory was developed to explain variation in the extent to which reproduction is monopolised among animal groups (Vehrencamp, 1983; Johnstone, 2000), but can be extended to the monopolisation of other resources such as wealth and power (Summers, 2005). There are two broad arguments to explain decreases in skew, namely that dominants concede matings to subordinates to incentivize them to stay (concession), and that dominants are unable to monopolize all matings (tug-of-war) (Kutsukake & Nunn, 2006). Specific factors that have been shown to affect skew include ecological and demographic factors such as outside options, i.e., opportunities to breed elsewhere (decrease skew), relatedness among group members (increases skew), differences in fighting ability (increase skew), or group size (decreases skew). For instance, the number of males in a group was found to be a strong negative predictor of skew across primate species because monopolization becomes increasingly difficult for dominants in larger groups (Kutsukake & Nunn, 2006).

These theories reflect how patchiness impacts resource defensibility, and the importance of relative bargaining power through fighting ability and outside options. Dominants monopolize resources when they can, but concede

to others if they must, to the point of offering other commodities in exchange for support when bargaining power is more equal.

3.2. Explaining variation in hierarchies and inequality among chimpanzees and bonobos

There is substantial variation in dominance hierarchies within and between chimpanzee communities (Table 1). Females compete to establish home ranges in productive areas, resulting in rank effects on fitness (Pusey et al., 1997), and higher levels of competition due to increased female density result in increased aggression, including female-led infanticide (Townsend et al., 2007). Males compete for access to fertile females (see Section 1.2), but male mating success is not only a function of individual fighting ability but also influenced by coalitions with other males as dominants concede matings to their allies or are unable to completely monopolize access to females (Watts, 1998; Duffy et al., 2007; Wröblewski et al., 2009; Gilby et al., 2013a). However, the effects of demographic factors (such as the number of males) on mating skew seem to be limited (Langergraber et al., 2013). In order to recruit support, dominants therefore invest in alliances by exchanging grooming and food, especially meat (Nishida et al., 1992; Watts, 2002; Mitani, 2006b; Gomes & Boesch, 2011; Jaeggi & van Schaik, 2011). The steepness of the dominance hierarchy affects patterns of exchange: exchanges of coalitionary support, food, and grooming tend to be more reciprocal in egalitarian groups, but more one-sided in despotic groups (Jaeggi et al., 2010b; Gomes & Boesch, 2011; Kaburu & Newton-Fisher, 2015). Gains from cooperation such as in hunting (Boesch & Boesch-Achermann, 1989; Boesch, 1994) and territorial defence (see Section 4.2) could further reduce hierarchies through subordinate leverage; indeed, species that have a history of cooperation are more averse to inequity (Brosnan, 2011), bolstering the idea that a need for cooperation creates subordinate leverage which over time may shape species-typical psychology (Figure 4).

Bonobo dominance hierarchies are described as more relaxed than chimpanzee hierarchies due to reduced female feeding competition and reduced male mating competition (see Section 2.2), and are typically characterized by several females ranking highest in the group (White & Wood, 2007; Furuichi, 2011; Surbeck & Hohmann, 2013). This female (co-)dominance may be caused by females' ability to form coalitions against otherwise dominant males, reduced male fighting ability in large groups, male deference in conflicts over resources that are more limiting to female fitness (food), past and

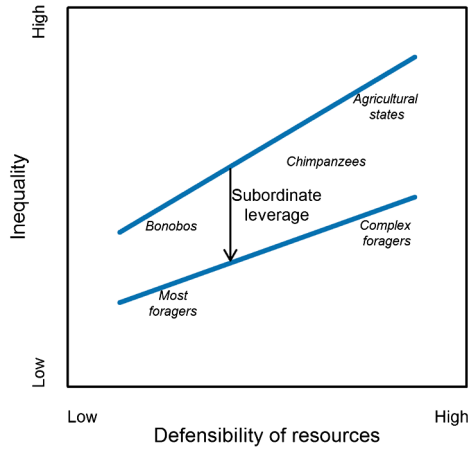


Figure 4. Across species, the extent to which resources are defensible should positively associate with resultant inequality as dominants are able to hoard larger shares. However, the elevation of this reaction norm can decrease if subordinates maintain leverage due to a need for coalitions in resource defence, cooperative production, outside options, or reduced differences in fighting ability. The slope might decrease as depicted here if the importance of collective action, and hence subordinate leverage, in procuring and protecting resources increases with defensibility as might be the case for complex foragers and chimpanzees. Placement of example populations is tentative, see Section 3 for details. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1568539x>.

