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## **Roving females and patient males: a new perspective on the mating strategies of chimpanzees**

Nicholas E. Newton-Fisher

### ABSTRACT

Mating strategies are sets of decisions aimed at maximizing reproductive success. For male animals, the fundamental problem that these strategies address is attaining mating access to females in a manner that maximizes their chances of achieving paternity. For chimpanzees (*Pan troglodytes*), despite substantial interest in mating strategies, very little attention has been paid to the most fundamental problem that mating strategies need to solve: finding mates. Only a single model, Dunbar's general model of male mating strategies, exists to explain mate-searching behaviour in chimpanzees. Under this model, males in most populations are regarded as pursuing a 'roving' strategy: searching for and sequestering fertile females who are essentially passive with respect to mate searching. The roving mating strategy is an assumption deeply embedded in the way chimpanzee behaviour is considered; it is implicit in the conventional model for chimpanzee social structure, which posits that male ranging functions both to monitor female reproductive state and to ward these females from other groups of males through collective territoriality: essentially, ranging as mating effort. This perspective is, however, increasingly at odds with observations of chimpanzee behaviour. Herein, I review the logic and evidence for the roving-male mating strategy and propose a novel alternative, a theoretical framework in which roving is a strategy pursued by female chimpanzees in order to engage successfully in promiscuous mating. Males, unable to thwart this female strategy, instead maximise the number of reproductive opportunities encountered by focusing their behaviour on countering threats to health, fertility and reproductive career. Their prolonged grooming bouts are seen, in consequence, as functioning to mitigate the negative impacts of socially induced physiological stress. In this new framework, the roving-male strategy becomes, at best, a 'best of a bad job' alternative for low-ranking males when faced with high levels of competition for mating access. Male chimpanzees do not search for mates, but for one another, for food, and, at times, for rivals in other communities. To the extent that female promiscuity functions to counter infanticide risk, mate searching by female chimpanzees—and any associated costs—can be seen as an unavoidable consequence of male sexual coercion. This novel framework is a better fit to the available data than is the conventional account. This review highlights the desperate need for additional work in an area of chimpanzee biology that has been somewhat neglected, perhaps in part because assumptions of roving males have remained unquestioned for too long. It also highlights the need, across taxa, to revisit and revise theory, and to test old assumptions, when faced with contrary data.

## I. INTRODUCTION

### I.1 Mating strategies

Mating strategies are sets of decisions aimed at maximizing reproductive success. For male animals, the fundamental problem that these strategies address is attaining mating access to females in a manner that maximizes their chances of achieving paternity. Female reproductive success is limited ultimately by resources and as a result, male strategies must accommodate the resulting distribution and grouping patterns of females (Trivers, 1972; Wrangham, 1980; Dunbar, 1988). The mating strategies available to males are therefore either to defend areas which encompass one or more females against other males, or to similarly defend groups of females directly (Emlen & Oring, 1977; Dunbar, 1988, 2000): males pursue either 'roving' or 'social' mating strategies, as determined by the relative pay-offs of each strategy (Dunbar, 2000).

For chimpanzees (*Pan troglodytes* Blumenbach, 1799), despite substantial interest in mating strategies including understanding the function of female anogenital swellings (Deschner et al., 2003, 2004; Emery & Whitten, 2003), the possible role of female mate choice (Tutin, 1979; Stumpf & Boesch, 2005; Stumpf, Emery Thompson & Knott, 2008; Emery Thompson & Wrangham, 2008b), and the complex tactics used by male chimpanzees in order to achieve paternity (Tutin, 1979; Nishida & Hosaka, 1996; Stanford, 1998; Watts, 1998; Duffy, Wrangham & Silk, 2007; Muller et al., 2007, 2011; Muller, Kahlenberg & Wrangham, 2009), very little attention has been paid to the most fundamental problem that mating strategies need to solve: finding mates. Only a single model, Dunbar's general model of male mating strategies (Dunbar, 1988, 2000), exists to explain mate-searching behaviour in chimpanzees. Under this model, male chimpanzees in most populations are regarded as pursuing a 'roving' strategy, searching at random through their home range for fertile females (who are seen as essentially passive with respect to the search for mates) and sequestering these females, together with the paternity opportunities that they present, once they are encountered (Dunbar, 1988, 2000). A sequestered female is one over whom the male has gained exclusive mating access for the duration of the window of conception. Females counter such efforts by engaging in frequent and highly promiscuous mating over an extended period.

Although initially cast in this light (Dunbar, 1988, p. 308), Dunbar's general model does not, in fact, model whether males should pursue a roving strategy. Instead, it specifically addresses the question of whether or not males should persistently associate with the females with whom they mate (i.e. remain with those females whether or not they are cycling, mating with them when they are: the alternative 'social' strategy in the model). The model predicts the fitness pay-offs for roving and social strategies as a function of a male's day journey length, the distance at which he can detect females, the local density of females and the size of female groupings. According to the model, a male should pursue the social strategy when the ratio between these two pay-offs is equal to, or less than, 1; where the ratio exceeds 1, the male should pursue the roving strategy. Given that only one of these two strategies involves searching, it might be preferable use a more encompassing term, such as 'mate-encounter' strategies.

For most study populations of chimpanzees, Dunbar's model generates ratios greater than one, and so correctly predicts that males should not persistently associate with females (Dunbar, 2000). It is easy, therefore, to regard male chimpanzees as pursuing a roving strategy—that they search for mates whether wandering at random through the home range as assumed in the model or actively searching. After all, the model allows for two strategies, and if it is not one, it must presumably be the other. The roving mating strategy is an assumption deeply embedded in the way chimpanzee behaviour is discussed (e.g. Wrangham, 1975, 1986; Dunbar, 1988, 2000; Newton-Fisher, 1997; Pusey, 2001; Mitani, 2008; Emery Thompson & Wrangham, 2008b), perhaps because across populations males are typically not in persistent association with females, and is largely unquestioned (but see Takahata, Ihobe & Idani, 1996; Newton-Fisher, 1997): male chimpanzees certainly range more widely than do females (Wrangham, 1977, 1979; Wrangham & Smuts, 1980; Chapman & Wrangham, 1993; Herbinger, Boesch & Rothe, 2001; Newton-Fisher, 2003) at times encountering females with whom they may mate. The general view appears to be that adult male chimpanzees cooperate to defend a communal territory that encompasses the core ranging areas of multiple adult females; within this territory, males monitor the reproductive status of these females and compete with one another for fertilization opportunities when these arise.

This view, however, represents an uneasy compromise between two functions proposed to explain sex differences in ranging patterns. The dominant view has been that males range widely in order to defend, collectively, access to multiple females who are dispersed in smaller, foraging core areas. Under this view, males necessarily rove within their territory, monitoring female reproductive status and searching for mates. This is ranging and territoriality as mating effort (Wrangham, 1979; Manson & Wrangham, 1991; Boesch & Boesch-Achermann, 2000). The opposing view is that males range widely to defend a sufficiently large feeding territory to support themselves, their offspring, and the adult females that they need to generate additional offspring (Goodall, 1990; Boone, 1991; Nishida, 1991; Watts & Mitani, 2001; Williams et al., 2004). This is ranging as indirect parenting effort, although if male territoriality increases survivorship of their offspring then parenting effort is also direct (Watts & Mitani, 2001).

The available data support the second view: that males defend land and the food resources it holds (Watts & Mitani, 2001; Williams et al., 2004; Mitani, Watts & Amstler, 2010). Male ranging, rather than searching female core areas for potential mates, appears to be a sequence of journeys from one food patch to the next, on roughly linear paths towards boundary zones (Bates & Byrne, 2009). Male chimpanzees do not make frequent turns to search restricted areas, seen in the travel patterns of females exploiting their core areas, as might be expected if males were actively searching; neither do they appear to travel at random through their home range (Bates & Byrne, 2009).

Despite such findings, the idea of male ranging as a mating strategy has considerable inertia, perhaps due to the clear predictions from Dunbar's general model, or for want of viable alternatives. Dunbar's model is, however, neutral with regard to whether males search for females, or are found by those females (Dunbar, 2000, p. 264). To the best of my knowledge, there is no clear evidence for active mate searching by male chimpanzees, who often seem more concerned with interacting with one another than with searching for females. Chimpanzees associate with one another in sub-groupings with fluid membership and variable duration and while the number of males in these 'parties' (Sugiyama, 1968) is certainly larger when more cycling females are present (Newton-Fisher, 1999a; Emery Thompson & Wrangham, 2006), it is not clear whether males (as predicted by the 'roving-male' strategy) or females are responsible for

initiating such mixed-sex groupings. Male chimpanzee association patterns appear to be driven by active decisions to associate with other adult males, rather than passively aggregating around resources as might be expected if they were independently searching for cycling females (Newton-Fisher, 1999a), and even when in a party with a potentially fertilizable female, males' attempts at mating can be sporadic (N. E. Newton-Fisher, personal observations; McGinnis, 1979) although such efforts may be restricted by energetic or competitive constraints.

Our understanding of mate-searching (or encounter) strategies in the chimpanzee (*Pan troglodytes*) lags behind that of other aspects of its reproductive behaviour yet is at the heart of any account of its social structure. Here, I argue for a new perspective, much of which is implicit in the existing literature but lacking a theoretical framework. While Dunbar's general model correctly predicts a non-social strategy (thereby implying 'roving') given real data for most (or perhaps all, as I argue below) study populations, observations of chimpanzee behaviour offer little support for a 'roving-male' mating strategy. Here, I argue that we can account for this discrepancy by switching the mate-searching strategy (roving) from males to females. This role reversal does not leave males passive (as females are in Dunbar's model) and I present a conceptual model of a new strategy for male chimpanzees: the 'patient-male' strategy. I contrast this with the established 'roving-male' strategy (see Fig. 1), and argue that the data that we have for chimpanzees better supports a framework in which males (largely) leave the mate searching to the females. My intention is to provide a novel, testable framework that I hope will encourage renewed interest in a somewhat neglected topic, and more generally stimulate rigorous re-examination of long-standing assumptions regarding the behaviour and biology of chimpanzees and other species.

## **1.2 Background on chimpanzees**

Chimpanzees live in multi-male, multi-female unit-groups or communities (Goodall, 1973; Nishida, 1979; Wrangham, 1986) that average around 40 adult and adolescent members, together with associated juveniles and infants, and have a sex ratio that is typically female biased (mean 1.6: Wrangham, 2000). These communities have a fluid or

fission-fusion social structure, with individuals moving between sub-groupings (parties: Sugiyama, 1968) in a flexible and dynamic fashion. All members share a common home range (Reynolds & Reynolds, 1965; Wrangham, 1986; Chapman & Wrangham, 1993; Herbinger et al., 2001; Newton-Fisher, 2003) within which males typically range more widely than do females, who often restrict their ranging to distinct, albeit overlapping, core areas within the community range (Wrangham, 1977; Wrangham & Smuts, 1980; Williams et al., 2002; Newton-Fisher, 2002a; Lehmann & Boesch, 2005; Kahlenberg, Emery Thompson & Wrangham, 2008b). In some communities these core areas are arranged into clusters, or neighbourhoods (Williams et al., 2002). Core areas vary in the quality of the resources they contain, which impacts female reproductive success (Emery Thompson & Wrangham, 2008a), and core residence leads to non-cycling females being dispersed through the community range. In some populations, male chimpanzees also have individual core ranging areas (Wrangham & Smuts, 1980; Newton-Fisher, 2000, 2002a) that may provide fall-back foraging locations during periods of food scarcity (Murray et al., 2008).

Male chimpanzees are territorial and neighbouring communities show mutual hostility, with the result that the periphery of a community's range and any boundary zones between communities are areas of high risk to all community members (Goodall et al., 1979; Nishida et al., 1985; Wrangham, 1999; Boesch & Boesch-Achermann, 2000; Wrangham, Wilson & Muller, 2006). Male chimpanzees patrol these areas intermittently and can show extreme, often lethal aggression towards members of other communities (e.g. Goodall et al., 1979; Muller, 2002; reviews: Wrangham, 1999; Newton-Fisher & Emery Thompson, 2012), including the snatching and killing of infants (Goodall, 1986; Newton & Nishida, 1990; Arcadi & Wrangham, 1999; Newton-Fisher, 1999b; Watts & Mitani, 2000). Both sexes show social dominance hierarchies, although these are much more pronounced for males (Simpson, 1973; Bygott, 1979; Goodall, 1986; Hayaki, Huffman & Nishida, 1989; Pusey, Williams & Goodall, 1997; Newton-Fisher, 2004, 2006). Adult male chimpanzees are typically more gregarious than (parous) females, spending less time alone (i.e. not in the company of other adults) and generally associating in larger parties (Goodall, 1986; Wrangham, 1986; Pepper et al., 1999; Emery Thompson & Wrangham, 2006). This may be because males appear to suffer lower costs



from being part of a group (Wrangham, 1986, 2000). Males also groom one another far more than do females and engage in substantially more coalitional behaviour (Wrangham, 1986; Nishida & Hiraïwa-Hasegawa, 1987; Boesch & Boesch-Achermann, 2000). The degree of these sex differences varies between populations, being most marked in East African chimpanzees (*Pan troglodytes schweinfurthii* Giglioli 1872), and less pronounced but still present in West African chimpanzees (*P. t. verus* Schwarz, 1934) (Lehmann & Boesch, 2008).

