



Review

The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression

Brian Hare^{a,*}, Victoria Wobber^b, Richard Wrangham^b^aDepartment of Evolutionary Anthropology and Center for Cognitive Neuroscience, Duke University, Durham, NC, U.S.A.^bDepartment of Human Evolutionary Biology, Harvard University, Cambridge, MA, U.S.A.

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Experiments indicate that selection against aggression in mammals can have multiple effects on their morphology, physiology, behaviour and psychology, and that these results resemble a syndrome of changes observed in domestic animals. We hypothesize that selection against aggression in some wild species can operate in a similar way. Here we consider the bonobo, *Pan paniscus*, as a candidate for having experienced this 'self-domestication' process. We first detail the changes typically seen in domesticated species including shifts in development. We then show that bonobos show less severe forms of aggression than chimpanzees, *Pan troglodytes*, and suggest that this difference evolved because of relaxed feeding competition. We next review evidence that phenotypic differences in morphology and behaviour between bonobos and chimpanzees are analogous to differences between domesticates and their wild ancestors. We then synthesize the first set of a priori experimental tests of the self-domestication hypothesis comparing the psychology of bonobos and chimpanzees. Again, bonobo traits echo those of domesticates, including juvenilized patterns of development. We conclude that the self-domestication hypothesis provides a plausible account of the origin of numerous differences between bonobos and chimpanzees, and note that many of these appear to have arisen as incidental by-products rather than adaptations. These results raise the possibility that self-domestication has been a widespread process in mammalian evolution, and suggest the need for research into the regulatory genes responsible for shifts in developmental trajectories in species that have undergone selection against aggression.

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Propensities for a specific type of behaviour such as aggression are sometimes not only surprisingly stable across various contexts but can also be correlated with other types of behaviour. Such correlations, or multitrait behavioural syndromes, occur at both the individual and species level and are found even in taxa as behaviourally flexible as primates (Thierry et al. 2000). For example, across macaque (*Macaca*) species, conciliatory tendency, reconciliatory contacts, bias for reconciliation with kin, and levels of counteraggression are all highly correlated after controlling for phylogeny. The correlation implies that these behaviours evolved in concert, although the mechanism responsible for covariation is unclear (Thierry et al. 2008). One possibility is that behavioural plasticity is limited partly by shared genetic or epigenetic mechanisms such that trait consequences are sometimes adaptive and sometimes nonadaptive. Thus, in cavity-nesting birds, individual

levels of aggression covary across interspecific and intraspecific contexts, but only levels of interspecific aggression have high fitness effects (Duckworth 2006). Behavioural syndromes can therefore incur evolutionary trade-offs that present special challenges for adaptive explanations (Price & Langen 1992; Gosling 2001; Sih et al. 2004a, b).

The challenge is particularly apparent in domesticated animals because they tend to exhibit correlations across traits that are not only behavioural but also morphological, physiological and cognitive, including variations in body coloration, cranial shape, dentition, brain size, activation of the hypothalamic–pituitary–adrenal (HPA) axis and problem-solving abilities. Experimental breeding of a variety of mammals suggests that this 'domestication syndrome' is largely the by-product of selection against aggression (Trut et al. 2009). Two stages of such selection have been proposed for dogs, *Canis familiaris*, in their evolution from wolves, *Canis lupus*. The first involved natural selection or 'self-domestication' in the absence of intentional breeding by humans. During this stage less aggressive and fearful wolves gained a selective advantage because they were able to approach human settlements relatively easily and therefore

* Correspondence: B. Hare, Department of Evolutionary Anthropology and Center for Cognitive Neuroscience, Duke University, Durham, NC 27708, U.S.A.

E-mail address: b.hare@duke.edu (B. Hare).

better exploit novel ecological opportunities (e.g. Peterson et al. 2004) such as human garbage and faeces. After proto-dogs began reliably behaving pro-socially towards humans, a second stage of intentional breeding of dogs could begin (Zeuner 1963; Morey 1994; Coppinger & Coppinger 2001; Hare & Tomasello 2005; Wobber et al. 2009). We suggest that the first hypothesized phase of selection leading to the evolution of dogs from wolves is a useful model for self-domestication (i.e. selection for reduced aggressiveness within a species). If so, consistent with the results of experimental selection against aggression, a self-domestication process could explain a range of correlated phenotypic differences in wild species that show low levels of aggression. We call this the self-domestication hypothesis (cf. Morey 1994).

Here we explore the potential utility of the self-domestication hypothesis by comparing the socially tolerant bonobo, *Pan paniscus*, to its sister species the chimpanzee, *Pan troglodytes* (Won & Hey 2005). Chimpanzees, unlike bonobos, show severe forms of aggression. We first describe the domestication syndrome, evidence that it results from selection against aggression, and its association with developmental changes. We then show that important differences in behavioural and morphological traits between bonobos and chimpanzees conform to the expectations of the self-domestication hypothesis (Wrangham & Pilbeam 2001; Fig. 1). Finally we synthesize quantitative comparisons between the

psychologies of the two *Pan* species designed as a priori tests of the self-domestication hypothesis.

THE ROLE OF SELECTION AGAINST AGGRESSION IN DOMESTICATION

The main behavioural trait that unites domesticated species is a reduction in the expression of various forms of aggressive behaviour, including intraspecific, interspecific, offensive or defensive aggression. Wolves and feral dogs illustrate such reductions, being one of the best-studied pairs of wild ancestors and domesticated descendants. Territoriality among wolves is intense. Individuals avoid buffer zones, and lethal intergroup encounters have been recorded frequently (percentage of adult mortality due to intraspecific killing: 39–65% in Denali, AK, U.S.A.: Mech 1994; Mech et al. 1998; 5.4% in Yellowstone, WY, U.S.A.: Murray et al. 2010). In contrast, feral dogs rarely engage in physical aggression during intergroup interactions, despite the fact that feral dogs and wolves form groups of similar size (Boitani et al. 1995; Pal et al. 1999). Instead of showing contact aggression, feral dog packs tend to bark at each other at a distance until one group is intimidated and leaves (Boitani et al. 1995; MacDonald & Carr 1995; Pal et al. 1999; Bonanni et al. 2010). Only occasionally has a strange dog been observed entering into a group's territory and

