



Is social dispersal stressful? A study in male crested macaques (*Macaca nigra*)



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ABSTRACT

In gregarious species, dispersal events represent one of the most dramatic changes in social life and environment an animal will experience during life due to increased predation risk, aggression from unfamiliar conspecifics and the lack of social support. However, little is known about how individuals respond physiologically to dispersal and whether this process is stressful for the individuals involved. We therefore studied the physiological stress response during dispersal in the crested macaque, a primate species in which males often change groups. Over a period of 14 months and 14 dispersal events in 4 groups, we determined faecal glucocorticoid metabolite (FGCM) levels during the process of immigration into a new group and examined a variety of factors (e.g. male age, rank achieved, number of males in the group) potentially affecting FGCM levels during this process. We found that FGCM levels were significantly elevated in the first few days upon immigration, after which levels returned quickly to baseline. FGCM response levels upon immigration were significantly and positively influenced by the number of males in the group. The rank a male achieved upon immigration, aggression received, as well as the proximity to other males did not significantly influence FGCM levels. Our data confirm previous findings on other species demonstrating that in crested macaques immigration into a new social group is associated with an acute endocrine stress response. However, given that stress hormone levels remained elevated only for a short period of time, we do not expect males to experience high physiological costs during immigration. Given our limited knowledge on the physiological responses to dispersal in animals, this study contributes to our understanding of dispersal more generally, and particularly inter-individual differences in the stress response and the potential physiological costs associated with these.

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1. Introduction

In gregarious animals, certain individuals leave their natal group as a consequence of selective pressures from within-group competition and inbreeding avoidance (Clutton-Brock and Lukas, 2012; Crnokrak and Roff, 1999; Henzi and Lucas, 1980; Pusey, 1987). The dispersal of an individual from one social unit to another is likely to represent one of the most fundamental shifts in social life and environment in an animal's life (Smale et al., 1997). Dispersal is often accompanied by substantial benefits such as access to unrelated females but may also come with a number of costs to the individual involved. For instance, in comparison to philopatric individuals, conspecifics transferring from one group or territory to another often face increased predation risk and restricted

access to known food resources (e.g. Alberts and Altmann, 1995; Pärt, 1995; Ridley et al., 2008). Furthermore, upon arrival in a new social group, dispersing individuals may face an elevation in aggression (Teichroeb et al., 2011; Ydenberg et al., 1988), the need to establish a permanent residency and dominance rank, and unfamiliar competitors – which require them to adapt their behaviour accordingly (Smale et al., 1997). Dispersal from a social group and immigration into a new group represent therefore potentially highly stressful and costly life-phases for the dispersing individual. To date, however, information on the physiological response and potential costs of such dispersal events and, in particular, how stressful the different phases (i.e. transition, immigration, membership in new group) associated with dispersal events are, is scarce. Such information, however, would be important to better understand the implications of this event on the health, survival and consequently the fitness of individuals.

Generally, as an adaptation to cope with the new environment, increased predation risk, and social challenges during the transition

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period and upon immigration, dispersing individuals can be expected to show a physiological stress response, i.e. an activation of the hypothalmo-pituitary-adrenal (HPA) axis and the secretion of increased levels of stress hormone (i.e. glucocorticoid; GC) (e.g. Sapolsky, 2002). This stress response enables the mobilization of energy for immediate use (e.g. 'flight or fight') (Sapolsky, 2002). Enhanced cognition, analgesia, and sensory function, as well as decreased pain perception are further adaptive consequences of an acute physiological stress response increasing the chances to overcome stressful and life-threatening situations (Nelson, 2005; Sapolsky, 1992). A direct link between a physiological stress response and such situations (e.g. increased predation risk, food scarcity) has been shown in diverse taxa (e.g. amphibians: Narayan et al., 2013; insects: Adamo et al. 2013; mammals: Sheriff et al., 2009). Studies investigating the direct link between time spent outside a social group and its effect on GC levels are, however, scarce. To our knowledge, the only study to examine this relationship, showed that subordinate male meerkats (*Suricata suricatta*) show increased stress hormone levels when conducting extra-territorial forays (Young and Monfort, 2009). Elevated GC levels upon immigration into a new social group, the second important phase individuals face during dispersal, has been reported for a number of primate species (long-tailed macaques (*Macaca fascicularis*): van Schaik et al., 1991; yellow baboons (*Papio cynocephalus*): Alberts et al., 1992; chacma baboons (*Papio ursinus*): Bergman et al., 2005; gray-cheeked mangabeys (*Lophocebus albigena*): Arlet et al., 2009; but see black howler monkeys (*Alouatta pigra*): van Belle et al., 2009) and thus seems to be a more common pattern, at least in this taxon.