Mating in chimpanzees occurs in one of three contexts: possessive, opportunistic, and consortship (Tutin, 1979). Possessiveness occurs when males contest mating opportunities, attempting to prevent one another from accessing the female and controlling or coercing her behaviour. Success appears to depend on male social rank (Tutin, 1979) and if the number of competitors is particularly large, the use of allies (Watts, 1998). Opportunistic mating occurs when males neither contest mating with one another nor attempt to coerce the female. The consortship context occurs when a male attempts to remove the female from the company of other males such that he gains exclusive mating access (Tutin, 1979). Coercive aggression, mate guarding and the possessive mating context occur primarily with peri-ovulatory females (Tutin & McGinnis, 1981; Hasegawa & Hiraïwa-Hasegawa, 1983; Watts, 1998; Wrangham, 2000).

Most mating behaviour occurs between members of a single community and genetic studies show low rates of extra-group paternity (< 5% for East African chimpanzees *P. t. schweinfurthii*, ~10% for West African chimpanzees *P. t. verus*: Constable et al., 2001; Vigilant et al., 2001; Boesch et al., 2006; Wroblewski et al., 2009; Newton-Fisher et al., 2010). Females typically give birth to their first infant at between 10 and 14 years (see table 1 in Emery Thompson et al., 2007). Males are reproductively mature at 9–10 years (Goodall, 1986; Nishida & Hiraïwa-Hasegawa, 1987; Reynolds, 2005) and while the earliest age of a father for a genetically confirmed paternity is 10 years (Boesch et al., 2006), the majority of infants (88 – 95%: Boesch et al., 2006; Wroblewski et al., 2009; Newton-Fisher et al., 2010) are fathered by fully adult males (those of full body size, reached at around 16 years).



## II. ROVING FEMALES

Females are the dispersing sex in chimpanzees; they may transfer between communities on a permanent or temporary basis, in the latter case sometimes returning pregnant (Pusey, 1979; Pusey et al., 1997; Boesch & Boesch-Achermann, 2000; Nishida et al., 2003; Sugiyama, 2004). Dispersal is part of the female reproductive strategy, an effort not only to acquire resources for the raising of offspring but also to locate males with whom to mate. Newly immigrated females appear to seek out and maintain associations with adult males in their new community possibly for protection from aggression by resident females (Kahlenberg et al., 2008a). For those females who mate before returning to their natal community, searching for and finding adult males is clearly reproductive effort.

Females seeking mates in other communities are likely to incur substantial costs; to understand the benefits they gain, it may be useful to draw a parallel between extra-group copulations (EGC) in chimpanzees — taking the female's home community males as her long-term collective 'pair bonded mate' — and extra-pair copulations (EPC) in superficially monogamous species [e.g. white-handed gibbons *Hylobates lar* Linnaeus 1771 (Reichard, 1995; Sommer & Reichard, 2000); many avian species (Westneat, Sherman & Morton, 1990)]. Such a comparison would suggest that, for dispersing females who mate before returning to their natal community or for females engaging in EGC after settling in a community, the benefits of such matings are likely to be either increased genetic diversity of offspring, or improved quality of offspring (Westneat et al., 1990). If this parallel holds, female chimpanzees should be sensitive to phenotypic markers of male quality, and we can predict that rates of EGC (and associated paternities) should be inversely related to both alpha male tenure and male success in territorial encounters. That is, females should look for mating opportunities elsewhere if they perceive males in their community of residence to be of poor quality. If females pursue genetic diversity of offspring, rates should be inversely related to the number of males in the female's community of residence, independent of male quality markers. If female pursuit of EGCs is facultative, these relationships may to an extent be mediated by prior experience or age. Females should also prefer EGC opportunities away from their natal communities. Understanding why female chimpanzees seek extra-group mating remains

unexplored, but these novel predictions may be testable with some of the larger long-term datasets collected on chimpanzee communities.

Within communities, sexually receptive females travel widely across the community range (Wrangham, 1986), show more male-like travel paths (Bates & Byrne, 2009), and have increased association with adult males (Goodall, 1986), when compared to non-cycling parous females. There are also anecdotal reports of sexually receptive females joining parties of males: Muller et al. (2009, p. 207), for instance, describe this as ‘a common occurrence’ among the Kanyawara community of chimpanzees from the Kibale Forest, Uganda. Observations of females leaving consortships to join other males (McGinnis, 1979; Tutin, 1979; Goodall, 1986) are also consistent with the idea that they are searching for mates. Searching for mates within their community of residence — roving — is central to the novel framework that I propose, and could be regarded as a simple extension of the mate-searching behaviour that characterises between-community female dispersal.

Female chimpanzees have a strong incentive to search for mates. They show a highly promiscuous mating strategy (Nishida, 1968; Sugiyama, 1968): during a single ovulatory cycle, a female can copulate hundreds of times (Wrangham, 2002). A cycling female characteristically produces a large perineal swelling (tumescence) during the follicular phase of her cycle that is bright pink and encompasses the full anogenital region. This signals, obviously if imprecisely, impending ovulation. Although females also show anovulatory swellings (Wallis & Lemmon, 1986), the swelling typically provides males with a probabilistic indicator of ovulation (Deschner et al., 2003; Emery & Whitten, 2003): a female will usually ovulate at some point during a 3 – 5 days window (Emery Thompson, 2005; Stumpf & Boesch, 2005) towards the end of the period of maximum swelling (approximately 11 days: Emery Thompson, 2005). These durations are long relative not only to the duration of copulation (mean 6 – 10 s: N. E. Newton-Fisher, unpublished data; Tutin & McGinnis, 1981; Hasegawa & Hiraiwa-Hasegawa, 1990; Wrangham, 2002; O’Hara, 2005; Stumpf et al., 2008), but also to duration of associations between individuals, which are typically measured in minutes or hours (Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2004; Reynolds, 2005). In consequence, females have the opportunity to find, and mate repeatedly with, most or all

adult males within their community (or, indeed, to make contact with extra-community males). The extent to which male behaviour may constrain such opportunities is discussed below. Detumescence is rapid, but may be delayed by a few days after ovulation has occurred (Graham, 1970; Deschner et al., 2003, 2004; Emery Thompson, 2005; Emery Thompson & Wrangham, 2008b).

Effective use of their mating strategy requires females to mate, probably repeatedly, with all or almost all potential fathers (adult and adolescent males). In theory, such promiscuous mating by females may be a counter-strategy to infanticidal behaviour by males, by providing all potential fathers with a non-zero probability of paternity and so creating 'paternity confusion' (Hrdy, 1979; Janson, 2000; van Noordwijk & van Schaik, 2000; Wolff & Macdonald, 2004). This is a plausible function for the mating strategy of female chimpanzees (Wrangham, 1993, 2002; van Schaik, 2000; Muller et al., 2007; Watts, 2007) given the risks of within-community infanticide (Nishida et al., 1985; Hamai et al., 1992; Uehara et al., 1994; Arcadi & Wrangham, 1999). Alternatively, it is possible that promiscuous mating functions to permit post-copulatory mate choice, selecting high-quality mates by provoking sperm competition (Parker, 1970; Stockley, 2004) for which chimpanzees show anatomical adaptations (Parker, 1970; Harvey & Harcourt, 1984; Moller, 1988; Anderson & Dixson, 2002; Snook, 2005).

Whatever the function of this promiscuity, allowing a single male to exclude all others from achieving a non-zero probability of paternity would incur potentially large costs. Such costs might be offset if the female has some means of selecting a high-quality male or if fathers can provide protection for their offspring against infanticidal males (van Schaik & Kappeler, 1997), as may well be the case in Gorilla (Savage, 1847) spp. (Harcourt & Greenberg, 2001). There is some evidence that female chimpanzees may be able to bias their mating behaviour to favour particular males (Tutin, 1979; Stumpf & Boesch, 2005; Emery Thompson & Wrangham, 2008b), but there is none to suggest that males provide specific protection for their own infants beyond collective territorial defence. The highly promiscuous, high-frequency mating behaviour typical of female chimpanzees suggests that they try hard to avoid incurring such costs: in turn this supports the idea that females have a strong incentive to find all potential fathers, and thus follow a roving mate-encounter strategy.

Despite this novel conclusion, Dunbar's (2000) analysis of chimpanzee mating strategies suggests that, in some populations, chimpanzees should follow the 'social' strategy of persistent association rather than the roving strategy. The particular study population to which this prediction applies lives in the Taï Forest, Cote D'Ivoire. Contrasts are often drawn between these West African chimpanzees and the multiple study populations of East African chimpanzees. The Taï chimpanzees have been described as 'bi-sexually bonded' (Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2009) and females in particular appear to differ from East African chimpanzees: they are more gregarious and sociable (Boesch, 1996; Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2008), and they show ranging patterns more similar to those of males, travelling widely though the community home range without restricting their activity to small core areas (Lehmann & Boesch, 2005). In common with East African chimpanzees (Wrangham, 2000), however, Taï Forest females range over smaller areas than do males (Lehmann & Boesch, 2005) and suffer foraging constraints on their sociability: the proportion of mixed-sex parties (Boesch, 1991) and female gregariousness (Riedel, Franz & Boesch, 2010) both decrease with declining abundance of fruit.

An analysis of Dunbar's model shows that it is particularly sensitive to both population density and to the distance at which a roving individual can detect a potential mating partner (N. E. Newton-Fisher, unpublished data). Replacing the figure of 9 adult females (see table 22.1 in Dunbar, 2000) with the 26 that Boesch & Boesch (1989) report living in the  $27\text{km}^2$  community home range, so correcting the local density of females, shifts the pay-off ratio from 0.4 to 1.3 and switches the model's prediction from 'social' to 'roving' (ratios in excess of 1.0 predict roving: see Section I.1). As a result, the 'non-roving' prediction is questionable for this population. Furthermore, Dunbar (2000) is very conservative with the detection distance specified in the model, restricting this to 0.05 km on either side of a travel path (a 100 m wide strip). While this might be appropriate for males looking for solitary, relatively stationary females, a roving female should have a better chance of detecting males. Human observers certainly find it easier to locate adult male chimpanzees than other age/sex classes, often by listening for the loud 'pant-hoot' vocalisations and drumming on tree buttresses that males commonly perform. These

signals can carry hundreds of metres through forested habitat (personal observations), and at times serve to coordinate the movements of chimpanzees (Mitani, 1994; Notman & Rendall, 2005). In Dunbar's model, increasing the detection distance to a value greater than 0.1 km (a search strip in excess of 200 m) changes the prediction for Tai chimpanzees to one of roving, independently of any change to the local density of females. In fact, the conditions under which the model predicts a social strategy given real data on chimpanzees are quite restricted, and roving is the more general prediction for this species.

Across species, a focus on resources as the limiting factor in female reproductive success has resulted in the idea of females as reproductive opportunists often being unappreciated. With the rise in sexual conflict theory (Parker, 1979; Arnqvist & Rowe, 2005) it has become clear that male and female reproductive interests can often diverge and that infanticide by males has driven a variety of female adaptations (van Schaik & Janson, 2000). It is now common to read debates on the extent to which females from a variety of taxa pursue their own reproductive goals, including surreptitious mating with males, being proceptive rather than merely receptive, engaging in promiscuous mating, or attempting to be selective over the fathers of their offspring. Sexual conflict sets the stage for an 'arms race' between males and females in their adaptations.

### III. MALE MATING STRATEGIES

Promiscuous mating by females, regardless of its function, creates a fundamental problem that male mating strategies must address. This problem is compounded for male chimpanzees by the dispersion of females through the community home range. The question, then, is what mate-encounter strategy would maximize their reproductive success, given spatially dispersed, promiscuous females?

#### **III.1 An alternative to roving?**

The initial presentation of the roving-male strategy was based entirely around scramble competition (Dunbar, 1988): benefits fall to the first male to encounter a fertile female,

although this depends critically on whether males can thwart the female strategy of promiscuity by sequestering the female (monopolizing mating and the paternity opportunity that each female presents). Given the arguments above, females should actively resist efforts to be sequestered and continue searching for other (non-roving) males across the relatively long period for which they are fertile (perhaps as much as 10 days in a single cycle: Emery Thompson & Wrangham, 2008b). Thus efforts to sequester the female and prevent her mating with other males are likely to be both time-consuming and energetically demanding. The assumption of sequestration is fundamental to the roving-male strategy: without it the effort put into searching is wasted (while it is possible to conceive of the roving strategy as constantly searching, non-sequestering males, pausing long enough only for a single copulation before resuming the search, this is so unlike observed chimpanzee behaviour that it will not be considered further here). This will apply even for a male pursuing a roving strategy in a population of non-roving males, as the female should continue searching for these other males.