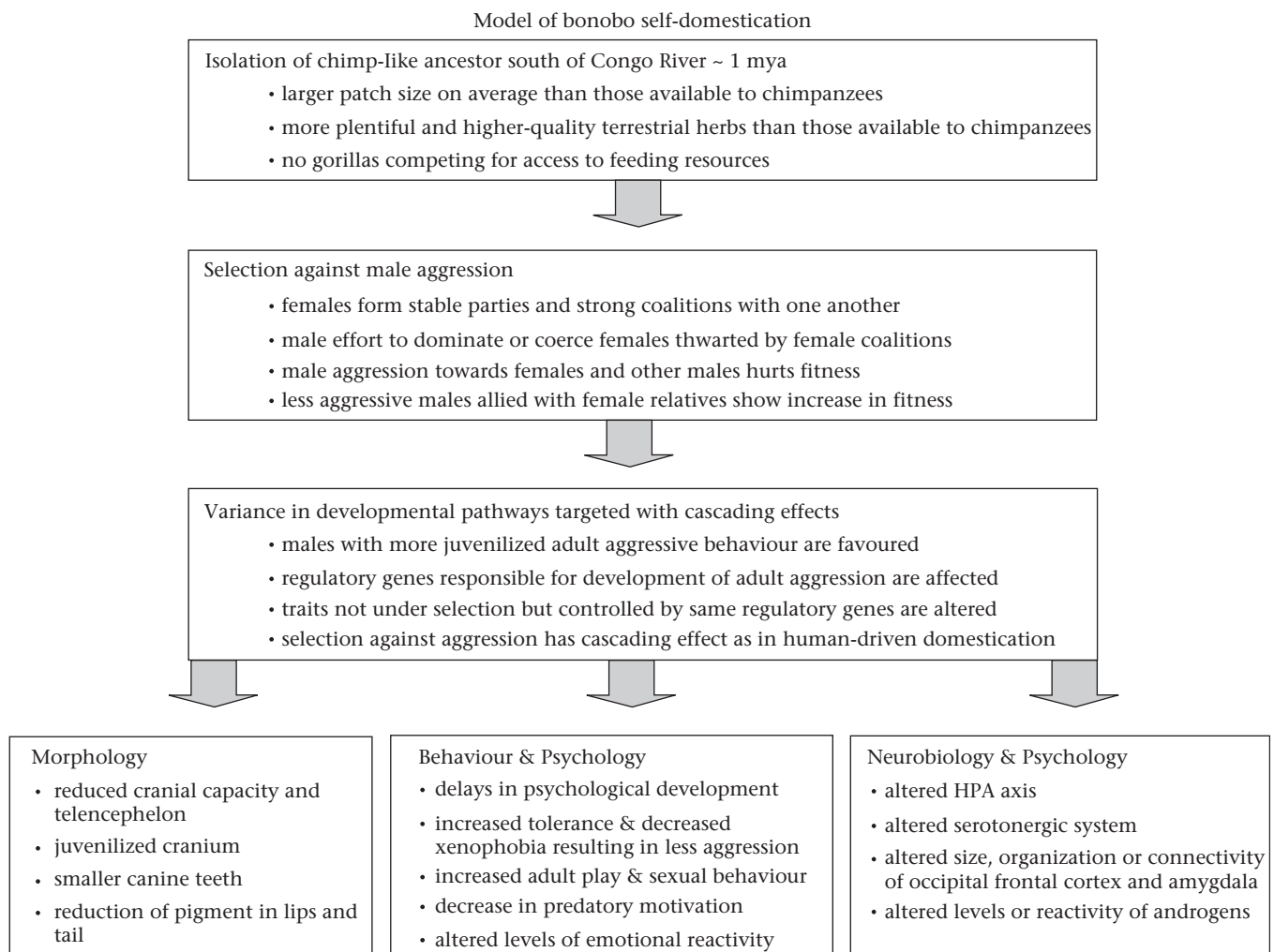


Figure 1. A model of bonobo evolution due to selection for tolerance and against aggression.

being physically attacked or killed (in one case) when it did not retreat (MacDonald & Carr 1995). Levels of within-group aggression show similar reductions in dogs relative to wolves. In wolves, reproductive competition among females includes dominant females readily attacking and sometimes killing the pups of subordinate females (McLeod 1990; Derix et al. 1993; McLeod et al. 1996; Sands & Creel 2004). Among feral dogs there is little evidence for reproductive suppression and no reported cases of infanticide (Boitani & Ciucci 1995; MacDonald & Carr 1995; Pal et al. 1999). Furthermore, a more subtle indication that dogs are less aggressive than wolves is that dogs tend to tolerate the inspection of their anogenital region by a stranger, while wolves can become aggressive even towards group members that attempt anogenital inspections (Bradshaw & Nottingham 1995).

The ethological comparison of wolves with feral dogs indicates that the effects of being reared in captivity do not fully explain the differences in aggressiveness between wild ancestors and domesticates. Captive experiments with a range of species support this conclusion. Kunzl et al. (2003) kept wild cavies, *Cavia aperea*, in captivity for 30 generations without any selection for domestication. Despite the multiple generations of being reared in captivity, there was no evidence of change in aggressive behaviour. Thus, the captive cavies had to be kept in single male groups to prevent adult males from attacking and potentially killing their fully grown sons (Kunzl et al. 2003). Their behaviour contrasted markedly with that of domesticated descendants (guinea pigs, *Cavia aperea f. porcellus*), in which attenuation of aggression allowed multiple males to be housed in a single group without risk. Similar reductions in aggressiveness and increases in social tolerance are characteristic of a variety of domestic species (Price 1998; Trut 2001).

In domesticated species, the characteristic down-regulation of aggressiveness and increased tolerance is accompanied by other differences, many of which serve no obvious function. Together with reduced aggression and increased tolerance these constitute the domestication syndrome. Traits in the domestication syndrome occur with varying degrees of consistency and fall into four major categories. First, physiological changes include those related to aggression, such as reduced reactivity of the hypothalamic–pituitary–adrenal (HPA) axis (Kunzl & Sachser 1999), as well as others with no clear relation to aggression, such as more frequent reproductive cycles (Hemmer 1990; Trut 1999). Second, behavioural changes include reduced aggression and increased tolerance, and also increased pro-social behaviours, particularly play, non-conceptive sexual behaviour and grooming (Hemmer 1990; Clutton-Brock 1992; Coppinger & Coppinger 1998; Kunzl & Sachser 1999; Gariépy et al. 2001). Third are anatomical changes such as reduction in cranial capacity, shortening of the face, reduction in tooth size, depigmentation of parts of the body, floppy ears and reductions in sexual dimorphism of crania (Hemmer 1990; Stuermer et al. 2003; Kruska 2005). Fourth, cognitive changes are suggested by evidence of differences in problem-solving abilities where domesticates and nondomesticates have been compared (Frank et al. 1989; Miklósi et al. 2003; Hare & Tomasello 2005; Miklósi 2008; Topál et al. 2009; Hare et al. 2010; Lewejohann et al. 2010).