current selection for tolerant males, or some combination thereof (Surbeck & Hohmann, 2013). Adaptation to relaxed dominance hierarchies in extant bonobos is exemplified by a lack of formalized submission vocalizations (i.e., pant grunts) compared to chimpanzees (Hare et al., 2012). Nonetheless, some males, especially those without powerful female allies, are routinely excluded from prime feeding sites and from access to preferred social partners and fertile females, resulting in rank effects on male fitness, and steep male hierarchies (Surbeck et al., 2011; Table 1). Little is known to date about the steepness of female hierarchies (cf., Table 1) or rank effects on female fitness in wild bonobos. Captive studies illustrate the extent and limits of reaction norms in hierarchy formation as clumped resources, small group size, and an inability to fission can lead to very hierarchical groups with highly unequal distribution of food, grooming, mating, and other benefits (Stevens et al., 2005, 2008; Jaeggi et al., 2010b). Perhaps due to an absence of formalized submission signals, hierarchies in these captive groups are less stable

than among chimpanzees, leading to constant re-negotiation of ranks and thus greater levels of escalated aggression (Stevens et al., 2008).

In summary, while chimpanzee hierarchies typically confer fitness benefits on high-ranking individuals, concessions in the form of mating or resource access, meat sharing, or grooming reduce variance among group members. Bonobo hierarchies differ due to reduced competition and female power, which might explain species differences in male temperament and formalized submission signals. Future research should examine the use of hierarchy steepness and other socio-metrics to characterize variation in *Pan* hierarchies and link this variation to resource distribution and access.

3.3. Explaining variation in hierarchies and inequality among human populations

Like other primates, humans have been selected to maximize access to valuable resources, but since men's mate quality partly depends on their productivity and wealth (see Section 2.3) food and other material resources may be limiting for both sexes' fitness. In contrast to most nonhuman primates then, human males should compete over control of resources and not just directly over mating (Foley & Gamble, 2009; Kaplan et al., 2009). This link between material resources and male fitness amplifies the potential for variance in male reproductive success, resulting in great variation in social stratification and inequalities throughout human history as dominants tried to monopolize resources while subordinates struggled to level inequalities, with resource defensibility and bargaining power turning the scales (Cashdan, 1980; Boehm, 1993; Summers, 2005; Foley & Gamble, 2009; Kaplan et al., 2009; Powers & Lehmann, 2014).

Among foraging societies, social structure varies from egalitarian to highly stratified (or "complex") groups (Marlowe, 2005; Kelly, 2013). Several socio-ecological factors have probably contributed to relatively egalitarian hierarchies and low levels of resource inequalities for much of human prehistory (though perhaps not preceding our species: Foley & Gamble, 2009), in spite of an evolved tendency for individuals to accumulate power and resources whenever they can: (i) foraging returns are often unpredictable, and resource pooling is an effective means of buffering the risk of shortfalls, thus creating interdependence among individuals (Winterhalder, 1986; Gurven, 2004); (ii) mobility of prey and seasonal variation in food availability require residential mobility and flexible grouping patterns, allowing subordinates to 'vote with their feet' and move away from would-be

dominants (Woodburn, 1982; Bell & Winterhalder, 2014); and (iii) projectile weapons and other technology effectively equalized dyadic fighting ability and facilitated levelling coalitions that can directly select against would-be dominants (Boehm, 1993, 1999; Okada & Bingham, 2008; though unequal access to weapons increases inequality as discussed below).

Despite these levelling factors and the absence of formal hierarchies, differences in status and fitness outcomes persist even among egalitarian foragers (von Rueden, 2014), consistent with some variation in individual quality (e.g., hunting skills) and the need for leadership in within-group coordination (Hooper et al., 2010; Powers & Lehmann, 2014; von Rueden et al., 2014). Indeed, the association between male status and fitness is equally strong in foraging societies as in other subsistence economies (though it is lower than in other primates; von Rueden & Jaeggi, data not shown), suggesting a long history of positive selection for status-seeking behaviour. Less is known about female hierarchies, but status competition among females is also common in subsistence populations (Rucas et al., 2006; Hess et al., 2010).

