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Chimpanzees use multiple strategies to limit aggression and stress during spatial density changes

Luke Mangaliso Duncan*, Megan Anne Jones, Mathew van Lierop, Neville Pillay

School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, South Africa

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ABSTRACT

The regulation of aggression in captive animals is an important welfare concern. Captive environments typically provide limited space for animals and many species exhibit heightened aggression in response to spatial restriction. However, primates appear to regulate aggression under these conditions. These findings have led to the proposal of three models for responses to spatial density changes: the density-intensity, tension-reduction and conflict-avoidance models. Our study aimed to investigate whether spatial restriction in two groups of captive chimpanzees at the Johannesburg Zoo, South Africa, supported the hypotheses of one or more of these models. In addition, a forth model based on the coping hypothesis of stereotypic behaviour was tested. Behavioural observations of both chimpanzee groups were conducted during the nine month reconstruction of the chimpanzee exhibit, and the associated variation in spatial limitation. Both chimpanzee groups used a tension-reduction tactic to limit aggression in the outdoor environments under high spatial density. In the indoor environments, the one (orphan) group of chimpanzees adopted a tension-reduction tactic to limit aggression while the other (family) group adopted a conflict-avoidance tactic. In both groups, indoor high-density conditions generated significant increases in abnormal behaviour. Our findings provide mixed support for the tension-reduction and conflict-avoidance models, while offering no clear evidence for the density-intensity model. The outcomes suggest that the chimpanzees may also have utilised abnormal behaviour as an outlet for the stress of spatial restriction. Together with evidence from other studies, our results suggest that chimpanzees are flexible in their response to the stress of spatial restriction and may employ aggression-mediation tactics in a context dependent manner. With regard to primate welfare, our findings suggest that aggression during spatial restriction may not necessarily be as prominent a welfare concern as previously thought but redirected and abnormal behaviour may still compromise animal wellbeing under spatial restriction.

1. Introduction

With an estimated 26 billion captive animals worldwide (Mason, 2010), there is an ethical (Seamer, 1998) and often legal (Line et al., 1990) responsibility to ensure that animals are maintained in environments that promote wellbeing. In order to ensure animal welfare, the social, behavioural, physiological and psychological requirements of captive animals must be considered (Hancocks, 2001) and appropriate resources provided. These resources necessary for normal biological functioning may be species-specific and range from basic requirements such as food (Veissier et al., 2008) to appropriate and adequate space (Nicol, 2007).

* Corresponding author at: 1 Jan Smuts Avenue, Braamfontein, Johannesburg 2050, South Africa. Tel.: +27 723120330; fax: +27 117176494.
E-mail address: luke.mangaliso.duncan@gmail.com (L.M. Duncan).

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Space is crucial to animals not only because other resources are spatially distributed, but space functions as a resource itself, providing a physical area in which to perform behaviour (Nicol, 2007). Moreover, space is also critical in regulating group social dynamics because individuals within groups possess limits on their inter-individual spacing, typically enforced through aggression (McBride, 1971). Because the social and spatial environments are linked, captive animals exhibit changes in aggression associated with physical environmental change and the resulting effect on social organisation (de Waal, 1989). The effects of changes in available space have been extensively studied, particularly with regard to the effects of spatial restriction in captive environments.

Preliminary observations of the effects of spatial restriction lead to the development of a 'density-intensity' model (*sensu* Nieuwenhuijsen and de Waal, 1982). Rodent studies such as those of Calhoun (1962) and Christian (1955a,b, 1961) exemplified the idea that reduced available space led to increased social stress and escalating aggression. Various subsequent studies of primates (Erwin and Erwin, 1976; Nash and Chilton, 1986; Demaria and Thierry, 1989) and non-primates (Blanc and Thériez, 1998; Blanc et al., 1999; Li et al., 2007) provided support for the density-intensity model.