Experimental research suggests that the components of the self-domestication syndrome emerge as correlated by-products of selection against aggression, rather than each trait being under direct selection. The longest-running selection experiment has been conducted with silver foxes, *Vulpes vulpes*, in Siberia since 1959 (Belyaev 1979; Trut et al. 2004; for similar work with mink, mice and rats see: Trut 1999; Gariépy et al. 2001; Albert et al. 2008). Individuals in an experimental population of foxes had minimum contact with humans throughout life but were chosen for breeding if they showed a low-level of reactivity towards a human at

7 months of age (as measured by the absence of biting and presence of approach behaviour towards a human standing in front of their cage). A control line was reared under identical conditions but bred randomly in regard to their behaviour towards humans (Trut 2001). Based solely on this selection criterion, successive generations of experimental foxes increasingly began to approach humans instead of running away or trying to bite when touched. After 20 generations most experimental foxes were as friendly towards humans as were dogs (even wagging their tails as a human approached). Mapping experiments have identified similar genetic loci on the experimental fox and dog chromosome VU12 that are associated with the degree that animals wag their tails, approach humans and allow humans to touch them (Kukekova et al. 2006, 2011; vonHoldt et al. 2010), suggesting genetic convergence between the experimental fox population and domesticated dogs.

Numerous features of the domestication syndrome were observed to emerge in the selected foxes (Trut et al. 1991; Trut 2001). Changes in the adrenal cortex, serotonergic and limbic systems related to a down-regulation of the HPA axis were identified within 20–40 generations (Kulikova et al. 1989; Popova et al. 1997; Trut 1999, 2001; Popova 2004). Behavioural changes include higher levels in the experimental population of tail wagging, submissive posturing and high-pitched whining in the presence of humans, similar to how fox kits respond their mothers (Trut et al. 2004, 2009). The experimental population also showed a higher prevalence than the control population of floppy ears, piebald coats and curly or shortened tails. While the males in the experimental population had larger bodies than those in the control population, their faces became wider and flatter and their skulls lost both width and length relative to those of the control males (Trut et al. 2006). Skulls of the males in the experimental population also showed evidence of feminization while a minority of experimental females became fertile biannually as opposed to annually, like dogs but not wolves (Trut et al. 2006). Finally, when compared for their spontaneous ability to use basic human communicative gestures (e.g. the same gestures that nonhuman apes do not use spontaneously; Hare & Tomasello 2005), experimental fox kits were as skilled as dog puppies and more skilled than control fox kits even though social problem-solving skills had not been a target of selection by humans (Hare et al. 2005).

THE ONTOGENY OF DOMESTICATION

The fox data thus show that selection for low levels of aggression and/or a high level of social tolerance leads to a series of traits emerging as by-products. They also suggest that this process of correlated evolution is responsible for the domestication syndrome. Finally, the fox experiment also indicates that the mechanism by which these by-products occur is through changes in development.

The proposal that the domestication syndrome is in large part a consequence of changes in development originates with the idea that selection for reduced aggression tends to favour regulatory genes that affect neuroendocrine maturation (Trut 2001). As a result, adult aggression in domesticates is reduced relative to the ancestral state (Gariépy et al. 2001; Trut et al. 2004). In support, patterns of aggression in domesticated animals, and in experimental populations selected for reduced aggression, show similarities to those found in juveniles of unselected populations (Belyaev et al. 1985; Wayne 1986; Trut 1999, 2001; Coppinger & Coppinger 2001; Gariépy et al. 2001). For example, in the absence of conspecifics, wolf puppies can be socialized with humans, whereas adult wolves cannot. By contrast, dogs retain the puppy-like propensity to be socialized to a much greater extent at later points in their lives (Zimen 1987; Serpell & Jagoe 1995). Furthermore, while wolves

show an increase in the number and complexity of agonistic signals used in aggressive contexts throughout their lives, domestic dogs display only a few, juvenile-like agonistic signals into adulthood (Fox 1969, 1970; Miklósi 2008). Likewise, mice experimentally selected to be nonaggressive towards conspecifics show delays in the timing and development of social behaviours when compared to aggressive mice, suggesting that heterochronic changes in the pattern and/or pace of ontogeny may be responsible for the observed behavioural differences. Gariépy et al. (2001) directly compared the developmental patterns of lines of male mice selected for low and high levels of aggression towards conspecifics. They found that after only four generations the adult 'low-aggression' males maintained levels of attack behaviour typical of juveniles in the original ancestral line. In addition, even though there was no direct selection on freezing behaviour, a behaviour that functions to relieve social tension, the adult 'low-aggression males' showed a similar delay in that this behaviour did not go extinct, unlike the ancestral stock or the 'aggressive line' males, in which it did. With detailed knowledge of both the selection pressure exerted on the experimental populations as well as developmental data on the aggressive and freezing behaviours of each of 13 generations, Gariépy et al. (2001) concluded that juvenilization of selected and unselected social behaviours was due to alterations in developmental pathways in the low aggression line.

As a result, selection for juvenile levels of aggression could explain the cascade of behavioural, physiological and morphological traits typical of juveniles that tend to be retained in adults of the descendant domesticated species (Trut 2001). Paedomorphic aggressive responses may derive from the delayed development of physiological responsiveness in domesticated animals. The brains of experimentally domesticated foxes and rats exhibit elevated levels of serotonin and tryptophan hydroxylase (an enzyme involved in the synthesis of serotonin) relative to unselected populations (Popova et al. 1980, 1997; Kulikova et al. 1989; Hammer et al. 1992; Trut 1999; but see Albert et al. 2009). Given that serotonin levels are generally higher in the brains of immatures than in the brains of adults, and that increased serotonin leads to decreased impulsive aggression, the patterns observed in the foxes and rats suggest paedomorphism in the serotonergic system (Niehoff 1999; Murrin et al. 2007). The domesticated foxes also had lower corticosteroid levels and less corticosteroid reactivity compared to the control foxes, with these differences arising via a developmental delay in the responsiveness of the experimental line and changes in gene expression in the HPA axis (Plyusnina et al. 1991; Gulevich et al. 2004; Trut et al. 2004). These results support the hypothesis that delayed ontogenesis of physiological responses may underlie the paedomorphic aggressive responses in domesticated species.

Why selection for paedomorphic behaviour should lead to paedomorphic morphology is unknown, but such correlated changes can in theory derive from a variety of mechanisms including common regulatory genes, linkage disequilibrium and an epigenetic interaction (Zohary et al. 1998; West-Eberhard 2003, 2005; Ruff et al. 2006; Stock 2006; Zhang & Meaney 2010). For example, a positive correlation between depigmentation and less reactive temperaments in domesticated animals may be related to the fact that dopamine, adrenaline and melanin have the same biochemical precursor while dopamine is thought to inhibit the hormone that stimulates pigment cells to produce melanin (melanocyte stimulation hormone; Ferry & Zimmerman 1964; Tilders & Smelik 1978; Belyaev 1979). Thus, change in an animal's stress response might lead to changes in pigmentation patterns via effects on shared biochemical pathways. Experimentally domesticated animals should ultimately provide the strongest tests of the genetic mechanisms underlying these developmental shifts in mammals. For example, quantitative trait locus-mapping studies

may be able to identify whether the correlations between tame behaviour and distinct morphological shape components are due to a common genetic basis that results in co-segregation of behaviour and morphology (Trut et al. 2006). Taken together, the domestication syndrome suggests that across species, selection on developmental pathways controlling the physiological systems responsible for reduced aggressiveness may also have led to by-product paedomorphosis, or juvenility, in restricted traits governed by the same regulatory genes or physiological systems (contra Gould 1977, who suggested global paedomorphosis of the human phenotype relative to chimpanzees).