In chimpanzees, operational sex ratios are highly skewed and paternity opportunities rare. Female chimpanzees have an inter-birth interval of 5 – 7 years (Boesch & Boesch-Achermann, 2000) and, in East African chimpanzees at least, typically cycle no more than three or four times for a single conception (Wrangham, 2002). Assuming a peri-ovulatory period (POP) of 5 days and three cycles to conception, each female provides, on average, a window of opportunity for males of only around 15 days every 6 years. If roving males are expected to converge on tumescent females and then compete — directly, or indirectly via social dominance—with one another for paternity opportunities (introducing contest competition into the model), contesting for these opportunities effectively increases the scarcity of paternity opportunities for any one male still further. Ultimately, it is the number of paternity opportunities encountered that sets a limit on male reproductive success, with more encounters resulting in significantly greater reproductive success (Wroblewski et al., 2009). Maximising the number of opportunities encountered is the fundamental purpose of any mate-encounter strategy and an effective strategy for male chimpanzees has to address this scarcity.

The roving-male strategy is poor choice for male chimpanzees: there is little if any advantage in being the first to find a female. Not only are individual ovulation events rare

and unpredictable, but these events must also be contested with other males in the community. While males able to win such competition should in principle benefit from roving, the female strategy renders it a poor choice for these males as well, as discussed below. Yet males would do worse by pursuing the alternative social strategy because they would miss paternity opportunities entirely (Dunbar, 1988, 2000). If we accept that the roving predicted by Dunbar's general model is, as suggested here, females searching for males, the optimal choice for males is, I propose, a new mate-encounter strategy: the 'patient-male' strategy.

To cope with the effective scarcity of paternity opportunities, males need to pursue a strategy that ensures they encounter multiple opportunities through time and that they maintain fertility in order to take advantage of these, opportunistically, as and when they occur: this is the 'patient-male' strategy. In contrast to the roving-male strategy, the patient-male strategy assumes that males are unable to counter the female strategy of promiscuity effectively and are forced therefore into a probabilistic competition for paternity. They are unable to sequester fertile females, either because it is not feasible to do so, or because it is simply too costly (e.g. Watts, 1998). That is, they can neither fully prevent females pursuing a promiscuous mating strategy, nor prevent other males from taking advantage of this. Unable to thwart the female strategy of promiscuity, they exploit it. Under this new framework, male chimpanzees do not search, but wait to be found; they use time that might otherwise have been lost in searching (if following a 'roving' strategy) to engage in behaviour that mitigates, or buffers against, threats to health and fertility and thereby maintain reproductive and competitive viability across multiple opportunities, essentially prolonging their reproductive careers. While such behaviour may also contribute to improved longevity relative to other strategies, the patient-male strategy is not a strategy for longevity (in the life-history sense of a later age at senescence) per se; males are not foregoing reproductive opportunities in order to 'out-last' competitors, which would make little sense as maturing males will replenish losses in any particular male's pool of rivals.

Life expectancy in the wild for adult chimpanzees—at the age of 15 years—is only 15 further years, and is lower for males than for females with only 11% of males who reach age 15 expected to survive to age 40 (Hill et al., 2001). With such levels of adult



mortality across populations, there should be a strong selective advantage for, amongst other things, behavioural strategies that maintain health and reproductive viability and thereby allow surviving males to continue to compete for paternity. Evidence from long-term studies of wild chimpanzees shows that some males father infants over a long career and into old age (Boesch et al., 2006; Wroblewski et al., 2009; Newton-Fisher et al., 2010). In the Budongo Forest, Uganda, paternity success increases with age, peaking in the early 30's, with a second peak for males who reach their 40's (calculated from data in table 1 of Newton-Fisher et al., 2010). Average age of a father is 26.9 years. In the Tai Forest, Cote D'Ivoire, average age of fathers is 24.1 years (Boesch et al., 2006), not significantly different. In both populations, males estimated at 40 years old or more are successful in achieving paternity. By contrast, fathers at Gombe are significantly younger (mean 20.4 years: Wroblewski et al., 2009) than in Budongo ( $Z = 3.31$ ,  $n_1 = 21$ ,  $n_2 = 33$ ,  $P = 0.001$ ): although males achieve paternity during their 20s and 30s, those aged 15–19 years are most successful. In comparison to these other sites, Gombe is a highly seasonal environment, and it has been suggested (Wroblewski et al., 2009) that male fertility may decline more rapidly, consequently reducing success in sperm competition; this may also account for the higher incidence of consortship—the mating context in which males avoid sperm competition—in this population (Wroblewski et al., 2009). Gombe chimpanzees also suffer elevated mortality due to SIV infection (Keele et al., 2009).

In summary, under the patient-male strategy male chimpanzees avoid the costs of mate searching (time, energy and risk), and seek to maximise paternity opportunities by mitigating threats to a prolonged reproductive career behaviourally, trading the time and opportunities that a roving strategy would otherwise require in order to do so. This strategy, as with 'roving' and 'social', is a means of maximising the number of paternity opportunities encountered and, in common with the 'social' strategy, is a 'waiting' rather than a 'searching' approach. The patient-male strategy assumes that males cannot sequester females and that time-constraints restrict the behavioural mitigation of threats to non-roving individuals. In contrast to conventional assumptions, male chimpanzees do not search for fertile females but leave the search for mates to the females, whose mating strategy requires them to locate multiple mates. If this female roving is driven by the need to mate promiscuously to minimize infanticide risk, males are essentially forcing females

to bear the costs of mate searching. This, I propose, is the male chimpanzees' solution to the problem created by the promiscuous mating strategy of spatially dispersed females.

### *III.2 The alpha male paradox*

Securing high, particularly alpha, social rank also increases male reproductive success: alpha males often make efforts to competitively exclude other males from mating, particularly towards the end of a female's POP, and can achieve around 30–40% of paternities (Boesch et al., 2006; Wroblewski et al., 2009; Newton-Fisher et al., 2010), in most cases a strongly disproportionate share. We might predict, therefore, that alpha males would benefit by pursuing the roving-male strategy, while lower ranking males follow the patient-male strategy. The ability for alpha males to succeed under a roving model that includes contest competition is doubtful, however. Despite being socially dominant to all other members of the community, an alpha male's share of paternities falls with increasing numbers of male competitors (Boesch et al., 2006; Newton-Fisher et al., 2010), indicating that even for alpha males, costs associated with sequestration of an unwilling female are likely to be prohibitive. With females pursuing a roving strategy, alpha males may do better to save the costs of searching and wait for these females to find them. The competitive abilities of alpha males that make roving seem an attractive strategy mean that, paradoxically, they do not need to be the first to encounter a fertilizable female, so long as other males cannot stop females from roving and females start searching for mates sufficiently early in their period of tumescence. Alpha males show greatest mating interest during the last few days for which a female is tumescent, suggesting that they are indeed 'waiting to be found' (i.e. not pursuing the roving male strategy).

The one situation in which roving might become viable for alpha males is during periods when community females are not cycling. In such circumstances, searching for possible mates among extra-community females might be advantageous for all males but, given that the same competitive constraints apply, the benefits will largely fall to the alpha. Either the alpha male slips away from the other males to avoid the costs of contest competition and, despite the associated search costs, roves alone (which may account for

the otherwise unusual periods of absence for a past alpha male, DN, from the Sonso, Budongo Forest, community: personal observations), or other males follow the alpha to exploit his inability to sequester completely any female encountered (as argued in section IV.1). If this latter possibility — that males rove en masse when there are no cycling females within their own home range — holds, it suggests that at least some patrols into the territories of neighbouring communities are mate-searching endeavours. Available evidence indicates, however, that such incursions are instead concerned with the elimination of males in those communities and the annexation of their territory (Mitani et al., 2010). These considerations indicate that roving is an unlikely strategy even for an alpha male.

### ***III.3 Best of a bad job?***

Instead, might roving be a viable option for low-ranking, less competitive males, as the ‘best of a bad job’ (Krebs & Davies, 1987)? Any male who mates with a promiscuous female during her fertile period should have a non-zero probability of achieving paternity, but in group mating contexts, opportunities for low-ranking males to mate successfully may be highly restricted by the efforts of multiple higher-ranking competitors attempting to increase their own share of matings. In such circumstances, finding a potentially fertile female before she has encountered a group of higher-ranking males might in principle be a better option for these less competitive males. Despite not being able to sequester the female, they may thereby increase the number of copulations that they achieve while avoiding the costs of contest competition (but incurring costs associated with travel and reduced sociality). Roving would at least then allow them to ‘buy a ticket in the lottery’ (Parker, 1982) of sperm competition even if their chances of ‘winning’ remain low. In practice, such copulations are unlikely to coincide with ovulation, however, and whether active searching in this case would actually increase paternity success any more than incidentally encountering cycling females (a null hypothesis of no searching) is unclear. Benefits of roving might increase if multiple females are cycling and ovulation is tightly synchronised, as a male focused on fertilizing one female may be unable to compete for a second, but only if roving females do not

converge on the same males. If males are unable to stop females from roving, the impact of reproductive synchrony on male reproductive skew is likely to manifest itself via its impact on mating opportunities within a party, rather than promoting roving amongst males.

Low-ranking, less competitive, males may do better to pursue multiple paternities over time by means of: (i) the patient-male strategy, (ii) seeking opportunities to rise in social rank in order to have better success in contest competition for copulations that coincide with ovulation, or (iii) ‘convincing’ females by means of coercive aggression to engage in consortships, than they would do by pursuing a roving-male strategy, particularly if the costs associated with roving of reduced sociality with other males are significant.

#### ***III.4 A mixed strategy?***

As with Dunbar’s general model, where males are regarded as pursuing either roving or social strategies, the novel framework proposed here requires males to choose between the roving and the patient strategy. Roving is unlikely to be a good choice for males, as they cannot sequester females whom they encounter. Nevertheless it is possible to at least conceive of a mixed strategy, whereby male chimpanzees engage in some mate-searching (roving) while also waiting for searching females and attempting to ensure that they encounter multiple paternity opportunities over time (patient). Whether they do this is an empirical question that should be resolved as the ideas presented here are tested, although ‘part-time roving’ seems unlikely to do much except generate costs—those associated with searching as well as opportunity costs. Unless males are able to mitigate threats to health and fertility in a time-limited fashion that is not compromised by the necessarily lone search for fertile females, males who are ‘patient’ will do better than those who ‘rove’, unless roving males can sequester females and thwart female promiscuity.

On the other hand, ‘status-striving’ (rank-acquisition) is a complementary strategy to both roving and patient strategies: high-ranking, socially dominant, males should have an advantage under either. Roving-male and patient-male are both mate-encounter (or search) strategies concerned with maximizing the number of paternity opportunities. By

contrast, status striving is a strategy to address contest competition among males for mating opportunities, and particularly the timing of copulations relative to a female's POP, once a potential mate has been encountered. To be clear, males following the patient-male strategy can (and probably should) also strive for social dominance.

#### IV. MATING TACTICS

The proposal that females, rather than males, are concerned with mate searching does not mean that males are uninterested in mating: male chimpanzees are clearly highly aroused by the sight of fully tumescent females (Nadler & Bartlett, 1997). It does, however, raise the question of how males should behave when in the company of such females: which mating tactics should they pursue once in a mating context, i.e. once the search for mates is successful. Male mating tactics, as decision sets nested within a higher level set of strategic decisions (Dunbar, 1988), concern who, what, when and where — the choice of mate, the timing and location of mating, and the use of aggression to coerce others' behaviour: both contesting mating opportunities with other males and sexual coercion (Smuts & Smuts, 1993; Clutton-Brock & Parker, 1995; Muller et al., 2007) of females.

##### *IV.1 Sequestering or biasing?*

Chimpanzee males show forms of restrictive mating (Tutin, 1979; Tutin & McGinnis, 1981; Hasegawa & Hiraiwa-Hasegawa, 1983; Watts, 1998; Wrangham, 2000) that seem to produce significant mating biases, but it is not at all clear that such tactics lead to sequestering of paternity opportunities: that is, isolating the female for duration of the period for which she can be fertilized. Possessive mating involving a single male does not typically last the duration of the POP (Tutin, 1979; Hasegawa & Hiraiwa-Hasegawa, 1983; Watts, 1998) and not all attempts to monopolize mating are successful at excluding other males from mating (although this may be due to constraints imposed by the competitive ability of other males, or the fickleness of females). More telling, perhaps, is that males will sometimes abandon mate-guarding efforts to engage in male-focused activities such as hunting (Watts, 1998), even if generally less likely to hunt when mating

opportunities exist (Gilby et al., 2006), and that not all mating contexts are possessive (Tutin, 1979; Boesch et al., 2006; Wroblewski et al., 2009). Recent genetic studies have demonstrated that paternities are distributed more widely than would be predicted by the roving-male model: lower ranking males typically do better, and high-ranking males worse, than expected (Wroblewski et al., 2009; Newton-Fisher et al., 2010, cf. Boesch et al., 2006).

We need to be careful not to conflate the possessive mating context and associated behaviours with sequestration (the consortship mating context and sequestration are considered in Section IV.2). Male tactics such as mate-guarding, disrupting the copulations of other males, and aggressive coercion of female behaviour might be regarded as evidence that males are attempting to sequester females (e.g. Hasegawa & Hiraiwa-Hasegawa, 1983; Goodall, 1986; Boesch & Boesch-Achermann, 2000; Muller et al., 2009), but equally well could be interpreted as attempts by males to bias the mating behaviour of females who cannot be sequestered (e.g. Muller et al., 2011). Among Kanyawara community chimpanzees, aggression is thought to dissuade females from mating with other males (Muller et al., 2009), so increasing the aggressor's share of copulations. Males direct aggression more frequently towards females who are maximally swollen (0.074 versus 0.019 times/h) and have higher copulation rates with those females to whom they are most aggressive (Muller et al., 2007).

