



## Ecology rather than psychology explains co-occurrence of predation and border patrols in male chimpanzees



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The intense arousal and excitement shown by adult male chimpanzees, *Pan troglodytes*, during territorial attacks on other chimpanzees and predation upon monkeys suggest that similar psychological mechanisms may be involved. Specifically, it has been proposed that hunting behaviour in chimpanzees evolved from intraspecific aggression. Over 32 years, chimpanzees at Gombe National Park, Tanzania were significantly more likely to engage in a territorial border patrol on days when they hunted red colobus monkeys (*Procolobus* spp.), and vice versa, even after statistically controlling for male chimpanzee party size. We test the hypothesis that this correlation arises because hunting and patrolling are components of a species-level aggressive behavioural syndrome; specifically that predation arose as a by-product of territorial aggression in this species. However, hunting was equally likely to occur after a patrol and/or an intergroup interaction as it was before, and the occurrence of an intergroup interaction in which the chimpanzees approached strangers did not increase subsequent hunting probability. We also reject the hypothesis that hunting and patrolling reflect an individual-level behavioural syndrome. We identified two 'impact hunters' whose presence increased hunting probability. Similarly, there were also three 'impact patrollers', who increased the likelihood that a visit to the periphery of the community range resulted in a patrol. While this discovery has important implications for our understanding of the proximate causes of cooperation, it does not explain the temporal correlation between patrolling and hunting, since no males had such an impact in both contexts. Instead, the data suggest that the correlation arose because patrols typically involved males travelling long distances, which increased the probability of encountering prey. Additionally, parties that travelled to the periphery were more likely to encounter colobus in woodland, where hunts are more likely to occur and to succeed. Therefore, we conclude that ecological, rather than psychological, factors promote the co-occurrence of hunting and territorial aggression in this species.

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Male chimpanzees, *Pan troglodytes*, collectively defend group territories by conducting boundary patrols, advertising territory ownership with vocalizations and aggressively repelling members of other groups, sometimes injuring or killing them (Wrangham 1999; Wilson & Wrangham 2003; Watts et al. 2006; Boesch et al. 2008). Male chimpanzees also engage in group hunts of monkeys, particularly red colobus monkeys, *Procolobus* spp. (reviewed by Gilby 2012), which involve many of the same behavioural elements as aggression against conspecifics. The intense arousal and excitement shown during attacks on both chimpanzees and monkeys has prompted the suggestion that similar physiological and psychological mechanisms may be involved in predation and intergroup aggression (Goodall et al. 1979; van Hooff 1990; Wrangham & Peterson 1996; Wrangham 1999; Watts & Mitani 2001). Specifically, predation by

chimpanzees may have evolved as a by-product of selection for intraspecific territorial aggression (Kortlandt 1972; Eibl-Eibesfeldt 1975; Wrangham 1999). This idea contrasts with the finding that distinct mechanisms underlie predation and intraspecific aggression in other taxa (e.g. rodents: Parmigiani & Palanza 1991; Wersinger et al. 2007; but see Siegel & Victoroff 2009).

We used long-term data on wild chimpanzees in the Kasekela community in Gombe National Park, Tanzania to test the hypothesis that predation and territoriality are components of an 'aggressive' behavioural syndrome in this species. A behavioural syndrome is a suite of similar traits that evolved in concert due to shared genetic or epigenetic mechanisms (Sih et al. 2004a, b). In addition to explaining interindividual behavioural variation (personality), a behavioural syndrome may also account for species-level differences (Sih & Bell 2008). For example, Thierry et al. (2008) found that several traits associated with conflict resolution existed as 'an integrated suite of characters' across nine macaque (*Macaca*) species.

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Chimpanzees hunt red colobus monkeys wherever the two species are sympatric (Uehara 1997; Mitani 2009). At all sites where predation by chimpanzees has been studied in detail, the probability of a hunt occurring is positively correlated with the number of adult male chimpanzees present in the subgroup that encounters red colobus monkeys (Stanford et al. 1994a; Boesch & Boesch-Achermann 2000; Hosaka et al. 2001; Mitani & Watts 2001; Gilby et al. 2006; Gilby & Wrangham 2007). Thus, while chimpanzees do sometimes hunt alone (Gilby et al. 2006, 2008), hunting more often involves several individuals. While there is debate over the degree to which hunters coordinate their actions (Boesch 1994; Gilby & Connor 2010), the probability of a kill is positively correlated with the number of male chimpanzees present at a hunt (Mitani & Watts 2001; Gilby et al. 2006, 2008). During a hunt, males exhibit signs of great excitement, including piloerection, loud vocalizations, grimaces and embraces (Goodall 1986). When a chimpanzee captures a large monkey that fights back (posing a threat to its captor), the hunter typically bites, pounds and drags the victim until it is incapacitated. Goodall (1986, page 334) describes such behaviour as 'retaliatory aggression', noting similarities with attacks on chimpanzees from neighbouring communities (Goodall 1986, pp. 529–530).