REDUCED AGGRESSION IN BONOBOS RELATIVE TO CHIMPANZEES

Given that experiments demonstrate that selection against aggression can generate the domestication syndrome, the question arises as to whether an analogous phenomenon can result from natural selection against different forms of aggression in the wild. The variance in dominance styles and the degree of territoriality observed across mammals and particularly in primates (e.g. ranging from despotic to egalitarian; Kappeler & van Schaik 2002) indicate that selection against aggression could play an important role in shaping the psychology of a variety of species. Bonobos and chimpanzees are closely related species with extensive phenotypic similarities, yet they have striking differences in the severity of the aggression exhibited. Furthermore, morphological comparison indicates that, at least anatomically, bonobos appear relatively derived compared to chimpanzees (Shea 1983; Wrangham & Pilbeam 2001). These congeneric apes therefore offer an opportunity to investigate the applicability of the self-domestication hypothesis. We begin by comparing inter- and intragroup aggression in the two species.

Chimpanzees display intense forms of aggression, both intra- and intergroup. Male chimpanzees use aggression routinely to compete for dominance rank, fight for resources and intimidate females (Goodall 1986; Muller 2002; Watts & Mitani 2002; Wilson et al. 2002; Muller et al. 2007). They use elaborate displays to intimidate rivals and females, often culminating in intense physical aggression that can lead to wounds, or sometimes direct interference with copulations (Watts 1998). Male aggression towards females can also be severe and costly for females, partly as a sexually coercive tactic (Muller 2002; Wrangham 2002; Muller et al. 2007; Muller & Wrangham 2009). In addition, adolescent males systematically target adult females for aggression, so that young adult males are socially dominant to all adult females (Goodall 1986). Aggression among females is less frequent than among males but can be equally severe in leading to wounds or deaths (Pusey et al. 2008). For example, females can wound each other, and both males and females may commit infanticide within groups (Arcadi & Wrangham 1999; Townsend et al. 2007; Pusey et al. 2008). Between communities, chimpanzee groups are highly territorial, cooperatively defending their home range from neighbouring chimpanzee groups, and attack vulnerable neighbours (Goodall 1986; Wrangham 1999; Boesch & Boesch-Achermann 2000; Mitani & Watts 2010). In particular, large groups of males patrol the boundaries of their territories, watching and listening for signs of unfamiliar individuals (Goodall 1986; Watts & Mitani 2001). Intergroup encounters are always hostile and occasionally lethal, with males killing the infants of neighbouring mothers or solitary adult males (Wrangham 1999; Muller 2002; Wrangham et al. 2006).

The severity of bonobo aggression is markedly reduced compared to that of chimpanzees in all of these contexts (Wrangham & Peterson 1997; Doran et al. 2002; Furuichi 2011). Within groups, male aggression remains at relatively low intensity;

unlike chimpanzees, bonobos do not express dominance through formal signals and have very low-intensity displays relative to those of chimpanzees (Kano 1992; Parish 1996; Furuichi 1997; Vervaecke et al. 1999, 2000a, b; Hohmann & Fruth 2003a, b; Paoli et al. 2006). Even when displays by male bonobos include running and dragging branches near or at a group member, they rarely end in aggressive physical contact, nor do they vary between individuals or become highly elaborated as in the case of chimpanzees (Mori 1983; Kano 1992). Male bonobos do not aggressively interfere with or attempt to prevent each other's matings and do not form alliances with one another to monopolize matings (Furuichi 1997; Hohmann & Fruth 2003a, b). Instead, male bonobos form the strongest bonds with their mothers, and male–female alliances are more frequent in bonobos than in chimpanzees (Kano 1992; Furuichi et al. 1998; Hohmann & Fruth 2002; Stevens et al. 2006; Surbeck et al. 2011). Male aggression towards females is likewise muted. Males that attempt to intimidate females are easily retaliated against by a coalition of females (Kano 1992; Parish 1996; Vervaecke et al. 1999, 2000a; Fruth & Hohmann 2002; Hohmann & Fruth 2003a, b). This reduction in male–female aggression is associated with females showing feeding priority over males, with no group of bonobos having been observed to have a male (or coalition of males) as the highest-ranking member(s) (White & Wood 2007). Male bonobos in the Eyengo community at Lomako are slightly more aggressive towards young females or towards those in oestrus than they are towards lactating adult females, but intersexual aggression in the context of mating is infrequent and has not been observed to be an effective mating strategy (Hohmann & Fruth 2003a, b; Surbeck et al. 2011). For example, as many as five of eight adult males in one bonobo community have sired similar numbers of offspring according to initial mitochondrial DNA paternity analysis, suggesting maternal rank as a strong influence reproductive success (Gerloff et al. 1999). As a result, female choice appears to play a significant role in bonobos, in contrast to chimpanzees (Hohmann & Fruth 2003a, b; Schaller et al. 2010; Muller et al. 2011; Surbeck et al. 2011).

Intergroup interactions between bonobos are also less aggressive than those among chimpanzees even though, like chimpanzees, bonobos are territorial and can have hostile intergroup interactions in which males and females display at members of neighbouring groups (Kano 1992; Hohmann & Fruth 2002). These interactions infrequently result in physical contact aggression (e.g. the highest recorded rate is 8 of 23 of such encounters in the Eyengo community at Lomako during 1993–1998; Hohmann & Fruth 2002) and more often result in one group simply leaving the contested area without incident (Badrian & Badrian 1984; Kano 1992; Hohmann 2001; Myers-Thompson 2002). In addition, intergroup interactions can sometimes be highly social events with members of both groups sitting in close proximity, playing, and in some cases, even copulating (Itani 1990; Idani 1991; Furuichi 2011). Bonobos have not been described as conducting border patrols as seen in chimpanzees, and there is no evidence for lethal aggression (Wrangham 1999; Furuichi 2011). This intergroup tolerance is reflected in the ease by which aggression in captive bonobo social groups is managed relative to that of chimpanzees (where fatalities often occur because of conspecific aggression in captivity; de Waal 1986; Brent 2001; Seres et al. 2001). Typically, a new bonobo, even as an infant, can be introduced without incident; and two groups, including multiple adult males separated for weeks, months or years, can be reintegrated with little more than play and sexual contact as a result (B. Hare, V. Wobber & R. Wrangham, personal observations). This is consistent with the lack of observations of aggressive infanticide among wild bonobos (Fowler & Hohmann 2010; Furuichi 2011). In corroboration of the behavioural evidence, museum collections reveal a high incidence of skeletal

trauma in wild chimpanzees, but not in wild bonobos, that appear to have been inflicted from fights with conspecifics (Jurmain 1997; Novak & Hatch 2009). Furthermore, canine height is reduced in both male and female bonobos compared to that of chimpanzees (Kelley 1995).