In practice, it may be difficult to distinguish between successful attempts to bias mating and failed attempts at sequestering, but we need to question why we might assume a function for the male's behaviour over and above that which is immediately apparent. Ideas of mate searching by males, formalised in the roving-male model, lead to an expectation of sequestration and in consequence we explain male behaviour in this light. The roving-female/patient-male framework allows us to dispense with this expectation, and to consider the behaviour as observed: the consequence of male mating tactics is a bias in the share of mating achieved (or the particular timing thereof), and achieving this bias is their function.

This conclusion is supported by even the briefest consideration of chimpanzees' anatomical adaptations. Male chimpanzees simply do not show the extreme weaponry,

body size, or wounds that would be expected under the high levels of intra-sexual competition and selection that would be generated if they were able to sequester paternity opportunities. Sexual dimorphism is only moderate, with adult males around 25% heavier than adult females (Leigh & Shea, 1995). It is useful to draw a contrast with a highly sexually dimorphic (non-primate) species that demonstrates the classic ‘rove-and-sequester’ strategy. In an ursid such as the polar bear (*Ursus maritimus* Phipps, 1774), males are on average twice the size of females and show an accumulation of wounds, scars and broken canines with age that is not seen in females. Male polar bears rove great distances to find highly dispersed solitary females, scrambling to find them before other males, and engaging in fierce, bloody battles with rivals to sequester females and the paternity opportunities they present (Derocher et al., 2010). Chimpanzees are capable of inflicting great violence upon one another, particularly when working in concert (reviewed by Newton-Fisher & Emery Thompson, 2012), but this does not happen in the context of mate-guarding and the contesting of paternity opportunities.

Chimpanzee males clearly compete for mating opportunities, but the evidence that sperm competition also plays an important role in contests for paternity is strong. Chimpanzee males have enormous testes, both absolutely and relative to body size (Pan: 120g, body mass 47kg; cf. Gorilla: 30g, body mass 170 kg: Short, 1979 in Harcourt, 1997), which provide a large volume of sperm for multiple, repeated mating. Ejaculates have high sperm counts, and sperm show morphological and physiological adaptations for enhanced motility and longevity (Harvey & Harcourt, 1984; Moller, 1988; Harcourt, 1997; Anderson & Dixson, 2002; Anderson et al., 2007).

#### ***IV.2 The case of consortships***

The one context in which males do seem to achieve complete sequestration is the consortship (defined above, and see Tutin, 1979; also Muller et al., 2009). Far less is known about chimpanzee consortships than other mating contexts, but they may be of little relevance to whether the optimal encounter strategy for males is the roving or patient strategy. Consortships can last from a matter of hours to months (3h–28 days: Tutin, 1979; 3 days–3 months: Wallis, 1997) but successful consortships (those that result



in conception) are rare. In the Kasakela community at Gombe, of 175 consortships by 7 different males, only 41% included the female's POP (calculated from table 16.7 in Goodall, 1986), while Wallis (1997) reported that only 14 (11.9%) of 117 consortships were thought to result in conception. Despite early views that consortships provided the mating context for 25% or more of conceptions in the Kasekela community (Goodall, 1986; Wallis, 1997), recent genetic analysis suggests that only 9% of conceptions in this community occur during consortships (Wroblewski et al., 2009). In the Mahale Mountains M-group community, only 1 of 12 conceptions (8.3%) could be ascribed to a consortship context (Hasegawa & Hiraiwa-Hasegawa, 1990). For the Taï Forest chimpanzees only 1 of 17 consortships (5.9%) resulted in conception, of 1 of the 10 infants whose paternity was confirmed genetically (Boesch & Boesch-Achermann, 2000).

Male initiation of consortships is often aggressive, a form of indirect sexual coercion (Goodall, 1986; Smuts & Smuts, 1993; Muller et al., 2009), yet female compliance appears to be critical in ensuring that a consortship persists and that the male is successful in gaining exclusive mating access (personal observations; Tutin, 1979; Goodall, 1986; Boesch & Boesch-Achermann, 2000). Females have been seen slipping away from inattentive consorting males (Goodall, 1986), and a female often only has to vocalise in order to draw the attention of other males, thereby ending the consortship. Such vocalisations may be screams produced in response to male aggression, but as these may provoke further male aggression (Goodall, 1986) some degree of compliance with the consorting male (e.g. not vocalising) may be coerced by the threat of male violence (McGinnis, 1973; Muller et al., 2009). Quantitative data on the ending of consortships are scarce, although Tutin (1979) reports that 2 of 11 consortships (18%) ended with the female leaving the male, while in a third case, the female vocalised in response to hearing other males resulting in other males joining the consorting pair and ending the consortship; so in this small dataset, 27% of consortships failed due to female non-compliance.

By changing their mating behaviour, and not attempting to recruit or locate other males, females reduce the costs associated with sequestering: a male does not have to work as hard to control the female's behaviour, and does not have to contend with contest competition from other males. It might be most useful, therefore, to view consortships as

the outcome of alternate mating tactics, at least for females who become selective rather than promiscuous. Females may use participation in consortships to favour preferred males (Tutin, 1979; Stumpf & Boesch, 2005; Stumpf et al., 2008; Emery Thompson & Wrangham, 2008b): in the Tai forest, only males who had held or would go on to hold alpha rank successfully pursued consortships (Boesch & Boesch-Achermann, 2000), whereas for low-ranking males among the Gombe chimpanzees they were an effective means of securing paternity (Constable et al., 2001). These observations suggest that females may be responding to male phenotypic quality prior to males being able to demonstrate this through rank acquisition, or may perhaps be attempting to increase genetic diversity in offspring (in which case we can predict that rates of compliance in consortships with non-alpha males should increase with the length of alpha male tenure. In principle, compliance should also be greater where the consorting male has not previously sired one of the female's surviving offspring, but this requires females to have a means, if only probabilistic, of identifying 'non-sires').

If consortships remain rare and not all result in conception, females may be able to exploit them to exert mate choice or at least endure the resultant restriction of promiscuity without incurring increased infanticide risk. While non-consorting males can impose heavy costs on those returning from a consortship (Tutin, 1979), they should be relatively relaxed to the few paternities that arise: tolerating a degree of paternity uncertainty may provide their own offspring with a defence against infanticide (Boyko & Marshall, 2009; Henzi et al., 2010).

### ***IV.3 Detecting ovulation***

A female searching for males is likely, as a consequence of male gregariousness, to encounter groups of males. Given that she seeks to mate with all males, how should males respond? If males can reliably detect ovulation, they should withhold mating efforts until such time as copulation will coincide with ovulation. Various studies have presented data to support the hypothesis that males can detect the POP (Goodall, 1986; Hasegawa & Hiraiwa-Hasegawa, 1990; Wallis, 1992; Watts, 1998; Deschner et al., 2003, 2004; Emery Thompson, 2005; Emery Thompson & Wrangham, 2008b), and by

implication time their mating behaviour to coincide with ovulation.

Male sexual interest in females is greatest during the 10 – 13 days for which the perineal swellings show full tumescence. Possessive behaviour and copulation rates peak in the last few days of the maximally swollen period (Goodall, 1986; Hasegawa & Hiraiwa-Hasegawa, 1990), typically, if imprecisely, coinciding with the POP (Wallis, 1992; Deschner et al., 2003, 2004; Emery Thompson, 2005). There is a similar peak in the persistence with which males inspect female genitals: they may be looking for cues to ovulation in subtle changes in swelling size that continue across the period of ‘full’ tumescence until ovulation occurs (Deschner et al., 2003) and vaginal fatty acids (Matsumoto-Oda et al., 2003) that are consequences of changing levels of follicular oestrogen (Emery & Whitten, 2003; Deschner et al., 2004; Emery Thompson & Wrangham, 2008b). Deschner et al. (2004) suggest that subtle increases in size allow the swelling to function as a graded signal of fertility (Nunn, 1999).

Deschner et al. (2004) also report, however, that maximum swelling size was sustained after ovulation for up to 4 days, while Emery Thompson & Wrangham (2008b) provide evidence that conception is possible across the period of maximal swelling. Emery Thompson (2005) and Emery Thompson & Wrangham (2008b) also found that while male mating interest was greater during the POP (determined from endocrine data to be day 7 to day 3 prior to detumescence) than earlier in the period of maximal swelling, male copulation rates peaked at the start of the POP (days 7 and 6). In addition, they found that mating effort by the alpha male peaked at the end of, and after, the POP (in days 3, 2 and 1). Thus the alpha male, who should have fewest constraints on his mating behaviour, appeared to be timing his mating effort in relation to either size or duration of the swelling (mating when the swelling is largest, and when the female has been swollen for longest) rather than some other indicator of ovulation (as this is likely to happen prior to the alpha male’s peak mating effort). Furthermore, while male (and female) mating effort was greater in cycles in which females subsequently conceived (Emery Thompson & Wrangham, 2008b) copulation rates with alpha males did not differ significantly (Emery Thompson, 2005).

On current evidence, male chimpanzees ability to pinpoint ovulation is imprecise.

Ovulation in chimpanzees is not tightly coupled to swelling size or duration, and females seem to be doing a good job of keeping the precise timing of ovulation concealed within the period of tumescence. Males are likely, therefore, to be limited in the information available to them — beyond the approximate timing of the POP — when it comes to determining appropriate mating tactics. If males cannot be entirely sure when a female is ovulating, the most appropriate tactic on encountering a swollen female might be to mate with her immediately — in case ovulation is imminent — but at the last of any males present to do so — in case ovulation is hours or days away — as that copulation will be closer to ovulation than those that precede it (so improving the likelihood of sperm viability and egg fertilization windows overlapping). Mating after a rival might also serve, at least in theory, to displace that males' sperm. For these reasons, we can make the novel prediction that males should benefit most by being both the first and last to mate with a female in any particular encounter (note that specific mating-order effects have not been studied in chimpanzees and sperm competition is generally assumed to operate as a lottery: Dixson, 1998; Watts, 1998).

In such circumstances, where the information on the timing of ovulation that is available to males is limited, we would expect (i) a flurry of mating when a female is first encountered, with males competing and attempting to exclude rivals; (ii) subsequent periods of apparent disinterest during which male chimpanzees are attentive to mating attempts by other males; (iii) bursts of mating initiated by lower ranking males given the potential for high-ranking males to aggressively exclude other males; (iv) higher ranking males mating with swollen females following, and as a consequence of, mating attempts by lower ranking males. Flurries of mating behaviour and periods of apparent disinterest among males in a party with a swollen females are seen in wild chimpanzees (personal observations; McGinnis, 1979) and it is known that alpha males often delay the bulk of their mating effort until the end of a female's POP (Hasegawa & Hiraiwa-Hasegawa, 1983; Emery Thompson, 2005; Emery Thompson & Wrangham, 2008b). A lack of information regarding ovulation might explain these observations. The expectations are clearly testable, but I know of no systematic studies that have done so.

The assumption that selection should have favoured males capable of precisely detecting ovulation stems, it seems, from the expectation that males are attempting to

sequester females: the closer a female is to ovulating, the lower the costs of sequestering. If instead selection has favoured efforts to bias a female's promiscuity, selection for precision may be less strong. Being able to pinpoint it to within a few days, every 5 or 6 years might be enough, particularly if males actually benefit from a degree of paternity confusion (Boyko & Marshall, 2009). Females pursuing a roving strategy with promiscuous mating should seek out and associate with males as ovulation approaches; in consequence, even if they do not solicit copulations, they make themselves more available for them.

## V. BEYOND MATING

### *V.1 Social grooming*

If male chimpanzees pursue the proposed patient-male strategy, they should attempt to mitigate or buffer against threats to health and fertility. While many such threats may the same time to be ambient environmental hazards that they must accept as part of the trade-off necessary to meet energy budgets and secure copulations, where threats can be countered we should see appropriate behaviour.

Interactions between adult male chimpanzees are characterised by extensive bouts of social grooming (Newton-Fisher, 1997, 2002b; Boesch & Boesch-Achermann, 2000; Watts, 2000a, 2002; Arnold & Whiten, 2003; Mitani, 2006, 2009; Gomes, Mundry & Boesch, 2009; Newton-Fisher & Lee, 2011). While the most obvious potential benefit is hygienic — the removal of ectoparasites (Saunders & Hausfater, 1988; Tanaka & Takefushi, 1993; Zamma, 2002) — bouts are far longer than would be expected if this were its only purpose; across catarrhine (old world) primates, time spent grooming correlates with group size rather than body size (Dunbar, 1991; Lehmann, Korstjens & Dunbar, 2007). While parasite load may, at least in principle, increase with group size (Altizer et al., 2003; Johnson, Stopka & Macdonald, 2004), compensating for this is considered to be unlikely as the primary function of social grooming in catarrhine primates (Dunbar, 1991).