In more recent history, changes in the resource base and increases in population density led to predictable shifts away from egalitarianism. Thus, complex hunter-gatherers typically occupied productive patches with predictable and controllable resources, were highly sedentary and lived at high densities, resulting in hereditary leadership and political inequality, and even slavery to increase household production and food storage, along with the associated changes in cultural norms and values (Marlowe, 2005; Kaplan et al., 2009; Kelly, 2013). Even though highly productive coastal foraging patches might have been around for a long time (de Vynck et al., 2015), the high population densities required to shift foragers towards these sedentary patterns probably did not arise until recently (Binford, 2001). Incipient market integration among extant foragers provides another illustration of the adaptable nature of social stratification and inequality; among the Kalahari !Kung, residence structures, property rights, and sharing norms quickly changed with the advent of new types of resources (Cashdan, 1980; Yellen, 1990), and have probably done so repeatedly in the past (Solway & Lee, 1990). Among the Tsimane' of Bolivia, access to market wealth has not measurably eroded traditional sharing practices (yet) (Gurven et al., 2015), even though inequalities in wealth and power seem to be increasing.

The domestication of plants and animals may further increase inequalities. Agricultural production is limited by fertile land (thus reducing residential mobility), can be increased by coerced labour, and generates predictable surpluses, all of which results in the potential for exploitation by dominants and ultimately the rise of states and empires (Carneiro, 1970; Betzig, 1986; Boone, 1992; Powers & Lehmann, 2014). Yet not all farming societies are stratified, and not all are stratified to the same degree. Horticulturalists practicing slash-and-burn farming where production is mostly limited by labour input are relatively egalitarian and acephalous, whereas those inhabiting islands where production is limited by fertile land instead are typically chiefdom-based, and have more heavily regimented property rights (Kaplan et al., 2009; Gurven et al., 2010). Even among intensive agriculturalists stratification can vary due to crops differing in their storability, predictability and taxability, resulting in varying degrees of stratification.

Power differentials between dominants and subordinates also fluctuate as a function of technological developments and access to effective weaponry, resulting in variation in inequality (Summers, 2005); for instance, knights were viewed as invincible by untrained and unarmed peasants but were rendered obsolete by the invention of longbows and eventually guns, leading to a reduction in despotism. Finally, variation in the extent to which fitness-limiting capital can be transmitted across generations influences levels of inequality; foragers and horticulturalists are mostly limited by embodied and relational capital, which is not strongly heritable thus allowing each generation to get a fresh start, whereas pastoralists and agriculturalists are limited by material capital which can be transferred to the next generation, thus perpetuating inequality (Borgerhoff Mulder et al., 2009).

In sum, there has been much variation in hierarchies, (in)equality, and resource access in human societies, even though the conditions for highly stratified societies (defensible resources, limited mobility, high population density) probably arose only recently. What emerges is a clear pattern of increased inequality when fitness-limiting resources are defensible by dominants, and decreased inequality when subordinates have bargaining power due to cooperative production, outside options, or levelling coalitions.

4. Intergroup relationships

4.1. Theoretical background: territoriality and gains from intergroup cooperation

The economic defensibility of territories determines relationships among neighbouring individuals or groups across a wide range of species (Brown, 1964; Davies & Houston, 1984). Defending a territory requires time and energy to patrol the perimeters and keep others out, which is only economical when the resources in a territory are worth defending, i.e., highly productive and clumped, and so can be patrolled in a reasonable amount of time (Mitani & Rodman, 1979). Furthermore, territorial defence is costly to individuals yet some benefits of a defended territory are shared by everyone in a group, potentially resulting in a collective action problem, wherein each individual is better off free-riding on the efforts of others, but the group as a whole is better off if territories are defended (Willems et al., 2013, 2015). If resources are clumped and defensible, and groups can overcome this collective action problem (through aligned interests or the action of individuals who benefit disproportionately), interactions among neighbouring individuals or groups can be hostile (Emlen & Oring, 1977; Sterck et al., 1997; Willems et al., 2015). If resources are dispersed, neighbouring groups should not engage in direct competition, which, coupled with the collective action problem may explain the highly overlapping home ranges in many primate species (Willems et al., 2013, 2015).