While bonobos display less severe aggression than chimpanzees, this does not mean bonobos are nonaggressive. Groups of female bonobos can attack and seriously injure males (e.g. Parish 1996; Stevens et al. 2006; Hohmann & Fruth 2011). In addition, while bonobos tend not to attack nongroup members, they are not always tolerant of them (Hohmann 2001). Although yet to be observed in bonobos, it is possible that forms of severe aggression only observed in chimpanzees might be observed occasionally, as suggested by bonobos and chimpanzees being similarly sexually dimorphic in terms of their canine height and body mass (Kelley 1995; Smith & Jungers 1997; but see Kinzey 1984). However, all current evidence indicates that bonobos display less severe aggression than chimpanzees.

THE DOMESTICATION SYNDROME IN BONOBOS

In addition to showing less severe forms of aggression compared to chimpanzees, bonobos show differences in phenotypic traits and developmental patterns that appear analogous to the domestication syndrome (see Table 1). First, morphological similarities between bonobos and domesticates include reduced cranial size (Coolidge 1933; with as much as a 20% reduction in male cranium; Cramer 1977; also see S. Durrleman, X. Pennec, A. Trouve, N. Ayache & J. Braga, unpublished data), a reduction in facial projection (McHenry 1984; Shea 1989) and decreased mandible and tooth size (Cramer 1977; Zihlman & Cramer 1978; Latimer et al. 1981; McHenry & Corruccini 1981; Pilbrow 2006). Bonobos also show diminished sexual dimorphism in their brains and crania compared to chimpanzees (Cramer 1977; see also McHenry & Corruccini 1981; McHenry 1984). Systematic comparisons between the skulls of bonobos and chimpanzees have consistently interpreted differences as developmental delays in bonobos (Schultz 1941; Shea 1983, 1984, 1989; Kappelman 1996; Lieberman et al. 2007; but see Mitteroecker et al. 2005). The strongest test to date examined the two major units of the skull separately in a developmental sample of bonobo and chimpanzee skulls that included males and females in four age categories (infant to adult) and found that the bonobo cranium, but not the face, was paedomorphic (Lieberman et al. 2007). Lieberman et al. (2007) suggested that the observed pattern is probably due to smaller neonate size in bonobos and may be driven by regulatory shifts occurring early in fetal or even embryonic development. The potential for early developmental differences is supported by indirect morphological evidence that suggests chimpanzees are hyper-androgenized relative to bonobos in utero (McIntyre et al. 2009; see also Lutchmaya et al. 2004).

Further morphological differences in bonobos relative to chimpanzees include a white tail-tuft and pink lips that can last throughout life and result from a loss of pigmentation, an increase in the duration and frequency of female sexual swelling and retention of the labia majora (Dahl 1985, 1986; Kano 1992; de Waal & Lanting 1997). These traits appear analogous to the changes in pigmentation and extended reproductive seasons observed in domesticated animals (Trut 2001). They may also result from developmental shifts since white tail-tufts are only observed in juvenile chimpanzees and the temporal pattern of sexual swelling in parous bonobos resembles that of nulliparous chimpanzees (Wrangham 2002).

Behaviourally, bonobos are similar to many domesticates (e.g. Kunz & Sachser 1999) in showing intensified sexual behaviour. Not only do bonobos show an overall increase in the frequency of

Table 1
Evidence for the domestication syndrome across species

	Bonobo–Chimpanzee	Dog–Wolf	Experimental–Control fox	Domestic–Wild guinea pigs; Experimental–Control rodents
Aggression	Lower intensity inter- and intragroup aggression in bonobos ^a	Lower intensity inter- and intragroup aggression in feral dogs ^b	Exp. foxes but not controls nonaggressive towards humans ^c	Guinea pigs and exp. rodents are less aggressive to conspecifics than are caviae and controls ^d
Physiology	Bonobos have more passive coping response to social stress; bonobo females are receptive for more of sexual cycle ^e	Dogs show muted stress response when interacting with humans; multiple periods of sexual receptivity in female dogs but not wolves ^f	Higher basal serotonin and lower corticosteroids in exp. foxes; multiple periods of sexual receptivity in exp. foxes but not controls ^g	Guinea pigs/exp. rodents show muted physiological stress response when interacting with conspecifics and when exploring ^h
Morphology	Bonobos show reduced cranial capacity; less canine dimorphism; depigmentation of lips and tail tufts ⁱ	Dogs show reduced cranial capacity; smaller canines; less canine dimorphism; depigmentation of coat ^j	Exp. foxes show feminized skull; less canine dimorphism; depigmentation of coat ^k	Guinea pigs show reduced cranial capacity; depigmentation of coat ^l
Prosocial behaviour	Bonobos show more play and sociosexual behaviour as adults; voluntarily share food and are more food tolerant ^m	Dogs show more play and sociosexual behaviour as adults, and are more attracted to humans than they are to conspecifics ⁿ	Exp. foxes are more attracted and interested in playing and interacting with humans as adults ^o	Guinea pigs are more playful and show more sexual behaviour than caviae; exp. rodents show more social freezing ^p
Delay in development	Bonobos are more dependent on mothers; develop social skills more slowly in tasks related to foraging and feeding competition ^q	Onset of adult fear response delayed in dogs; retain juvenile communicative repertoire into adulthood ^r	Onset of adult fear response delayed in exp. foxes; retain juvenile communicative repertoire into adulthood ^s	Lower aggression in exp. rodents is due to developmental delay; retain juvenile communicative repertoire into adulthood ^t
Cognition	Bonobos are more sensitive to human social cues and more skilled at tasks requiring social tolerance ^u	Dogs are more sensitive to human social cues ^v	Foxes are more sensitive to human social cues ^w	Guinea pigs are more skilled than caviae at spatial learning tasks ^x

Dogs, foxes, guinea pigs and rodents experimentally selected for reduced aggression are less aggressive while showing similar changes in physiology, morphology, prosocial behaviour, development and cognition when compared to their wild progenitor or control populations (i.e. those not selected for low-aggression phenotypes). Bonobos show an analogous phenotypic pattern when compared to chimpanzees (see footnote for references).