Conventionally, then, these grooming interactions are interpreted as efforts to build

and maintain relationships, valuable social bonds of some form that exist outside of the grooming interactions, although largely constituted by grooming interactions and for which grooming can provide an index (Newton-Fisher, 1997, 2002b; Boesch & Boesch-Achermann, 2000; Watts, 2000b, 2002; Arnold & Whiten, 2003; Mitani, 2006, 2009; Gomes et al., 2009). These relationships, in turn, function to provide 'trust' and so permit alliances and coalitions to form (de Waal & van Roosmalen, 1979; Dunbar & Sharman, 1984; Dunbar, 1988; Muller & Mitani, 2005). This provides a social function for grooming that is said to account for the cross-species relationship between group size and time spent grooming. The benefits of grooming are substantially delayed, coming through the rank and reproductive advantages associated with successful use of coalitions. Such coalitions provide a means of increasing relative social dominance as well as social support, buffering against harassment (aggression, displacement at feeding sites, disruption of activity) from other members of the social group.

Relationships (*sensu* Hinde, 1976) are, however, essentially proximate descriptors of interaction patterns. Repeated bouts of grooming (in this instance) create a history of interactions that provides the context for future interactions, but such relationships exist as a consequence of these interactions (Carpenter, 1945): that is, in contrast to the conventional view, catarrhine primates do not groom to form relationships; relationships form as a consequence of their grooming. If the behaviour that constitutes the interaction has clear functional consequences, it may be both unnecessary and misleading to search for adaptive value at the level of the relationship (cf. Cameron et al., 2009; Silk et al., 2010): to consider relationships functional rather than epiphenomenological, it is necessary to demonstrate that they provide benefits which are distinct from any that arise from their constituent interactions.

Social grooming has long been recognized to reduce tension (Terry, 1970; Dunbar, 1991); it provides stress reduction as a primary direct benefit for the recipient (Keverne, Martensz & Tuite, 1989; Feh & Demazieres, 1993; Aureli, Preston & de Waal, 1999) and potentially for the groomer as well (Shutt et al., 2007). We may not need, therefore, to look beyond the immediate benefits of grooming in order to discover a social function for this behaviour. Chronic levels of circulating corticosteroids depress the immune system, impair reproductive function, cause neurological damage and increase risks of

hypertension and atherosclerosis (Hansen, Alford & Keeling, 1984; Sapolsky et al., 1990; Coe, 1993; Packer et al., 1995; Dunbar, 1996; Sapolsky, 1996, 2004; Schapiro et al., 1998; Godbout & Glaser, 2006): reducing physiological stress should improve health and fertility (Sapolsky, Krey & McEwen, 2002). Larger, more complex social groups are likely to suffer from more conflicts of interest and increased social tension, thus the frequency of triggered stress responses is a socially induced problem that should increase with group size, particularly so in species such as chimpanzees where third parties can be drawn into others' conflicts, and where aggressive interactions can snowball. The tension-relieving or hedonistic nature of grooming might be the motivational mechanism that drives the performance of grooming (Dunbar, 1988), but it is the impact that these physiological changes have on chronic stress and thus on immunity, fertility and health (and so fitness) that should provide its adaptive function. That individuals will receive these benefits from interactions with others makes it a commodity that can be traded in a biological market and this perspective therefore represents a novel development of the existing biological markets (Noë & Hammerstein, 1994, 1995; Noë, 2001) 'grooming-trade' model (Barrett et al., 1999; Barrett & Henzi, 2001; Leinfelder et al., 2001) of primate social grooming in which the value of grooming is high, and lies in its ability to reduce physiological stress in recipients (Engh et al., 2006).

This argument provides a functional explanation for the prolonged bouts of grooming shown by male chimpanzees — stress reduction (or management) — over and above the grooming necessary to control parasite load (itself a threat to health and reproductive career). Adult male chimpanzees are unable to leave their natal communities, and are therefore trapped into a long history of interactions with their main competitors for reproductive success (Newton-Fisher, 2002b). Individuals experience frequent, regular harassment in the form of threats, including charging displays and chases; less common are attacks involving physical contact or wounding, but the risk is ever-present (Goodall, 1986). Reported rates of aggression between males vary among communities from 0.23 per hour (Sonso: Newton-Fisher, 2004) to 0.54 per hour (Mahale: Nishida & Hosaka, 1996; Tai: Boesch & Boesch-Achermann, 2000) and, while some of this variation is methodological (e.g. the Sonso figure excludes non-directed charging displays that are included elsewhere), it is clear that aggression is frequent. In the



Kasakela (Gombe) community in 1976 and 1978, individual adult males were attacked on average once every 62 h (range across individuals: 27 – 207 h: Goodall, 1986); among the Sonso (Budongo) chimpanzees in 1995, a male was victim of an attack on average once every 100h (N. E. Newton-Fisher, unpublished data). Furthermore, while the fission-fusion social system may counter some costs of grouping, it repeatedly creates social situations that are likely to trigger stress responses as well as exacerbating social unpredictability (Muller, 2002), which in itself should elevate stress levels (Sapolsky, 1993). Reproductive viability over time is likely to be compromised by unmanaged levels of chronic stress through increased susceptibility to both infectious and non-infectious disease and depression of fertility. Prolonged bouts of social grooming provide a potential counter to these threats.

It may be most parsimonious therefore to interpret grooming amongst male chimpanzees as a direct exchange of functionally significant behaviour (Newton-Fisher & Lee, 2011), as has been suggested for the grooming behaviour of baboons (*Papio ursinus*: Barrett et al., 1999; Barrett & Henzi, 2001). If chimpanzee males are trading a currency of stress reduction (as well as hygiene) through prolonged and repeated grooming exchanges, grooming should fluctuate in response to market forces: individuals vary in the need they have for the benefits it delivers, and this variation may account for apparent inequities in reciprocation (Newton-Fisher & Lee, 2011). Across individuals, grooming should vary in response to levels of social stability and stress, as has been reported for baboons (*Papio ursinus* Kerr, 1792: Crockford et al., 2008; Wittig et al., 2008). To the extent that social unpredictability increases rank instability, alpha males may in particular suffer elevated stress levels (Sapolsky, 2005). If, in consequence, holding alpha or high rank negatively impacts health or fertility, males may have to trade tenure at high rank against prolonged reproductive careers: for these individuals, tenure at high rank may be more critical for reproductive success. Mitigating rank-related costs through stress-ameliorating strategies such as grooming may help extend and exploit tenure, converting competitive success into paternity by maintaining fertility.

Adult male chimpanzees are, however, reproductive rivals and it may seem somewhat counterintuitive to suggest that they should cooperate in the exchange of grooming if this functions to promote the fitness of competitors: they might do better to

keep their rivals 'stressed' by withholding grooming and thereby gain a potential edge in, for example, sperm competition. Such a strategy may simply not be an option, however. These rivals are the source of the grooming that an individual needs, and so males may be forced into providing the stress-reducing benefits of grooming to rivals in order to secure those same benefits for themselves. Enhancing the fitness of reproductive rivals in this way may be an important but previously ignored cost to social grooming.

While male chimpanzees should seek out or exploit grooming opportunities to ensure that they receive the consequent benefits, they may be able to restrict the number of rivals that they aid in this way by cultivating preferred grooming partners (Mitani, 2009; Newton-Fisher & Lee, 2011). Simply by grooming those they have groomed before, any inequity in the distribution of grooming across potential partners will be magnified, and differentiated grooming relationships will emerge as a consequence of groomers making economic decisions to minimise associated costs. Such differentiated grooming relationships, with some dyads showing strongly reciprocal grooming, are common amongst male chimpanzees (Newton-Fisher, 1997, 2002b; Watts, 2002; Gomes et al., 2009; Newton-Fisher & Lee, 2011). This hypothesis provides an alternative explanation, to that provided by the concept of social bonds, for differentiated grooming relationships and persistent patterns of strong reciprocity restricted to particular dyads. Chimpanzees can be fickle in their allegiances (Nishida, 1983) and the assumption that high levels of affiliative interaction indicate bonds or 'friendships' may be unwarranted: in an extreme recent example, the prime motivators in the killing of an alpha male of the Mahale Mountains M-group were his two key affiliates in terms of both grooming and proximity prior to their attack (Kaburu et al., 2013).

This same logic can be extended to reconciliation and consolation, affiliative post-conflict behavioural interactions (de Waal & van Roosmalen, 1979; Kutsukake & Castles, 2004). Among wild chimpanzees, some form of reconciliation is seen in 12–16% of post-conflict situations (Arnold & Whiten, 2001; Kutsukake & Castles, 2004), although in captivity rates can be more than double this (27–35%: de Waal & van Roosmalen, 1979). Conventionally, these behaviours are regarded as functioning to repair valuable dyadic social relationships that have been damaged by aggressive interactions (de Waal & Aureli, 1997; Wittig & Boesch, 2005; Watts et al., 2006; Fraser, Stahl &

Aureli, 2008), although a study of post-conflict affiliative behaviour among wild chimpanzees did not find support for this ‘valuable relationships’ hypothesis (Kutsukake & Castles, 2004).

Although both reconciliation and consolation have been shown to reduce stress, or at least the correlated measures of behavioural anxiety (de Waal, 1996; Aureli & Schino, 2004; Fraser et al., 2008 Fraser, Stahl & Aureli, 2010), this is seen conventionally as a proximate mechanism that serves the ultimate function of maintaining strong dyadic relationships, which in some way enhance survival and reproductive success. If what matters to chimpanzees from an adaptive perspective, however, is the control of chronic stress levels, then it seems more parsimonious to explain the occurrence of these behaviours in terms of their direct functional benefits: whether by reconciling, consoling or grooming, chimpanzees may be trading a currency of stress reduction. The proximate reduction in stress that motivates these behaviours maps directly onto their adaptive function: mitigating the impact of chronic, socially induced, stress on immunity, fertility, and prolonged reproductive careers. This conclusion does not exclude the possibility that the quality of dyadic social relationships may moderate such benefits, for example by allowing longer grooming bouts, or by increasing (or decreasing) the value of a particular duration of grooming.

## ***V.2 Association patterns***

Chimpanzee parties are unstable associations, with individuals joining and leaving through multiple fission-fusion events over time. These parties provide the environment for social interactions, but often contain only a fraction of the community members (11–21% on average: Boesch, 1996); other individuals will be in other parties elsewhere in the community home range. Chimpanzees are therefore faced with on-going decisions regarding whether to stay in the current party, or to search for other companions.

Dunbar’s general model of male mating strategies pitches the pay-offs to males of persistently associating with females against searching for other females; it predicts therefore that male decisions to join or leave parties will be sensitive to the number of females present (Dunbar, 1988). If a male encounters a party with more than a critical

number of females he should stay (switch strategy from roving to social); if the number of females falls below that threshold, he should resume roving and leave (Dunbar, 1988). In direct contrast, the roving-female/patient-male framework predicts that males pursuing the patient-male strategy should be sensitive to the number of males in a party, not the number of females, when making decisions regarding joining and leaving as males provide opportunities for grooming, and thus management of chronic stress. More precisely, male decisions on party membership should be driven by the potential for interaction with other adult males, preferring parties with lowest potential for receiving aggression and highest potential for affiliative interactions such as grooming.

The two strategies also generate opposite predictions regarding male association decisions when a cycling, fully tumescent female is present. Males following the roving-male strategy should leave parties that contain a fully tumescent female if higher-ranking males, with whom they cannot compete, are present (Dunbar, 1988, p. 312). Thus, the number of adult males in a party should be lower than otherwise when a fully tumescent female is present: if the alpha male is in the party, all other males should leave. By contrast, males following the patient-male strategy should stay in parties that contain fully tumescent females regardless of the presence of higher-ranking males, to take advantage of male social interaction and female promiscuity. Data from wild chimpanzee populations show quite clearly that the number of adult males in a party is larger when a swollen, cycling female is present (Newton-Fisher, 1999; Emery Thompson & Wrangham, 2006). Although it might seem simplest to explain this in terms of lone, roving, males accumulating around a female (contra Newton-Fisher, 1999), these data in fact support the patient-male strategy. Following a similar logic to that laid out above, males pursuing the roving strategy should avoid parties with fully tumescent females that contain higher-ranking males, only joining those where they will be able to dominate; patient males should always join such parties, regardless of their relative social rank. These novel predictions provide a clear opportunity to test between the two strategies.