By contrast, some primate studies found inconsistent support for the density-intensity model. Captive chimpanzees *Pan troglodytes* displayed higher levels of aggression in their small indoor enclosure than their larger outdoor enclosure, but aggression was low relative to the size difference between the two enclosures (Nieuwenhuijsen and de Waal, 1982) and while aggression in socially housed Pigtail macaques *Macaca nemestrina* increased with increasing density, aggression was socially regulated (Anderson et al., 1977). Subsequently, de Waal (1989) proposed that because primates place great value in their social relationships, they thus modify their social interactions to counteract increased aggression risk, effectively placating would-be aggressors. de Waal's 'coping model' suggested that primates selectively employ various pre-existing social mechanisms, such as reconciliation and appeasement behaviours (Judge et al., 2006), to manage aggression under spatial high-density conditions (de Waal, 1989). Several studies provided support for the coping model (Demaria and Thierry, 1989; Clarke and Mayeaux, 1992; Cordoni and Palagi, 2007), but, as with the density-intensity model, some findings suggested an alternative coping tactic.

Some studies suggested that primates avoid conflict altogether by minimising social interactions, an alternative tactic to the social buffering effect of the coping model. Chimpanzees reduced activity levels and all forms of social contact under spatial restriction (Aureli and de Waal, 1997) and similar patterns of behaviour emerged for studies of Rhesus macaques *Macaca mulatta* (Judge and de Waal, 1993), Long-tailed macaques *Macaca fascicularis* (Aureli et al., 1995) and Olive baboons *Papio anubis* (Elton and Anderson, 1977) under spatial restriction.

Based on the findings of the primate spatial restriction studies, two coping strategies were suggested as constituents of the coping model: the tension-reduction and conflict-avoidance strategies (Videan and Fritz, 2007). Many studies have found mixed support for these strategies, whereby avoidance and social behaviours are employed together to apparently regulate aggression (Judge and de Waal, 1993; Cordoni and Palagi, 2007), suggesting that primates may employ several strategies in response to spatial restriction through behavioural plasticity (Judge and de Waal, 1993).

The lack of aggression displayed by many primates under spatially restricted conditions does not necessarily mean that they are not stressed (de Waal, 1989) and evidence suggests that individuals under spatial restriction experience heightened social stress (Aureli and de Waal, 1997; Cordoni and Palagi, 2007; Tacconi and Palagi, 2009). A number of studies (Elton and Anderson, 1977; Nieuwenhuijsen and de Waal, 1982; Judge et al., 2006) have described individuals displaying abnormal and stress-related behaviours during spatial restriction, such as self-directed scratching (Maestripieri et al., 1992), hair plucking (Reinhardt, 2005) and self-injurious behaviour (Reinhardt and Rossell, 2001). Even Calhoun's rat study described greater abnormal behaviour and social pathology, including cannibalism, in high spatial density populations (Calhoun, 1962). The function of abnormal behaviours remains unclear but many appear to be strongly related to stress alleviation (e.g. regurgitation/re-ingestion: Baker and Easley, 1996; self-injurious behaviour: Tiefenbacher et al., 2004) and may be responses to the restricting captive environment (Walsh et al., 1982). This idea was formalised in the 'coping hypothesis', originally coined by Rushen (1993), which suggests that abnormal behaviours may serve a coping role, by reducing the experienced stress of an individual.

Both the coping model, *sensu* de Waal (1989), and the coping hypothesis, *sensu* Rushen (1993) provide a framework of strategies for coping with stress but the mechanisms of each differ considerably (Coping model – social mechanisms: de Waal, 1989; Coping hypothesis – non-social mechanisms: Rushen, 1993). With regard to the coping hypothesis, abnormal and self-directed behaviours may provide an outlet for stress which minimises the risk of disrupting the established social relationships, considered to be critical to primate social functioning (de Waal, 1989). Yet, no studies of the effect of spatial density changes in primates have considered non-social abnormal behaviours as a possible outlet for the associated social stress of spatial restriction (Judge et al., 2006, noted displacement activities including pacing and self-scratching, but abnormal behaviour was not explicitly investigated).

We investigated the behavioural responses of two mixed-sex groups of captive chimpanzees to long-term spatial restriction during the reconstruction of their outdoor enclosures at the Johannesburg Zoo, South Africa. There has been a recent proliferation of large, complex 'naturalistic' enclosure designs in zoos worldwide (Ogden et al., 1990) which typically replicate both aesthetic and functional elements of the natural environment (Little and Sommer, 2002) and are considered as being beneficial for primate welfare as they typically promote natural behaviour (Maple and Finlay, 1989). However, the naturalistic enclosure construction process necessitates the