^aKuroda (1980); Itani (1990); Idani (1991); Kano (1992); Hohmann (2001); Pusey et al. (2008); Furuichi (2011); ^bMech (1994); Boitani et al. (1995); MacDonald & Carr (1995); Mech et al. (1998); Pal et al. (1999); Sands & Creel (2004); Bonanni et al. (2010); Murray et al. (2010); ^cTrut (1999); ^dGariépy et al. (2001); Kunz et al. (2003); Albert et al. (2008); ^eReichert et al. (2002); Hohmann et al. (2009); Wobber et al. (2010a); ^fZimen (1987); Derix et al. (1993); ^gKulikova et al. (1989); Popova et al. (1997); Trut (1999, 2001); Gulevich et al. (2004); Popova (2004); ^hHammer et al. (1992); Kunz & Sachser (1999); Kunz et al. (2003); ⁱCoolidge (1933); Schultz (1941); Cramer (1977); Latimer et al. (1981); Shea (1983, 1984, 1989); Kinzey (1984); Kano (1992); Lieberman et al. (2007); ^jWayne (1986, 2001); Kruska (1988, 2005); Clutton-Brock (1995); Coppinger & Schneider (1995); Coppinger & Coppinger (2001); but see Drake (2011); ^kTrut et al. (1991, 2006); ^lKruska (1988); ^mSavage-Rumbaugh & Wilkerson (1978); de Waal (1987); Enomoto (1990); Kano (1992); Furuichi & Hashimoto (2004); Palagi (2006); Hare et al. (2007); Palagi & Paoli (2007); Paoli et al. (2007); Hare & Kwtuenda (2010); Wobber et al. (2010b); ⁿHemmer (1990); Koler-Matznick et al. (2004); Miklósi (2008); ^oTrut (1999, 2001); Trut et al. (2004, 2009); ^pKunz & Sachser (1999); Kunz et al. (2003); ^qKuroda (1989); Furuichi & Ihobe (1994); De Lathouwers & Van Elsacker (2006); Herrmann et al. (2010); Wobber et al. (2010b); Furuichi (2011); Surbeck et al. (2011); ^rFox (1969, 1970); Zimen (1987); Coppinger & Coppinger (2001); Miklósi (2008); ^sBelyaev et al. (1985); Plyusnina et al. (1991); Trut (1999, 2001); Trut et al. (2004, 2006, 2009); Gogoleva et al. (2008); ^tGariépy et al. (2001); ^uHare & Kwtuenda (2010); Herrmann et al. (2010); Wobber et al. (2010b); ^vHare et al. (2002); Miklósi et al. (2003); Hare & Tomasello (2005); Miklósi (2008); Gácsi et al. (2009); Topál et al. (2009); ^wHare et al. (2005); ^xLewejohann et al. (2010).

heterosexual copulations, but they also display a substantial emancipation of sexual behaviour into nonconceptive functions that often involve same-sex partners (Savage-Rumbaugh & Wilkerson 1978; Kuroda 1984; Thompson-Handler et al. 1984; de Waal 1987, 1995; Kano 1989, 1992; Enomoto 1990; Dixon 1998; Hohmann & Fruth 2000; Furuichi & Hashimoto 2004; Paoli et al. 2007; Clay & Zuberbühler 2011; Woods & Hare 2011). Bonobo adults also initiate play, play more roughly (requiring more tolerance) and use play faces with other adults significantly more than do chimpanzee adults (Palagi 2006). In fact, play between adult bonobos is similar to that between juvenile chimpanzees and adults (Palagi 2006; Hare et al. 2007; Wobber et al. 2010b). These differences from chimpanzees appear similar to examples where juvenilized freezing behaviour reduces social tension in mice selected for low aggression (Gariépy et al. 2001).

The neurobiological sources of behavioural differences between chimpanzees and bonobos are generally unknown. However, there is evidence that the adult bonobo brain differs from the chimpanzee brain in areas related to emotional-reactivity, motor coordination and foraging (orbitofrontal cortex: Semendeferi et al. 1998; spinal cord: Rilling & Insel 1999; motor cortices: Schenker et al. 2005; hippocampus: Hopkins et al. 2009). Most recently, bonobos have been shown to possess more grey matter in areas implicated in perceiving distress in others, as well as a larger pathway linking the amygdala to ventral anterior cingulate cortex (implicated in mediating aggressive impulses; Rilling et al. 2011).

An alternative evolutionary scenario to the self-domestication hypothesis is that the observed behavioural differences are due to selection for severe aggression in chimpanzees from a bonobo-like ancestor. Equally, both *Pan* species could in theory be highly derived from a common ancestor that possessed a mosaic of traits seen in both species. The ontogeny of the bonobo skull argues against these ideas. During growth, chimpanzee skulls follow closely the ontogenetic pattern of their more distant relative, gorillas, *Gorilla gorilla* (Shea 1983, 1984, 1989), whereas the bonobo cranium remains small and juvenilized compared not only to chimpanzees but also to all other great apes, including australopithecines (Schultz 1941; Kappelman 1996; Lieberman et al. 2007). This means that the most parsimonious reconstruction is for the chimpanzee–gorilla pattern of cranial ontogeny to have been ancestral while the bonobo pattern is derived (Wrangham & Pilbeam 2001). Given that cranial ontogeny is related to brain development, this would also suggest that the behaviours observed in bonobos are derived as well. The low severity of aggression in bonobos is thus most plausibly seen as resulting from selection against aggressiveness.

THE SOCIOECOLOGY OF SELF-DOMESTICATION

Down-regulation of aggression can result from a variety of selection pressures, ranging from natural selection to unintended artificial selection by humans or deliberate experimental selection.

In the case of bonobos, natural selection is the only plausible mechanism. Unlike typical domesticated animals, but like some experimental populations (e.g. [Gariépy et al. 2001](#)), such selection in bonobos would have been driven solely by changes in intra-specific rather than interspecific interactions (i.e. with humans). Therefore, the self-domestication hypothesis does not propose that the exact cause(s) of the selection pressure, the precise neurobiological or developmental mechanisms it affects and the resulting phenotype are all identical when comparing bonobos to different domesticates.