## VI. CONCLUSIONS

- (1) A fresh look at the results from the last 40 years of field studies suggests that the conventional model of chimpanzee mating strategies, in which male ranging is mating effort, is based on some rather shaky assumptions—males search for and are able to sequester females—that persist in the face of contrary data (e.g. male travel patterns; the spread of paternity across male rank; use of coercive aggression to bias female mating). Instead, the reproductive component of male ranging appears to be parenting effort, while the available data suggest that ranging as mate-searching (roving) is a female, not male, strategy. Conventional presentations of ‘roving’ males searching for ‘passive’ females appear to have the strategies reversed: it is the females who should benefit from roving. Males, by contrast, seem unlikely to do so under most circumstances. Female chimpanzees appear to have a strong incentive to search for mates: under a fluid, or fission-fusion, social system with individuals dispersed and at relatively low density, it is the only way they can effectively pursue a promiscuous mating strategy. There is evidence to support explanations of female promiscuity both as a counter to infanticide risk, and as a means of promoting post-copulatory mate choice through sperm competition. If the threat of infanticide drives this mating strategy, mate searching by female chimpanzees—and any associated costs—should be seen as an unavoidable consequence of male sexual coercion.
- (2) The function of male chimpanzee behaviours that lead to restrictive mating is, it is argued, to achieve biases in mating patterns and a consequent shifting of the odds of achieving paternity. Interpreting such behaviours as failed or constrained efforts to sequester females and the paternity opportunities they present is conventional, but it is not parsimonious, and seems driven by a desire to fit the data to theoretical expectations rather than using the discrepancy to challenge theory. The consortship mating context is the best evidence for sequestration but these events are rare and appear to be the result of a switch of mating strategy by the female, rather than success by males in overcoming female promiscuity.

(3) The function of social grooming in chimpanzees, and probably other catarrhine primates, is, it is argued, to mitigate the adverse consequences of socially induced chronic stress on immunity, fertility, and health (and so fitness). The conventional interpretation of grooming as promoting 'social bonds' with delayed fitness returns is flawed through a conflation of proximate and ultimate functions. Grooming reduces social tension and physiological stress, and the impact of this on the negative fitness consequences of chronic stress provides plausible adaptive benefits. These benefits are provided by one individual to another, grooming gains currency as a consequence, and thus the way individuals distribute grooming is likely to have been shaped by selection as modelled by biological markets theory. Recognising that grooming (and the same logic applies to behaviours such as reconciliation and consolation) may provide important fitness benefits challenges the need to postulate 'social bonds' or 'relationships' (that exist outside the grooming interactions) to account for grooming patterns. Under a strict Hindean definition, catarrhine primates do not groom to form relationships; relationships form as a consequence of their grooming. It seems both unnecessary and misleading to search for adaptive value of grooming interactions in terms of 'relationships', which themselves may be little more than abstracted descriptors of interactions, if this value is no more than the cumulative benefits provided by the grooming behaviour itself.

(4) This paper proposes a new mating strategy for male chimpanzees, which is to maximize paternity opportunities through promoting a prolonged reproductive career. This is the 'patient-male' strategy. Under this, instead of scrambling for access to females, males are able to spend time together engaged in prolonged and repeated grooming exchanges that counter socially induced chronic stress, thereby protecting immunity, health and fertility. Males settle, with sporadic shakeups, into a nested set ('hierarchy') of dyadic dominance relationships that reduce the frequency or intensity of aggressive confrontation and compete directly at each opportunity for paternity using a mix of rank-mediated contest, and post-copulatory sperm competition. Roving becomes, it is proposed, a potential (but perhaps unlikely) alternative strategy for

males when intra-community females are not cycling, and possibly a ‘best of a bad job’ strategy for low-ranking males faced with large numbers of high-ranking competitors.

- (5) This roving female/patient male framework is clearly testable, and at the very least it demands that some long-held assumptions about chimpanzee behaviour are challenged, and rejected if found wanting. This paper highlights numerous new hypotheses that emerge as a result of shifting away from the ‘roving-male’ model, e.g. mate-searching by female chimpanzees is a general strategy that encompasses within-and between-group mating, and female dispersal; rates of extra-group copulations (and paternities) should be inversely related to markers of male quality (alpha male tenure and male success in territorial encounters) as well as, independently, the number of males in the female’s home community; male association decisions should be sensitive to the number of males in a party; males should stay in parties that contain maximally swollen females regardless of male competitors; male mating tactics such as mate-guarding function to generate mating biases—they are not (doomed) attempts at sequestration; male roving is only likely to benefit alpha males, but if females rove such males should not search for mates. Exploring this novel framework as an alternative to the ‘roving-male’, ‘ranging-as-mating-effort’ model—testing, accepting or rejecting the various hypotheses with high-quality quantitative data—will lead to a substantially improved understanding of chimpanzee biology. More generally, this paper illustrates the need to revisit and revise theory in the light of accumulating data, rather than attempting to squeeze those data into an increasingly poorly fitting theoretical framework.

## VII. ACKNOWLEDGEMENTS

I thank Sarah Johns and Stefano Kaburu for various discussions that helped shape my thinking on these topics. I also thank Louise Barrett, in particular, as well as various anonymous reviewers, for constructive, thought-provoking and useful comments on previous drafts of this manuscript. I was supported by grant F/00236/Z from The Leverhulme Trust.



## VIII. REFERENCES

- Altizer, S., Nunn, C., Thrall, P., Gittleman, J., Ezenwa, V., Pulliam, J., Pedersen, A., Dobson, A., Poss, M., Cunningham, A., Antonovics, J. & Jones, K. (2003). Social organization and disease risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics* 34, 517–547.
- Anderson, M. J., Chapman, S. J., Videan, E. N., Evans, E., Fritz, J., Stoinski, T. S., Dixon, A. F. & Gagneux, P. (2007). Functional evidence for differences in sperm competition in humans and chimpanzees. *American Journal of Physical Anthropology* 134, 274–280.
- Anderson, M. J. & Dixon, A. F. (2002). Sperm competition: motility and the midpiece in primates. *Nature* 416, 496.
- Arcadi, A. C. & Wrangham, R. W. (1999). Infanticide in chimpanzees: review of cases and a new within-group observation from the Kanyawara study group in Kibale National Park. *Primates* 40, 337–351.
- Arnold, K. & Whiten, A. (2001). Post-conflict behaviour of wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Behaviour* 138, 649–690.
- Arnold, K. & Whiten, A. (2003). Grooming interactions among the chimpanzees of the Budongo Forest, Uganda: tests of five explanatory models. *Behaviour* 140, 519–552.
- Arnqvist, G. & Rowe, L. (2005). *Sexual Conflict*. Princeton University Press, Princeton.
- Aureli, F., Preston, S. D. & de Waal, F. B. M. (1999). Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. *Journal of Comparative Psychology* 113, 59–65.
- Aureli, F. & Schino, G. (2004). The role of emotions in social relationships. In *Macaque Societies: A Model for the Study of Social Organization*, pp. 38–55. Cambridge University Press, New York.
- Barrett, L. & Henzi, S. P. (2001). The utility of grooming in baboon troops. In *Economics in Nature* (eds R. Noë, J. A. R. A. M. van Hooff and P. Hammerstein), pp. 119–145. Cambridge University Press, Cambridge.
- Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 266, 665–670.
- Bates, L. A. & Byrne, R. W. (2009). Sex differences in the movement patterns of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*): foraging and border checking. *Behavioral Ecology and Sociobiology* 64, 247–255.
- Boesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117, 221–242.
- Boesch, C. (1996). Social grouping in Tai chimpanzees. In *Great Ape Societies* (eds W. C. McGrew, L. F. Marchant and T. Nishida), pp. 101–113. Cambridge University Press, Cambridge.
- Boesch, C. & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology* 78, 547–573.
- Boesch, C. & Boesch-Achermann, H. (2000). *The Chimpanzees of the Tai Forest*. Oxford University Press, Oxford.
- Boesch, C., Kohou, G., Nene, H. & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Tai forest. *American Journal of Physical Anthropology* 130, 103–115.
- Boone, J. L. (1991). Comments on Manson, J. H. & Wrangham, R. W. 'Intergroup aggression in chimpanzees and humans'. *Current Anthropology* 32, 377.
- Boyko, R. H. & Marshall, A. J. (2009). The willing cuckold: optimal paternity allocation, infanticide and male reproductive strategies in mammals. *Animal Behaviour* 77, 1397–1407.
- Bygott, J. D. (1979). Agonistic behaviour, dominance, and social structure in wild chimpanzees of the Gombe National Park. In *The Great Apes* (eds D. A. Hamburg and E. R. McCown), pp. 405–428. Benjamin/Cummings Publishing Company, Menlo Park.

- Cameron, E. Z., Setsaas, T. H. & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences of the United States of America* 106, 13850–13853.
- Carpenter, C. R. (1945). Concepts and problems of primate sociometry. *Sociometry* 8, 56–61.
- Chapman, C. A. & Wrangham, R. W. (1993). Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organization. *American Journal of Primatology* 31, 263–273.
- Clutton-Brock, T. H. & Parker, G. A. (1995). Sexual coercion in animal societies. *Animal Behaviour* 49, 1345–1365.
- Coe, C. L. (1993). Psychosocial factors and immunity in non-human primates: a review. *Psychosomatic Medicine* 55, 298–308.
- Constable, J. L., Ashley, M. V., Goodall, J. & Pusey, A. E. (2001). Noninvasive paternity assignment in Gombe chimpanzees. *Molecular Ecology* 10, 1279–1300.
- Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. A. & Cheney, D. L. (2008). Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior* 53, 254–265.
- Derocher, A. E., Andersen, M., Wiig, O. & Aars, J. (2010). Sexual dimorphism and the mating ecology of polar bears (*Ursus maritimus*) at Svalbard. *Behavioral Ecology and Sociobiology* 64, 939–946.
- Deschner, T., Heistermann, M., Hodges, K. & Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour* 66, 551–560.
- Deschner, T., Heistermann, M., Hodges, K. & Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. *Hormones and Behavior* 46, 204–215.
- Dixon, A. F. (1998). *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human Beings*. Oxford University Press, Oxford.
- Duffy, K. G., Wrangham, R. W. & Silk, J. B. (2007). Male chimpanzees exchange political support for mating opportunities. *Current Biology* 17, R586–R587.
- Dunbar, R. (1996). *Grooming, Gossip and the Evolution of Language*. Faber & Faber, London.
- Dunbar, R. I. M. (1988). *Primate Social Systems*. First Edition. Croom Helm, London.
- Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. *Folia Primatologica* 57, 121–131.
- Dunbar, R. I. M. (2000). Male mating strategies: a modeling approach. In *Primate Males: Causes and Consequences of Variation in Group Composition* (ed. P. M. Kappeler), pp. 259–268. Cambridge University Press, Cambridge.
- Dunbar, R. I. M. & Sharman, M. (1984). Is social grooming altruistic? *Zeitschrift für Tierpsychologie-Journal of Comparative Ethology* 64, 163–173.
- Emery, M. A. & Whitten, P. L. (2003). Size of sexual swellings reflects ovarian function in chimpanzees (*Pan troglodytes*). *Behavioral Ecology and Sociobiology* 54, 340 – 351.
- Emery Thompson, M. (2005). Reproductive endocrinology of wild female chimpanzees (*Pan troglodytes schweinfurthii*): methodological considerations and the role of hormones in sex and conception. *American Journal of Primatology* 67, 137–158.
- Emery Thompson, M., Jones, J. H., Pusey, A. E., Brewer-Marsden, S., Goodall, J., Marsden, D., Matsuzawa, T., Nishida, T., Reynolds, V., Sugiyama, Y. & Wrangham, R. W. (2007). Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. *Current Biology* 17, 2150 – 2156.
- Emery Thompson, M. & Wrangham, R. W. (2006). Comparison of sex differences in gregariousness in fission-fusion species: reducing bias by standardizing for party size. In *Primates of Western Uganda* (eds J. D. Paterson, V. Reynolds, N. E. Newton-Fisher and H. Notman), pp. 209–226. Cambridge

University Press, Cambridge.