Male chimpanzees jointly defend group territories (Wilson & Wrangham 2003; Boesch et al. 2008; Mitani 2009), by advertising territory ownership with vocalizations and by attempting to repel or kill any strangers that they encounter (except for reproductively active females, especially those without infants). Encounters with neighbours ('intergroup encounters' hereafter) occur most often in boundary areas (Wilson et al. 2012) and may include lethal aggression, which can account for a substantial proportion of total mortality (e.g. 9.3% at Gombe, 3.8% at Mahale Mountains National Park, Tanzania; Wilson 2013). Similar to hunting red colobus monkeys, the outcome of an intergroup encounter depends on the number of participants; parties with more males are more likely to call in response to vocalizations from simulated (Wilson et al. 2001) and real (Wilson et al. 2012) intruders. During an intergroup encounter in which the numerical odds are favourable or even, males behave in much the same way as they do during hunts of red colobus monkeys (e.g. bristling, embracing and vocalizing loudly). Killings appear most likely to occur when one side has an overwhelming numerical advantage (Manson & Wrangham 1991), reducing the risk of injury for attackers (Manson & Wrangham 1991). Like large red colobus monkey prey, chimpanzee victims are dragged, pummelled and bitten until incapacitated. The aggressors twist limbs and tear flesh, behaviours that are typically not seen during intracommunity aggression (Goodall 1986, page 529).

Given the importance of numerical odds in intergroup encounters, chimpanzees are more likely to visit the periphery when in parties with more males (Wilson et al. 2007, 2012). Visits to the periphery may include boundary patrols (Goodall et al. 1979; Watts & Mitani 2001), in which males spend more time travelling and less time feeding than usual (Amsler 2010), apparently searching for neighbours to attack. Therefore, we treat such patrols as examples of intraspecies aggression; by joining a patrol, each participant is committing to a potential conflict with hostile conspecifics.

Understanding the relationship between hunting and intergroup aggression has important implications for studies of aggression in general. For example, some argue that the considerable psychological and developmental differences between chimpanzees and their closest genetic relative, the bonobo, *Pan paniscus*, are due to a physiological link between aggressive and predatory behaviour. Bonobos exhibit considerably lower rates of both between-group aggression and hunting than chimpanzees (Surbeck & Hohmann 2008; Surbeck et al. 2009; Hare et al. 2012), a difference that has been proposed to result either from selection

against within-group aggression in the bonobo lineage, with an associated (but unselected) reduction in between-group aggression (Wrangham & Peterson 1996; Hare et al. 2012), or from selection specifically against lethal raiding due to larger, more stable parties in bonobos (Wrangham 1999). This has been proposed to explain the considerable psychological (Hare et al. 2007), physiological (Wobber et al. 2010) and morphological (Wrangham & Pilbeam 2001) differences between the two species. To evaluate this proposal, we must understand to what extent, and why, hunting and intergroup aggression are related in these species.

We begin by demonstrating that among the Gombe chimpanzees, hunting and territoriality are temporally related: over 32 years, hunts were more likely to occur on days with patrolling and vice versa. We then test the hypothesis that this correlation can be explained by a behavioural syndrome. However, we find that extrinsic, ecological factors explain the co-occurrence of hunting and patrolling in this population.

### *Hypotheses and Predictions*

#### *H1: species-level behavioural syndrome*

Several investigators have argued that hunting by chimpanzees is part of a species-wide behavioural syndrome, in which hunting emerged as a by-product of selection for other traits (Kortlandt 1972; Eibl-Eibesfeldt 1975; Goodall et al. 1979; van Hooff 1990; Wrangham 1999). Kortlandt (1972) suggested that hunting is a redirection of intraspecies aggression towards another species. More recently, Wrangham (1999) hypothesized that communal predation by chimpanzees evolved as a by-product of intraspecific coalitionary killing. For example, increases in testosterone associated with aggression (Muller & Wrangham 2004) may lead to an increase in hunting. Accordingly, males should be 'primed' to kill monkeys after patrolling or encountering hostile conspecifics. This predicts that, upon encountering red colobus monkeys, chimpanzees will be more likely to hunt them (1) after a patrol and/or an intergroup interaction than before such events, and (2) after an intergroup interaction in which they approached the strangers than after an intergroup interaction in which they did not approach the strangers (Table 1).

#### *H2: individual-level behavioural syndrome*

If hunting and intergroup aggression share underlying physiological or psychological mechanisms, this should be evident in the behaviour of individuals. Some individuals appear particularly motivated to hunt, raising the possibility that such individuals may also be inclined to participate in intergroup aggression. Moreover, such highly motivated individuals may play a catalytic role in the occurrence of group-level predation and aggression. For example, at Kanyawara (Kibale National Park, Uganda), the presence and behaviour of two particular chimpanzees affected hunting probability (Gilby et al. 2008). Upon encountering prey, a chimpanzee party almost never hunted unless one or both of these males (AJ or MS) were present. When at least one of them was present, other adult males did not hunt unless either AJ or MS did. At Ngogo (Kibale National Park, Uganda), MO was usually one of the first male chimpanzees to hunt, apparently prompting others to follow (D. P. Watts, personal communication). Boesch & Boesch (1989) attributed an increase in group hunting success at Taï National Park (Côte d'Ivoire) to the maturation of one particularly persistent hunter. Gilby et al. (2008) and Gilby & Connor (2010) proposed that such 'impact' hunters have a catalytic effect on other potential hunters via a simple by-product mutualism: the actions of particularly motivated individuals create opportunities for others to hunt in circumstances when they would normally refrain. For example, an 'average' hunter might be initially wary of being the sole target

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