In addition to resource density and predictability, the extent to which there are potential gains from cooperation among neighbouring groups should affect intergroup relationships (Kelly, 2013; Figure 5). Consider a situation in which a group experiences high variance in food abundance. They have two options to buffer the risk of shortfalls: (a) store food during periods of surplus for consumption in bad times (in the form of body fat or food caches), or (b) rely on neighbours for help during bad times and help them in return during good times, when the marginal costs of sharing are low. Option b may lead to reciprocal tolerance of land use, as well as potential trade among groups; but option b is a viable strategy only if good and bad times are uncorrelated among neighbours; otherwise option a should prevail and may include territorial defence to limit poaching and even warfare and slavery to steal food stores and increase one's own production. Finally, if variance in production is low within groups but high between groups, where

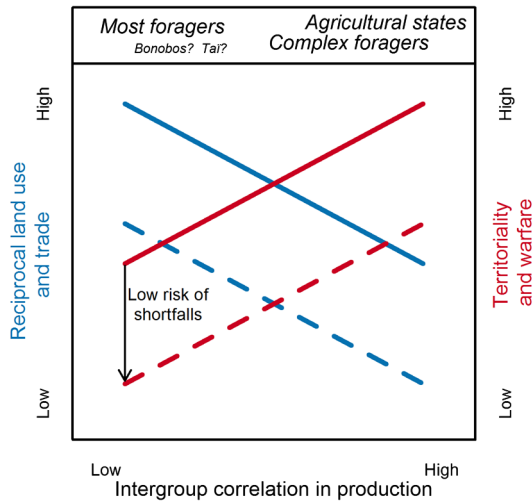


Figure 5. Intergroup correlation in production (resource abundance) changes the gains to raiding or trading. If the correlation is low, one group will have plenty when others have little and vice versa, creating the opportunity to benefit from reciprocal land use and trade, e.g., among most foragers and perhaps bonobos and Tai chimpanzees where females may visit neighbouring groups for extended periods of time. When neighbours experience good and bad times simultaneously, this increases the gains to territoriality and warfare, e.g., among complex foragers and agriculturalists. The benefits from both kinds of intergroup interactions are reduced when the risk of shortfalls is lower (dashed vs solid lines). After Kelly (2013), his Figures 6–8. See Section 4 for details and examples. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1568539x>.

neighbouring groups produce different commodities, the potential gains to trade should motivate more peaceful exchange relationships. Thus, intra- and intergroup variance in production change the pay-offs to raiding or trading (Figure 5).

In sum, as in previous sections, the distribution of resources and differences in bargaining power, but also potential gains from cooperation should pattern variation in inter-group interactions.

4.2. Explaining variation in intergroup relationships among bonobos and chimpanzees

All long-term field studies of chimpanzees to date have reported lethal intergroup aggression, however virtually no such occurrences have been observed at any bonobo sites (Wilson et al., 2014). Chimpanzee territorial behaviour can best be understood as a form of resource-defence polygyny, wherein

coalitions of males defend a territory encompassing valuable resources (e.g., fruit trees) that attract females; the more successful males are in expanding their territory, the more productive the territory becomes, the more females it attracts and/or the higher the resident females' reproductive rates (Manson & Wrangham, 1991; Mitani et al., 2002; Williams et al., 2004; Wilson et al., 2012, 2014). Territorial defence may involve border patrols and incursions into neighbouring territory, wherein outnumbered strangers of all age-sex classes may be attacked if a certain asymmetry in power is reached (Wrangham & Peterson, 1996; Sobolewski et al., 2012; Wilson et al., 2012; Pradhan et al., 2014). In extreme cases, neighbouring groups may be systematically diminished to the point of extinction (at Mahale: Nishida et al., 1985; at Gombe: Wilson, 2012). Participation in territorial defence is facilitated by male philopatry (a derived trait), allowing males to reside with their male kin and form life-long alliances, which might help to overcome the collective action problem of territory defence. Furthermore, individuals who stand to gain a greater share of the benefits may be more willing to participate in defence (Willems et al., 2015). Indeed, males that patrol most tend to have high mating success (Mitani & Watts, 2001; Gilby et al., 2013b) and are more likely to patrol with their allies (Mitani & Watts, 2001). In some populations, females may also participate in aggressive intergroup encounters (Boesch et al., 2008). Rates of lethal aggression vary across chimpanzee populations (Boesch et al., 2008; Wilson et al., 2014), ranging from 0 deaths/year of observation for some Tāi groups to about 1.6 deaths/year at Ngogo (Table 1). Lower death rates could be due to higher gregariousness making strong asymmetries less likely (though Ngogo is a strong counterexample, having both the highest death rate and mean party size among chimpanzee communities; cf., Table 1), or lower resource defensibility and therefore gains to territoriality.