- Emery Thompson, M. & Wrangham, R. W. (2008a). Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. *American Journal of Physical Anthropology* 135, 171–181.
- Emery Thompson, M. & Wrangham, R. W. (2008b). Male mating interest varies with female fecundity in *Pan troglodytes schweinfurthii* of Kanyawara, Kibale National Park. *International Journal of Primatology* 29, 885–905.
- Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of social systems. *Science* 197, 215–223.
- Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Seyfarth, R. M. & Cheney, D. L. (2006). Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proceedings of the Royal Society B: Biological Sciences* 273, 707–712.
- Feh, C. & Demazieres, J. (1993). Grooming at a preferred site reduces heart-rate in horses. *Animal Behaviour* 46, 1191–1194.
- Fraser, O. N., Stahl, D. & Aureli, F. (2008). Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America* 105, 8557–8562.
- Fraser, O. N., Stahl, D. & Aureli, F. (2010). The function and determinants of reconciliation in *Pan troglodytes*. *International Journal of Primatology* 31, 39–57.
- Gilby, I. C., Eberly, L. E., Pintea, L. & Pusey, A. E. (2006). Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour* 72, 169–180.
- Godbout, J. P. & Glaser, R. (2006). Stress-induced immune dysregulation: implications for wound healing, infectious disease and cancer. *Journal of Neuroimmune Pharmacology* 1, 421–427.
- Gomes, C. M., Mundry, R. & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B: Biological Sciences* 276, 699–706.
- Goodall, J. (1973). Cultural elements in a chimpanzee community. In *Precultural Primate Behaviour, Fourth IPC Symposia Proceedings* (Volume 1, (ed. E. W. Menzel), pp. 144–184. Karger Press, Basel.
- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of behaviour*. First Edition. Belknap Press, Cambridge.
- Goodall, J. (1990). *Through a Window: My Thirty Years with the Chimpanzees of Gombe*. Goerge Weidenfeld & Nicolson Ltd., London.
- Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., Pierce, A. & Riss, D. (1979). Intercommunity interactions in the chimpanzee population of the Gombe National Park. In *The Great Apes* (eds D. A. Hamburg and E. R. McCown), pp. 13–53. Benjamin/Cummings, Menlo Park.
- Graham, C. E. (1970). Reproductive physiology of the chimpanzee. In *The Chimpanzee*, Volume 3, Immunology, Infections, Hormones, Anatomy, and Behavior of Chimpanzees, pp. 183–220. University Park Press, Baltimore.
- Hamai, M., Nishida, T., Takasaki, H. & Turner, L. A. (1992). New records of within-group infanticide and cannibalism in wild chimpanzees. *Primates* 33, 151 – 162.
- Hansen, J. F., Alford, P. L. & Keeling, M. E. (1984). Diffuse myocardial fibrosis and congestive heart-failure in an adult male chimpanzee. *Veterinary Pathology* 21, 529 – 531.
- Harcourt, A. H. (1997). Sperm competition in primates. *American Naturalist* 149, 189 – 194.
- Harcourt, A. H. & Greenberg, J. (2001). Do gorilla females join males to avoid infanticide? A quantitative model. *Animal Behaviour* 62, 905–915.
- Harvey, P. H. & Harcourt, A. H. (1984). Sperm competition, testes size, and breeding systems in primates. In *Sperm Competition and the Evolution of Animal Mating Systems*, pp. 589–600. Academic Press, Orlando.
- Hasegawa, T. & Hiraiwa-Hasegawa, M. (1983). Opportunistic and restrictive mating among wild chimpanzees in the Mahale Mountains, Tanzania. *Journal of Ethology* 1, 75–85.

- Hasegawa, T. & Hiraiwa-Hasegawa, M. (1990). Sperm competition and mating behavior. In *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies* (ed. T. Nishida), pp. 115–132. University of Tokyo Press, Tokyo.
- Hayaki, H., Huffman, M. A. & Nishida, T. (1989). Dominance among male chimpanzees in the Mahale Mountains National Park, Tanzania: a preliminary study. *Primates* 30, 187–197.
- Henzi, S. P., Clarke, P. M. R., van Schaik, C. P., Pradhan, G. R. & Barrett, L. (2010). Infanticide and reproductive restraint in a polygynous social mammal. *Proceedings of the National Academy of Sciences of the United States of America* 107, 2130 – 2135.
- Herbinger, I., Boesch, C. & Rothe, H. (2001). Territory characteristics among three neighboring chimpanzee communities in the Tai National Park, Cote d'Ivoire. *International Journal of Primatology* 22, 143–167.
- Hill, K., Boesch, C., Goodall, J., Pusey, A., Williams, J. & Wrangham, R. (2001). Mortality rates among wild chimpanzees. *Journal of Human Evolution* 40, 437 – 450.
- Hinde, R. A. (1976). Interactions, relationships and social structure. *Man* 11, 1–17. Hrdy, S. B. (1979). Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* 1, 13–40.
- Janson, C. H. (2000). Primate socio-ecology: the end of a golden age. *Evolutionary Anthropology* 9, 73–86.
- Johnson, D. D. P., Stopka, P. & Macdonald, D. W. (2004). Ideal flea constraints on group living: unwanted public goods and the emergence of cooperation. *Behavioral Ecology* 15, 181–186.
- Kaburu, S. S. K., Inoue, S. & Newton-Fisher, N. E. (2013). Death of the alpha: within-community lethal violence among chimpanzees of the Mahale Mountains National Park. *American Journal of Primatology* 75, 789–797.
- Kahlenberg, S. M., Emery Thompson, M., Muller, M. N. & Wrangham, R. W. (2008a). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour* 76, 1497 – 1509.
- Kahlenberg, S. M., Emery Thompson, M. & Wrangham, R. W. (2008b). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology* 29, 931–947.
- Keele, B. F., Jones, J. H., Terio, K. A., Estes, J. D., Rudicell, R. S., Wilson, M. L., Li, Y., Learn, G. H., Beasley, T. M., Schumacher-Stankey, J., Wroblewski, E., Mosser, A., Raphael, J., Kamenya, S., Lonsdorf, E. V., Travis, D. A., Mlengeya, T., Kinsel, M. J., Else, J. G., Silvestri, G., Goodall, J., Sharp, P. M., Shaw, G. M., Pusey, A. E. & Hahn, B. H. (2009). Increased mortality and AIDS-like immunopathology in wild chimpanzees infected with SIVcpz. *Nature* 460, 515–519.
- Keverne, E. B., Martensz, N. D. & Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology* 14, 155–161.
- Krebs, J. R. & Davies, N. B. (1987). *An Introduction to Behavioural Ecology*. Second Edition. Blackwell Scientific Publications, Oxford.
- Kutsukake, N. & Castles, D. L. (2004). Reconciliation and post-conflict third-party affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates* 45, 157–165.
- Lehmann, J. & Boesch, C. (2004). To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioral Ecology and Sociobiology* 56, 207–216.
- Lehmann, J. & Boesch, C. (2005). Bisexually bonded ranging in chimpanzees (*Pan troglodytes verus*). *Behavioral Ecology and Sociobiology* 57, 525–535.
- Lehmann, J. & Boesch, C. (2008). Sexual differences in chimpanzee sociality. *International Journal of Primatology* 29, 65–81.
- Lehmann, J. & Boesch, C. (2009). Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour* 77, 377 – 387.
- Lehmann, J., Korstjens, A. H. & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour* 74, 1617–1629.

- Leigh, S. R. & Shea, B. T. (1995). Ontogeny and the evolution of adult body size dimorphism in apes. *American Journal of Primatology* 36, 37–60.
- Leinfelder, I., De Vries, H., Deleu, R. & Nelissen, M. (2001). Rank and grooming reciprocity among females in a mixed-sex group of captive hamadryas baboons. *American Journal of Primatology* 55, 25–42.
- Manson, J. H. & Wrangham, R. W. (1991). Intergroup aggression in chimpanzees and humans. *Current Anthropology* 32, 369–390.
- Matsumoto-Oda, A., Oda, R., Hayashi, Y., Murakami, H., Maeda, N., Kumazaki, K., Shimizu, K. & Matsuzawa, T. (2003). Vaginal fatty acids produced by chimpanzees during menstrual cycles. *Folia Primatologica* 74, 75–79.
- McGinnis, P. R. (1973). *Patterns of sexual behaviour in a community of free-living chimpanzees*. PhD Thesis: University of Cambridge.
- McGinnis, P. R. (1979). Sexual behavior in free-living chimpanzees: consort relationships. In *The Great Apes* (eds D. A. Hamburg and E. R. McCown), pp. 429–439. Benjamin/Cummings Publishing Company, Menlo Park.
- Mitani, J. (1994). Ethological studies of chimpanzee vocal behavior. In *Chimpanzee Cultures* (eds R. W. Wrangham, W. C. McGrew, F. B. M. de Waal and P. G. Heltne), pp. 195–210. Harvard University Press, Cambridge.
- Mitani, J. C. (2006). Reciprocal exchange in chimpanzees and other primates. In *Cooperation in Primates and Humans: Mechanisms and Evolutions*, pp. 107–119. Springer, New York.
- Mitani, J. C. (2008). Chimpanzee behavior: there's no place like home. *Current Biology* 18, R166–R167.
- Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour* 77, 633–640.
- Mitani, J. C., Watts, D. P. & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology* 20, R507–R508.
- Moller, A. P. (1988). Ejaculate quality, testes size and sperm competition in primates. *Journal of Human Evolution* 17, 479–488.
- Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. In *Behavioural Diversity in Chimpanzees and Bonobos* (eds C. Boesch, G. Hohmann and L. F. Marchant), pp. 112–124. Cambridge University Press, Cambridge.
- Muller, M. N., Emery Thompson, M., Kahlenberg, S. M. & Wrangham, R. W. (2011). Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behavioral Ecology and Sociobiology* 65, 921–933.
- Muller, M. N., Kahlenberg, S. M., Emery Thompson, M. & Wrangham, R. W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society B: Biological Sciences* 274, 1009–1014.
- Muller, M. N., Kahlenberg, S. M. & Wrangham, R. W. (2009). Male aggression against females and sexual coercion in chimpanzees. In *Sexual Coercion in Primates and Humans* (eds M. N. Muller and R. W. Wrangham), pp. 184–217. Harvard University Press, Cambridge.
- Muller, M. N. & Mitani, J. C. (2005). Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior* 35, 275–331.
- Murray, C. M., Gilby, I. C., Mane, S. V. & Pusey, A. E. (2008). Adult male chimpanzees inherit maternal ranging patterns. *Current Biology* 18, 20–24.
- Nadler, R. D. & Bartlett, E. S. (1997). Penile erection: a reflection of sexual arousal and arousability in male chimpanzees. *Physiology & Behavior* 61, 425–432.
- Newton, P. N. & Nishida, T. (1990). Possible buccal administration of herbal drugs by wild chimpanzees, *Pan troglodytes*. *Animal Behaviour* 39, 798–801.
- Newton-Fisher, N. E. (1997). *Tactical behaviour and decision making in wild chimpanzees*. PhD Thesis:



University of Cambridge.

- Newton-Fisher, N. E. (1999a). Association by male chimpanzees: a social tactic? *Behaviour* 136, 705–730.
- Newton-Fisher, N. E. (1999b). Infant killers of Budongo. *Folia Primatologica* 70, 167 – 169.
- Newton-Fisher, N. E. (2000). Male core areas: ranging by Budongo forest chimpanzees. *Pan Africa News* 7, 10–12.
- Newton-Fisher, N. E. (2002a). Ranging patterns of male chimpanzees in the Budongo Forest, Uganda: range structure and individual differences. In *New Perspectives in Primate Evolution and Behaviour* (eds C. S. Harcourt and B. R. Sherwood), pp. 287–308. Westbury, Otley.
- Newton-Fisher, N. E. (2002b). Relationships of male chimpanzees in the Budongo forest, Uganda. In *Behavioural Diversity in Chimpanzees and Bonobos* (eds C. Boesch, G. Hohmann and L. F. Marchant), pp. 125 – 137. Cambridge University Press, Cambridge.
- Newton-Fisher, N. E. (2003). The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. *African Journal of Ecology* 41, 150 – 156.
- Newton-Fisher, N. E. (2004). Hierarchy and social status in Budongo chimpanzees. *Primates* 45, 81–87.
- Newton-Fisher, N. E. (2006). Female coalitions against male aggression in wild chimpanzees of the Budongo Forest. *International Journal of Primatology* 27(6), 1589 – 1599.
- Newton-Fisher, N. E. & Emery Thompson, M. (2012). Comparative evolutionary perspectives on violence. In *Oxford Handbook of Evolutionary Perspectives on Violence, Homicide, and War* (eds T. Shackelford and V. Weekes-Shackelford), pp. 41–60. Oxford University Press, New York.
- Newton-Fisher, N. E., Emery Thompson, M., Reynolds, V., Boesch, C. & Vigilant, L. (2010). Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *American Journal of Physical Anthropology* 142, 417 – 428.
- Newton-Fisher, N. E. & Lee, P. C. (2011). Grooming reciprocity in wild male chimpanzees. *Animal Behaviour* 81, 439–446.
- Nishida, T. (1968). The social group of wild chimpanzees in the Mahale Mountains. *Primates* 9, 167–224.
- Nishida, T. (1979). The social structure of chimpanzees of the Mahale Mountains. In *The Great Apes* (eds D. A. Hamburg and E. R. McCown), pp. 73–122. Benjamin/Cummings Publishing Company, Menlo Park.
- Nishida, T. (1983). Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates* 24, 318–336.
- Nishida, T. (1991). Comments on Manson, J. H. & Wrangham, R. W. ‘Intergroup aggression in chimpanzees and humans’. *Current Anthropology* 32, 381–382.
- Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Hunt, K. D., Itoh, N., Kawanaka, K., Matsumoto-Oda, A., Mitani, J. C., Nakamura, M., Norikoshi, K., Sakamaki, T., Turner, L., Uehara, S. & Zamma, K. (2003). Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology* 59, 99 – 121.
- Nishida, T. & Hiraiwa-Hasegawa, M. (1987). Chimpanzees and bonobos: cooperative relationships among males. In *Primate Societies* (eds B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. Struhsaker), pp. 165–177. University of Chicago Press, Chicago.
- Nishida, T., Hiraiwa-Hasegawa, M., Hasegawa, T. & Takahata, Y. (1985). Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. *Zeitschrift für Tierpsychologie* 67, 284–301.
- Nishida, T. & Hosaka, K. (1996). Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In *Great Ape Societies* (eds W. C. McGrew, L. F. Marchant and T. Nishida), pp. 114–134. Cambridge University Press, Cambridge.
- Noë, R. (2001). Biological markets: partner choice as the driving force behind the evolution of mutualisms. In *Economics in Nature* (eds R. Noë, J. A. R. A. M. van Hooff and P. Hammerstein), pp. 93–118. Cambridge University Press, Cambridge.