Evolutionary explanations for reduced aggressiveness in bonobos relative to that in chimpanzees have focused on bonobos' more predictable sociospatial associations. Bonobos form relatively stable parties (temporary associations) in which females are more gregarious than males and parties contain a larger proportion of the community (25–51%) than those of chimpanzees (9–30%) ([Furuichi 2011](#)). Stable parties allow for the formation of female–female alliances, which are much more frequent and effective against male aggression in bonobos than in chimpanzees ([Kano 1992](#); [Vervaeke et al. 1999, 2000a, b](#); [Furuichi 2011](#)). The characteristically extended female receptivity and less honest signals of ovulation in bonobos ([Reichert et al. 2002](#)) are also attributable to more stable parties, since females that can tolerate relatively permanent associates can afford to attract males over longer durations than a brief peri-ovulatory period ([Wrangham 2002](#)). As a result of extended female receptivity, males compete less intensely for each mating opportunity, including reduced sexual coercion and monopolization by dominant males. Thus, the benefits of high male rank are lower as a result of the lower value of each mating. Less aggressive males that avoid both the risks and the costs of physical aggression ([Sapolsky 2005](#)) and that use alternative means to access females (e.g. kinship ties with high-ranking mothers: [Kano 1992](#)) could then be favoured over more aggressive males ([Schaller et al. 2010](#); [Furuichi 2011](#); [Surbeck et al. 2011](#)). Female–female alliances and prolonged sexual receptivity can thus explain why more stable groups are associated with a reduced efficacy of male coercion of females and reduced value to high male rank ([Furuichi & Ihobe 1994](#); [Wrangham & Peterson 1997](#)). Stable parties would also have eliminated extreme imbalances of power in territorial encounters. A plausible result is that selection would no longer favour attempts to attack and injure members of neighbouring communities ([Wrangham 1999](#)). In this scenario selection would probably have been strongest against lethal male aggression (e.g. infanticide) and might have operated through female choice given the cost that female primates pay as a result of male aggression ([Engh et al. 2006](#)).

Since there is no evidence that the risks of predation differ between bonobos and chimpanzees, the ultimate explanation for the more stable parties of bonobos is normally thought to lie in their feeding ecology. The fact that female bonobos feed and travel together routinely, unlike female chimpanzees, which often travel alone, particularly when food is scarce, has implicated reduced scramble competition for food as a critical factor responsible for bonobo evolution ([Kuroda 1979](#); [White 1992](#); [Malenky & Wrangham 1994](#); [Williams et al. 2002](#); [Emery Thompson et al. 2007](#); [Furuichi 2011](#)). Although nutrient availability is not known to differ between the two species' habitats ([Hohmann et al. 2010](#)), food distribution may vary significantly. A potentially critical difference in food availability is a higher density of terrestrial foods in bonobo habitats, due to the absence of gorillas throughout the bonobos' geographical range ([Wrangham 1993](#); [Malenky & Wrangham 1994](#); [Wrangham & Peterson 1997](#)).

A challenge to testing these types of ecological hypothesis is a lack of data from long-term bonobo field sites and variation across chimpanzee field sites where long-term data exists ([Boesch et al.](#)

[2002](#)). In addition, a reduction in aggression does not necessarily have to occur because of systematic ecological differences. The frequency of male baboon aggression within a group has been observed to rapidly, albeit temporarily, decrease because of stochastic factors (i.e. disease that killed most of a cohort of aggressive individuals; [Sapolsky & Share 2004](#)). If an equivalent process occurred and female bonobos demonstrated a preference for less aggressive males, it is possible that stabilizing sexual selection could have played a large role in driving bonobo evolution. However, in the next section we provide a number of experimental comparisons between bonobos and chimpanzees that help test the predictions of the ecological hypothesis described above as well as a number of other predictions of the self-domestication hypothesis.

PSYCHOLOGICAL TESTS OF THE SELF-DOMESTICATION HYPOTHESIS

Subsequent to the proposal that behavioural and morphological similarity between bonobos and domestic animals have a parallel explanation ([Wrangham & Pilbeam 2001](#)), quantitative comparisons between the psychology of chimpanzees and bonobos have been conducted as a priori tests of the central predictions of the self-domestication hypothesis ([Hare 2007, 2011](#)).

First, the hypothesis predicts that bonobos should differ from chimpanzees in being more socially tolerant, for example, in relation to the sharing of food. [Hare et al. \(2007\)](#) tested this by studying cofeeding behaviour in an age- and sex-matched sample of captive bonobos and chimpanzees. They found that dyads of bonobos cofed, played and showed sociosexual behaviour more readily than dyads of chimpanzees. To assess the neuroendocrine basis for this difference, [Wobber et al. \(2010a\)](#) compared dyads of age-matched male bonobos and chimpanzees confronted by potential competition over food. In bonobos, but not chimpanzees, cortisol levels rose in anticipation of feeding competition (see also [Hohmann et al. 2009](#)). This pattern of response to potential social conflict reflects a passive coping style analogous to that observed in low-aggression strains of mice ([Veenema et al. 2004](#); also see [Herrmann et al. 2011](#)). In contrast to bonobos, prior to feeding competition, chimpanzee males showed increases in levels of testosterone but not in levels of cortisol. This pattern suggests that chimpanzees, like human males, respond to feeding competition as a dominance contest ([Schultheiss et al. 1999](#)).

Similar to domesticates, the passive coping style and high tolerance of bonobos also relate to how they solve social problems in experimental contexts. When tested for social skills related to reading the behavioural intentions of others, bonobos are more like dogs in being more responsive to human gaze direction than are chimpanzees ([Hare et al. 2010](#); [Herrmann et al. 2010](#)). In addition, when bonobos and chimpanzees were compared for their ability to spontaneously cooperate on a novel instrumental task, chimpanzees were highly constrained by intolerance while experimentally naïve bonobos outperformed even the most skilled chimpanzees because they shared the food rewards more easily ([Melis et al. 2006a](#); [Hare et al. 2007](#); see also [Petit et al. 1992](#); [Seed et al. 2008](#)). Bonobos have also been shown to cooperate by voluntarily sharing food in their possession with an unfamiliar conspecific ([Hare & Kwetuenda 2010](#)), consistent with their xenophilic tendencies observed in the wild ([Furuichi 2011](#)). Meanwhile, chimpanzees will only recruit to share food in this way with a familiar conspecific if they are necessary as partners in obtaining food that is out of reach and easily divisible ([Melis et al. 2006b](#)). However, the ability of bonobos to share may not always translate into active handing over of food in nondyadic interactions ([Jaeggi et al. 2010](#)).

Second, the self-domestication hypothesis suggests that during their evolutionary history, bonobos and chimpanzees experienced systematic differences in the intensity of feeding competition. Experimental evidence from other primates suggests that differences in feeding ecology across species can influence the psychology of feeding preferences relating to time and risk (e.g. Rosati et al. 2005; Stevens et al. 2005). Accordingly, feeding preferences are expected to differ between bonobos and chimpanzees. The apparently more stable and less competitive feeding conditions experienced by bonobos are expected to have lowered the benefits of taking risky foraging decisions (e.g. travelling alone, hunting or exploring more). Bonobos have indeed been found to be relatively averse to risky outcomes and to prefer immediate rather than delayed rewards when presented with foraging decisions, whereas chimpanzees are relatively risk prone, willing to wait for delayed rewards that are larger or of higher quality (Rosati et al. 2007; Heilbronner et al. 2008; Hare 2009). A. Rosati & B. Hare (unpublished data) also compared the spatial memory of bonobos and chimpanzees and found that adult chimpanzees remember many more locations where they saw food hidden and for a longer time than bonobos, whereas adult bonobos performed at the level of juvenile chimpanzees. These results support the hypothesis that reduced competition over food in bonobos has resulted in less developed memory and feeding preferences shifted towards risk aversion and greater impatience.