Among bonobos, about a third of intergroup encounters may involve physical aggression (and 87% involve aggressive displays), consistent with some territorial defence (Hohmann & Fruth, 2002); however, border patrolling and incursions are absent, intergroup encounters do not result in lethal aggression, and about half of them involve peaceful interactions among members of different groups (Hohmann & Fruth, 2002; Stumpf, 2007; Furuichi, 2011). As a result, home ranges of bonobo communities overlap more than those of chimpanzee communities. This qualitative difference in intergroup interactions is thought to arise from the relatively lower levels of feeding and mating

competition among bonobos (see Sections 2.2 and 3.2), which reduces the benefits of territorial defence (Stumpf, 2007; Furuichi, 2011). Given low gains to territoriality, we speculate that between-group interactions may be relatively friendly, particularly among females, because females encounter related or otherwise familiar individuals in neighbouring groups from which they immigrated. To some extent, such patterns are also observed among Tai chimpanzees, characterized by intermediate levels of feeding competition (see Section 2.2), where intergroup interactions can be peaceful and females may visit other groups for extended periods of time (Boesch et al., 2008). It is unclear what benefits females might be getting from these intergroup interactions or visits, but possibilities include protection from aggression in their own group or buffering of local resource shortfalls (cf., Figure 5). Another potential explanation for the lack of lethal aggression in bonobos is their large mean party size (Table 1), making it very unlikely for high power asymmetries to occur. However, wild bonobos show no signs of apprehension even when foraging alone at the edges of their range (F.J. White, unpublished data), and captive bonobos express strong curiosity towards strangers (Tan & Hare, 2013). This species difference in xenophobia (which is also well known in the management of captive populations) strongly suggests a relative absence of intergroup violence in ancestral bonobo populations and perhaps potential benefits to intergroup interactions and extended visits (lasting weeks or months at LuiKotale: Surbeck & Hohmann, 2013), which could function as a buffer against local resource shortfalls.

In summary, there seems to be a clear species difference in intergroup relations between chimpanzees and bonobos, despite great variation among chimpanzee populations (Table 1). Lower benefits of territorial defence due to reduced feeding competition, reconnecting with kin and familiar individuals in neighbouring groups, and small asymmetries in power may promote more peaceful interactions in bonobos and some chimpanzee groups. Future research should systematically investigate population differences in lethal aggression among chimpanzees as a function of resource defensibility and demographic factors, and test whether the observed intergroup visits at Tai and among bonobos indeed function to buffer local resource shortfalls as suggested here.

4.3. *Explaining variation in intergroup relationships among human societies*

All ethnographically known foragers have some way of managing spatial boundaries, ranging from subtle connections between individuals and land and so-called “social boundary control” (wherein neighbours have to ask for and are typically granted permission to use or pass land), to clearly marked territories with patrolled perimeters (Dyson-Hudson & Smith, 1978; Kelly, 2013). Territoriality and hostile intergroup interactions are only expected if valuable resources can be appropriated and defended (Kaplan et al., 2009), and if there are few gains to mutual aid due to correlated production (Kelly, 2013; Figure 5).

The resources that many egalitarian foragers rely upon are often dispersed, low density, and unpredictable; resource productivity is also largely uncorrelated among neighbouring groups (Kelly, 2013). This helps to foster the kind of peaceful intergroup interactions and reciprocal exchange often described among foragers (Fry, 2012, 2013). Intergroup interactions characterized by mutual benefits or avoidance were arguably the norm among the low-density populations prevalent during most human prehistory (Binford, 2001; Fry, 2013; Sterelny, 2014), and additionally bolstered by unique features of human social structure such as extended (affinal) kin networks that promote strong ties between multiple groups (Chapais, 2013; Dyble et al., 2015). Sedentism, high population density, and high defensibility of foraging patches changed the pay-off structure for complex hunter-gatherers who were more liable to exhibit territoriality and warfare, especially if they experienced frequent fluctuations in resource productivity that affected neighbouring groups concurrently (Dyson-Hudson & Smith, 1978; Kelly, 2013; Allen & Jones, 2014). Food storage then takes the place of exchange, and captives of war may be enslaved to increase production of otherwise unprofitable resources, as was the case for many Pacific Northwest Coast groups (Ames, 2003). In some cases, a wide range of variation could be found in the same region: in the Great Basin the Owens Valley Paiute were territorial because they had dense and predictable resources such as fish and acorns, the Reese River Shoshone were only territorial when exploiting piñon but not when gathering grass seeds, and the Kawich Mountain Shoshone were never territorial presumably due to low resource abundance (Thomas, 1981).