- Noë, R. & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology* 35, 1–11.
- Noë, R. & Hammerstein, P. (1995). Biological markets. *Trends in Ecology & Evolution* 10, 336–340.
- van Noordwijk, M. A. & van Schaik, C. P. (2000). Reproductive patterns in eutherian mammals: adaptations against infanticide?. In *Infanticide by Males and its Implications*, pp. 322–360. Cambridge University Press, Cambridge.
- Notman, H. & Rendall, D. (2005). Contextual variation in chimpanzee pant hoots and its implications for referential communication. *Animal Behaviour* 70, 177 – 190.
- Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour* 58, 229–246.
- O’Hara, S. (2005). *Female sexuality and male violence in wild chimpanzees*. PhD Thesis: University of Cambridge.
- Packer, C., Collins, D. A., Sindimwo, A. & Goodall, J. (1995). Reproductive constraints on aggressive competition in female baboons. *Nature* 373, 60–63.
- Parker, G. A. (1970). Sperm competition and its evolutionary consequences in insects. *Biological Reviews of the Cambridge Philosophical Society* 45, 525–567.
- Parker, G. A. (1979). Sexual selection and sexual conflict. In *Sexual Selection and Reproductive Competition in Insects* (eds M. S. Blum and N. A. Blum), pp. 123–166. Academic Press, New York.
- Parker, G. A. (1982). Why are there so many tiny sperm? Sperm competition and the maintenance of the two sexes. *Journal of Theoretical Biology* 96, 281–294.
- Pepper, J. W., Mitani, J. C. & Watts, D. P. (1999). General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology* 20, 613–632.
- Pusey, A. E. (1979). Intercommunity transfer of chimpanzees in the Gombe National Park. In *The Great Apes* (eds D. A. Hamburg and E. R. McCown), pp. 465–480. Benjamin/Cummings, Menlo Park.
- Pusey, A. E. (2001). Of genes and apes: chimpanzee social organisation and reproduction. In *Tree of Origin* (ed. F. B. M. de Waal), pp. 11–37. Harvard University Press, Cambridge.
- Pusey, A., Williams, J. & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277, 828–831.
- Reichard, U. (1995). Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). *Ethology* 100, 99–112.
- Reynolds, V. (2005). *The Chimpanzees of the Budongo Forest: Ecology, Behaviour and, Conservation*. Oxford University Press, New York.
- Reynolds, V. & Reynolds, F. (1965). Chimpanzees of the Budongo Forest. In *Primate Behaviour* (ed. I. DeVore), pp. 368–424. Holt, Rinehart and Winston, Inc., New York.
- Riedel, J., Franz, M. & Boesch, C. (2010). How feeding competition determines female chimpanzee gregariousness and ranging in the Tai National Park, Cote d’Ivoire. *American Journal of Primatology* 73, 305–313.
- Sapolsky, R. M. (1993). The physiology of dominance in stable versus unstable social hierarchies. In *Primate Social Conflict* (eds W. A. Mason and S. P. Mendola), pp. 171–204. State University of New York Press, Albany.
- Sapolsky, R. M. (1996). Stress, stress-related disease and personality: studies of wild baboons. In *XVIIth Congress of the International Primatological Society*. Madison.
- Sapolsky, R. M. (2004). Social status and health in humans and other animals. *Annual Review of Anthropology* 33, 393–418.
- Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science* 308, 648–652.
- Sapolsky, R. M., Krey, L. C. & McEwen, B. S. (2002). The neuroendocrinology of stress and aging: the glucocorticoid cascade hypothesis. *Science of Aging Knowledge Environment* 2002, cp21.
- Sapolsky, R. M., Uno, H., Rebert, C. S. & Finch, C. E. (1990). Hippocampal damage associated with



- prolonged glucocorticoid exposure in primates. *Journal of Neuroscience* 10, 2897–2902.
- Saunders, C. D. & Hausfater, G. (1988). The functional significance of baboon grooming behavior. *Annals of the New York Academy of Sciences* 525, 430–432.
- van Schaik, C. P. (2000). Social counterstrategies against infanticide by males in primates and other mammals. In *Primate Males: Causes and Consequences of Variation in Group Composition* (ed. P. M. Kappeler), pp. 34–54. Cambridge University Press, Cambridge.
- van Schaik, C. P. & Janson, C. H. (2000). *Infanticide by Males and its Implications*. Cambridge University Press, Cambridge.
- van Schaik, C. P. & Kappeler, P. M. (1997). Infanticide risk and the evolution of male–female association in primates. *Proceedings of the Royal Society of London B* 264, 1687 – 1694.
- Schapiro, S. J., Nehete, P. N., Perlman, J. E., Bloomsmith, M. A. & Sastry, K. J. (1998). Effects of dominance status and environmental enrichment on cell-mediated immunity in rhesus macaques. *Applied Animal Behaviour Science* 56, 319–332.
- Shutt, K., MacLarnon, A., Heistermann, M. & Semple, S. (2007). Grooming in Barbary macaques: better to give than to receive? *Biology Letters* 3, 231–233.
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology* 20, 1359–1361.
- Simpson, M. J. A. (1973). The social grooming of male chimpanzees. In *Comparative Ecology and Behaviour of Primates* (eds R. P. Michael and J. H. Crook), pp. 411 – 506. Academic Press, London.
- Smuts, B. B. & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behaviour* 22, 1–63.
- Snook, R. R. (2005). Sperm in competition: not playing by the numbers. *Trends in Ecology & Evolution* 20, 46–53.
- Sommer, V. & Reichard, U. (2000). Rethinking monogamy: the gibbon case. In *Primate Males* (ed. P. M. Kappeler), pp. 159–168. Cambridge University Press, Cambridge.
- Stanford, C. B. (1998). *Chimpanzee and Red Colobus*. Harvard University Press, Cambridge.
- Stockley, P. (2004). Sperm competition in mammals. *Human Fertility* 7, 91–97.
- Stumpf, R. M. & Boesch, C. (2005). Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Tai National Park, Cote d’Ivoire. *Behavioral Ecology and Sociobiology* 57, 511 – 524.
- Stumpf, R. M., Emery Thompson, M. & Knott, C. D. (2008). A comparison of female mating strategies in *Pan troglodytes* and *Pongo* spp. *International Journal of Primatology* 29, 865–884.
- Sugiyama, Y. (1968). Social organisation of chimpanzees in the Budongo Forest, Uganda. *Primates* 92, 225–258.
- Sugiyama, Y. (2004). Demographic parameters and life history of chimpanzees at Bossou, Guinea. *American Journal of Physical Anthropology* 124, 154–165.
- Takahata, Y., Ihobe, H. & Idani, G. (1996). Comparing copulations of chimpanzees and bonobos: do females exhibit proceptivity or receptivity? In *Great Ape Societies* (eds W. C. McGrew, L. F. Marchant and T. Nishida), pp. 146–155. Cambridge University Press, Cambridge.
- Tanaka, I. & Takefushi, H. (1993). Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthropological Science* 101, 187–193.
- Terry, R. L. (1970). Primate grooming as a tension reduction mechanism. *Journal of Psychology* 76, 129–136.
- Trivers, R. L. (1972). Parental investment and sexual selection. In *Sexual Selection and the Descent of Man 1871 – 1971* (ed. B. Campbell), pp. 136 – 179. Aldine Atherton, Chicago.
- Tutin, C. E. G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees

- (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology* 6, 29–38.
- Tutin, C. E. G. & McGinnis, P. R. (1981). Chimpanzee reproduction in the wild. In *Reproductive Biology of the Great Apes* (ed. C. E. Graham), pp. 239–264. Academic Press, New York.
- Uehara, S., Hiraiwa-Hasegawa, M., Hosaka, K. & Hamai, M. (1994). The fate of defeated alpha male chimpanzees in relation to their social networks. *Primates* 35, 49–55.
- Vigilant, L., Hofreiter, M., Siedel, H. & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences of the United States of America* 98, 12890–12895.
- de Waal, F. B. M. (1996). Macaque social culture: development and perpetuation of affiliative networks. *Journal of Comparative Psychology* 110, 147–154.
- de Waal, F. B. M. & Aureli, F. (1997). Conflict resolution and distress alleviation in monkeys and apes. *Annals of the New York Academy of Sciences* 807, 317–328.
- de Waal, F. B. M. & van Roosmalen, A. (1979). Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology* 5, 55–66.
- Wallis, J. (1992). Chimpanzee genital swelling and its role in the pattern of sociosexual behavior. *American Journal of Primatology* 28, 101–113.
- Wallis, J. (1997). A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Journal of Reproduction and Fertility* 109, 297–307.
- Wallis, J. & Lemmon, W. B. (1986). Social behavior and genital swelling in pregnant chimpanzees (*Pan troglodytes*). *American Journal of Primatology* 10, 171–183.
- Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology* 44, 43–55.
- Watts, D. P. (2000a). Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. *International Journal of Primatology* 21, 189–210.
- Watts, D. P. (2000b). Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. *International Journal of Primatology* 21, 211–238.
- Watts, D. P. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour* 139, 343–370.
- Watts, D. P. (2007). Effects of male group size, parity, and cycle stage on female chimpanzee copulation rates at Ngogo, Kibale National Park, Uganda. *Primates* 48, 222–231.
- Watts, D. P. & Mitani, J. C. (2000). Infanticide and cannibalism by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Primates* 41, 357–365.
- Watts, D. P. & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour* 138, 299–327.
- Watts, D. P., Muller, M., Amstler, S. J., Mbabazi, G. & Mitani, J. C. (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology* 68, 161–180.
- Westneat, D. F., Sherman, P. W. & Morton, M. L. (1990). The ecology and evolution of extra-pair copulations in birds. *Current Ornithology* 7, 331–369.
- Williams, J. M., Oehlert, G. W., Carlis, J. V. & Pusey, A. E. (2004). Why do male chimpanzees defend a group range? *Animal Behaviour* 68, 523–532.
- Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P. & Goodall, J. (2002). Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour* 63, 347–360.
- Wittig, R. M. & Boesch, C. (2005). How to repair relationships: reconciliation in wild chimpanzees (*Pan troglodytes*). *Ethology* 111, 736–763.
- Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M. & Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior* 54, 170–177.
- Wolff, J. O. & Macdonald, D. W. (2004). Promiscuous females protect their offspring. *Trends in Ecology*

- & *Evolution* 19, 127–134.
- Wrangham, R. W. (1975). *The Behavioural Ecology of Chimpanzees in the Gombe National Park*. PhD Thesis: Cambridge University.
- Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In *Primate Ecology* (ed. T. H. Clutton-Brock), pp. 504–538. Academic Press, London.
- Wrangham, R. W. (1979). Sex differences in chimpanzee dispersion. In *The Great Apes* (eds D. A. Hamburg and E. R. McCown), pp. 481–490. Benjamin/Cummings Publishing Company, Menlo Park.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour* 75, 262–300.
- Wrangham, R. W. (1986). Ecology and social relationships in two species of chimpanzee. In *Ecology and Social Evolution: Birds and Mammals* (eds D. I. Rubenstein and R. W. Wrangham), pp. 352–378. Princeton University Press, Princeton.
- Wrangham, R. W. (1993). The evolution of sexuality in chimpanzees and bonobos. *Human Nature* 4, 47–79.
- Wrangham, R. W. (1999). Evolution of coalitionary killing. *Yearbook of Physical Anthropology* 42, 1–30.
- Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In *Primate Males: Causes and Consequences of Variation in Group Composition* (ed. P. M. Kappeler), pp. 248 – 258. Cambridge University Press, Cambridge.
- Wrangham, R. (2002). The cost of sexual attraction: is there a trade-off in female *Pan* between sex appeal and received coercion? In *Behavioural Diversity in Chimpanzees and Bonobos* (eds C. Boesch, G. Hohmann and L. F. Marchant), pp. 204–215. Cambridge University Press, Cambridge.
- Wrangham, R. W. & Smuts, B. B. (1980). Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*. Supplement 28, 13–31.
- Wrangham, R. W., Wilson, M. L. & Muller, M. N. (2006). Comparative rates of violence in chimpanzees and humans. *Primates* 47, 14–26.
- Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H. & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour* 77, 873–885.
- Zamma, K. (2002). Grooming site preferences determined by lice infection among Japanese Macaques in Arashiyama. *Primates* 43, 41–49.

Fig. 1. A model of alternate male chimpanzee mating strategies. The direct route to paternity (dotted line), once accounting for the impact of resources on the distribution of females, is blocked by the female mating strategy. The roving-male and patient-male strategies present alternate approaches by which ‘non-persistently-social’ males can overcome this problem. Solid straight arrows link the core elements of each. Dashed arrows indicate negative impact of the male strategy on the female strategy, largely through increased infanticide risk. Curved arrows show predictions arising from each element: males pursuing a roving strategy should search alone, or only in the company of lower ranking individuals, show strong sexual dimorphism and/or weaponry as well as mate guarding that persists across the peri-ovulatory period (POP) and excludes all other males. Males following the patient strategy should be gregarious, engage in grooming and other threat-mitigating behaviours, exploit sperm competition and attempt to bias female mating behaviour.