Third, the self-domestication hypothesis suggests that psychological differences between bonobos and chimpanzees should in part be explained by developmental differences that promote juvenile behaviours and cognitive mechanisms in bonobos throughout life. Age- and sex-matched developmental comparisons have indeed revealed that bonobo psychology shows delayed development relative to that of chimpanzees. Wobber et al. (2010b, c) tested the prediction that the increased tolerance observed in bonobos relative to chimpanzees is a result of developmental differences in the two species. While juvenile bonobos and chimpanzees were both found to be highly tolerant, chimpanzees became increasingly intolerant with age but adult bonobos maintained juvenile levels of cofeeding. Because adult chimpanzees often needed to inhibit their desire to approach the food if placed with an intolerant partner, but bonobos did not, Wobber et al. (2010b) tested whether bonobos were developmentally delayed in tasks requiring social inhibition. As expected, in two different tasks, bonobos showed delayed development relative to chimpanzees in social situations requiring them to inhibit begging for food from certain social partners but not from others. V. Wobber, E. Herrmann, B. Hare, R. Wrangham & M. Tomasello (unpublished data) replicated and extended this finding using a large cross-sectional sample of bonobos and chimpanzees that were tested on a cognitive test battery, and they found that bonobos also demonstrate delayed development in tasks pertaining to their understanding of the physical world. Bonobos developed these abilities more slowly and never reached the level of competence observed in adult chimpanzees on tasks examining their spatial memory, their use of tools and their understanding of causality (similar to the findings of Gruber et al. 2010).

The observed cognitive differences are particularly compelling given that the two species are highly similar psychologically in domains where the self-domestication hypothesis does not make strong predictions. For example, the two species show comparable levels of inhibitory control in a detour-reaching task, and overall perform very similarly in a wide range of cognitive tasks not pertaining to foraging or feeding competition (Herrmann et al. 2010; Vlamings et al. 2010; Rosati & Hare 2011). It remains possible that several ecological variables have affected the cognitive skills assessed here. For example, increases in social tolerance among

primates have been predicted as a result of kinship bonds or as a result of cooperative breeding (Chapais & Berman 2004; Maestripieri 2007; Burkart et al. 2009). However, neither of these specific hypotheses makes predictions that can parsimoniously account for the syndrome observed and tested here for bonobos, given that patterns of kinship are similar in bonobos and chimpanzees, and that neither species breeds cooperatively. In the future the self-domestication hypothesis will need to be tested against these types of alternative ecological hypotheses.

FUTURE TESTS OF THE SELF-DOMESTICATION HYPOTHESIS

The presence of a domestication-like syndrome across a wide variety of species, potentially including the bonobo, underscores the importance of considering how different traits can reliably covary across a range of species when attempting to explain behavioural and psychological evolution. The self-domestication hypothesis posits that selection against aggression leads to a similar syndrome of phenotypic changes in captive populations under selective breeding as in wild animals in which natural selection has favoured less aggressive behaviour. We present bonobos as a test case of the hypothesis that natural selection for reduced aggression (or increased tolerance) can cause a suite of behavioural, physiological, morphological and psychological changes analogous to those seen in domesticates. The application of this model to bonobos is supported by initial comparisons between the psychology of bonobos and chimpanzees demonstrating that bonobos show increased tolerance, a passive coping style (evidenced by differential physiological responses to feeding competition), risk-averse foraging preferences and developmental delays in behaviour pertaining to feeding competition and foraging skills. Moreover, this model has the potential to explain morphological changes in bonobos (e.g. depigmentation, cranial reduction, etc.) that are otherwise difficult to understand as adaptive traits. Perhaps most importantly, the self-domestication hypothesis also leads to a number of novel, falsifiable predictions including: a relationship between gene expression or regulatory genes controlling aggressive behaviour and brain development in bonobos and domesticates (e.g. paedomorphic brain development; Sætre et al. 2004; Somel et al. 2009), an association between psychological and neurobiological differences related to reduced aggressiveness and juvenilized social behaviour (e.g. Rilling et al. 2011) and genetic or epigenetic links between reduced aggression and specific changes in morphology (e.g. Kukekova et al. 2011).

How applicable the self-domestication hypothesis will be to a wider range of species remains an open question. Even if future research strengthens the self-domestication hypothesis for bonobos, this species could still represent the product of an unusual evolutionary process (i.e. it may be that few wild animals have undergone 'self-domestication' even though there has been selection against aggression). Alternatively, there may be a host of species that show evidence of a domestication-like syndrome. Once documented, such diversity would allow for the application of more powerful phylogenetic tests than the pairwise test represented by the current bonobo–chimpanzee comparison (e.g. Thierry et al. 2008; MacLean et al. 2011). To test for other candidate species, comparisons will be needed between less fearful, less aggressive and/or more socially tolerant species and closely related taxa. Candidates might include species adapting to urban ecosystems (Ditchkoff et al. 2006), insular vertebrates that evolved with relaxed predation pressures (Stamps & Buechner 1985), or even primates with extreme levels of social tolerance (Thierry et al. 1994). Over the last 30 years the Florida Key deer, *Odocoileus virginianus clavium*, has increasingly encroached on urban areas. As a result, these deer have become less fearful, have larger

body mass, higher fitness and live in larger social groups across seasons than deer living farther away from urban areas (Harveson et al. 2007). Meanwhile, island vertebrates can demonstrate reduced aggressiveness towards conspecifics expressed as a lack of territoriality, increased tolerance towards intruders, acceptance of subordinates on the territory or a total lack of territoriality (Stamps & Buechner 1985). Island populations of rodents have also been found to be less aggressive, to have larger body mass and to live at higher densities than their mainland conspecifics (Adler & Levins 1994; also see Gray & Hurst 1998). Finally, there are other primates that might show some or all of the effects of self-domestication. Sulawesi macaque species are known to be relatively tolerant, with Tonkean macaques, *Macaca tonkeana*, being the best studied. Similar to bonobos, and unlike more despotic macaque species, Tonkean macaques have relatively tolerant relations within and between groups, live in more cohesive groups, are more capable of cofeeding and solving novel cooperative problems, play in closer contact and less competitively, have a more relaxed and playful use of facial expressions, and as infants interact with larger numbers of groupmates early in infancy (Thierry 1985; Petit et al. 1992, 2008; Thierry et al. 1994; Reinhart et al. 2010). Future research can examine morphological, cognitive and developmental differences in such species and their close relatives to test the polarity of changes in aggressiveness, and whether a domestication-like syndrome explains inferred reductions in aggression or fearfulness. The self-domestication hypothesis is therefore a potentially powerful tool for understanding the processes by which selection shapes both psychological and other seemingly unrelated traits, including those in humans (e.g. Leach et al. 2003; Dorus et al. 2004).

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