The domestication of plants and animals introduced more clumped and predictable resources such as land and livestock that could be contested

among neighbours (Keeley, 1996; Kaplan et al., 2009). Labour on agricultural land could also be more easily coerced and controlled than foraging effort, potentially leading to slavery, which provided an additional incentive for warfare (Boone, 1992). Furthermore, men could steal and control women from neighbouring groups when the need to provide for them was diminished, such as when surpluses were controlled by despots or when women could provide for themselves (Betzig, 1986; White & Burton, 1988; Kaplan et al., 2009). In societies where resources can be defended and appropriated and intergroup interactions are hostile, there may be increased cultural reverence for warrior-like traits (such as formidability or heroism) whereas among egalitarian foragers that emphasize sharing and interdependence, such traits are seen as threats against group-living (Boehm, 2012; Sterelny, 2014). As a consequence, warrior complexes and male supremacy are most prominent among pastoralists and agriculturalists (Divale & Harris, 1976; White & Burton, 1988) while cultural values emphasizing peace and interdependence prevail among egalitarian foragers (Fry, 2012).

Finally, the costs and benefits of territorial behaviour or intergroup trade are likely shared unequally among group members, and individual motivations should therefore differ in predictable ways. Lethal intergroup aggression in small-scale societies, if present, resembles intergroup aggression in chimpanzees, with low-risk attacks of male coalitions against outnumbered targets (Knauff, 1991; Manson & Wrangham, 1991; Wilson, 2013), though the majority of lethal aggression may be motivated by sexual jealousy or personal revenge rather than group-level benefits (Fry, 2013; Fry & Söderberg, 2013). In this context, individuals may be largely motivated by potential gains in inclusive fitness and the collective action problem may be limited (Glowacki & Wrangham, 2013; cf., Willems et al., 2015 for primates). In larger societies, where the risks of warfare may be greater and personal benefits more diluted, elaborate systems of reward and punishment may be necessary to sustain participation (Zefferman & Mathew, 2015). Similarly, individuals should differ in their ability and motivation to seek cooperative relationships with out-group members (Pisor, 2015), which can become a source of in-group prestige, e.g., for chiefs in the Pacific Northwest where connections to other groups were showcased in the context of the potlatch (Kelly, 2013).

In sum, ecological models of intergroup relationships can help explain variation in peaceful (i.e., trade or avoidance) and aggressive (i.e., territoriality or warfare) relationships among societies. Taking into account the role

of ecological factors in patterning variation among groups and over time provides a more nuanced understanding of the role of war and peace in human history.

5. Conclusions

We argued that a behavioural-ecological approach helps explain rather than just describe behavioural variation within and among species and therefore provides a useful perspective on catalysts and obstacles of cooperation in humans and our closest living relatives. Emphasizing behavioural reaction norms that predictably shift behaviour in response to socio-ecological conditions (Figures 1–5), this perspective can shed light on debates about human nature (as well as chimpanzee and bonobo natures). Cooperation and conflict are context-dependent, consistently expressed across species as a function of (i) the defensibility of fitness-limiting resources such as food, material wealth and females, and (ii) differences in bargaining power among individuals or groups due to differences in fighting ability, mate quality, social support, outside options, and gains to cooperation. While more data are needed to further support these links between socio-ecological conditions and behavioural variation, we hope that the theoretical framework described here can be useful for guiding future research. A better understanding of the “obstacles and catalysts of peaceful behaviour” is important as it can not only improve our understanding of human nature but may also help inform ethics (Kitcher, 2014) and social policy (Gibson & Lawson, 2015).

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