However, the duration of these elevations is mostly unknown despite its potential implication on an individual's health and fitness. Whereas a short term (i.e. acute) increase in GCs is adaptive and allows an individual to better cope with a stressful situation, long-term or frequent activation of the HPA axis may lead to chronically elevated GC levels that can lead to physiological costs and thus compromise fitness due to its diverse negative effects on health (e.g. immunosuppression, decreased growth, impaired reproduction), potentially even leading to death (Sapolsky, 1992; Balm, 1999; Nelson, 2005). As such, individuals that are better able to downregulate their physiological stress response experience diminished health and fitness impairments. If a stress response is purely adaptive, a rise in GC levels is expected to be followed by a quick return to baseline levels.

Although current data on the stress response following dispersal is extremely limited due to the difficulty to predict the timing of dispersal and immigration, we expect that both intrinsic factors (e.g. fighting ability/rank achieved) and extrinsic factors (e.g. number of males in the new group, aggression received) will predict inter-individual stress responses for the dispersing males. In primates, males are the dispersing sex in the majority of species, and newly-arriving individuals of high fighting ability often challenge resident males to achieve a high rank in the new group, often at the expense of high risks such as severe injuries (Marty et al., 2016; Drews, 1995). Immigrants with comparably lower fighting ability often only achieve a lower rank in the new group and develop strategies with which to circumvent contest, in this way reducing the potential costs of immigration (Clarke et al., 2008; Marty et al., 2016). Given these differences in immigration costs, males of different fighting ability can be expected to also differ in their stress hormone responses upon immigration.

Once arrived in a new group, a successful competition for mates does not only depend on intrinsic factors such as fighting ability but also on the number of competitors. We assume that the number of competitors and therefore the degree of male-male competition may have an influence on the males FGCM levels. FGCM levels are expected to be positively associated with the number of competitors in the group. Alternatively, males may circumvent competition by avoiding proximity to other males and becoming peripheral.

To investigate individual stress levels during dispersal and immigration, we studied crested macaques (*Macaca nigra*). Crested macaques

are an excellent model species as males are known to disperse from one group to another several times in their life (Marty et al., 2016). This species has a high reproductive skew leading to high male-male competition and a steep linear hierarchy (Neumann et al., 2011; Reed et al., 1997; Engelhardt et al., under review). Reproduction in crested macaques is moderately seasonal whereby females can give birth year round. Crested macaques are endemic to the island of Sulawesi (Indonesia) and show a social system typical for cercopithecines with groups consisting of several males and females. As in most primates, females are philopatric whereas males disperse after reaching their physical prime (Marty et al., in press). Predation risk during the transition between groups seems to be low (Marty et al., 2016). Immigrations into a new group are non-random and many males are observed to immigrate into a group around the same time as other males. Males who achieve a high rank upon immigration (i.e. high fighting ability) are mainly young adult males dispersing from their natal group for the first time, immigrate independent of other males, are more likely to get injured, and can expect high future reproductive success. Males who achieve a low rank upon immigration (low fighting ability) align their immigration to a recent change in the alpha male position (exclusively conducted from new immigrants) (Marty et al., in press).

The overall aim of this study was to investigate the pattern of stress hormone output shown by dispersing males of a gregarious primate, and, by doing so, to examine whether dispersal events are associated with long-term physiological costs to these animals. We also investigated the effect of a variety of factors potentially influencing stress hormone output during immigration. Generally, we posed the following predictions: for solitary living males in the transition between two social groups (transient males), we predict that (1) they will show higher FGCM levels than individuals living in a group (resident males). Directly upon immigration, we predict (2) elevated FGCM levels in the immigrants. However, due to differences in a males' physical condition and the target group constellation, inter-individual differences in the magnitude of the physiological stress response are expected. Specifically, we therefore predict (3) high rank achievers who usually challenge the top rank position upon immigration (Marty et al., 2016.) to initially show higher FGCM levels than males who achieve a low rank. Regarding male-male competition, we expect (4) males immigrating into groups with comparably more competitors, and males that spend more time in the vicinity of such males upon immigration (5) to experience higher FGCM levels.

2. Methods

2.1. Study subjects and study site

Four groups of wild crested macaques were studied from November 2011 until January 2013 (15 months) in the Tangkoko Reserve in North Sulawesi, Indonesia (1°33'N, 125°10'E) as part of an on-going long term project (Macaca Nigra Project, www.macaca-nigra.org). The reserve ranges from sea level to 1350 m and comprises 8867 ha of lowland rainforest (Rosenbaum et al., 1998). The groups live in a mixture of regenerating former gardens, secondary forest, and undisturbed primary forest. Two of the observed groups (R1 and R2) have been periodically studied during the last ten years (O'Brien and Kinnaird, 1997; Reed et al., 1997) and continuously since 2006 (e.g. Neumann et al., 2010), whereas the two other groups (PB and R3) were habituated in 2008 and 2010, respectively (for more details see Marty et al., 2016). All individuals were fully habituated to the presence of human observers and individually known by the observers. All dispersing males were fully adult and none of the males included in this study were considered to be of old age (i.e. worn down canines, skinny body and slower movement).

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