# **Coping with the cold: Predictors of survival in wild Barbary macaques, *Macaca sylvanus***

Richard McFarland[a,b,*] & Bonaventura Majolo[a]

[a]School of Psychology, University of Lincoln, Lincoln, U.K.

[b]Brain Function Research Group, School of Physiology, University of the Witwatersrand, Johannesburg, South Africa (richard.mcfarland@wits.ac.za)

*_Correspondence:_ R McFarland, School of Physiology, University of the Witwatersrand, Medical School, 7 York Road, Parktown, Johannesburg 2193, South Africa. Tel: +27(0) 1171 72152, E-mail: richard.mcfarland@wits.ac.za.

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We report the death of 30 wild Barbary macaques, living in two groups, during an exceptionally cold and snowy winter in the Middle Atlas Mountains, Morocco. We examined whether an individual's time spent feeding, the quality and number of their social relationships, sex, and rank predicted whether they survived the winter or not. The time an individual spent feeding and the number of social relationships that an individual had in the group were positive and significant predictors of survival. This is the first study to show that the degree of sociality affects an individual's chance of survival following extreme environmental conditions. Our findings support the view that sociality is directly related to an individual's fitness, and that factors promoting the establishment and maintenance of social relationships are favoured by natural selection.

*Keywords*: Climate change; Feeding; Fitness; Social relationships; Thermoregulation

## Introduction

Experiencing extremely cold temperatures over long periods can impose significant energetic costs to mammals. Given that a stable body temperature has to be maintained to avoid hypothermia, an animal's metabolism needs to be increased at cold temperatures by consuming enough food to sustain thermoregulation [1]. Moreover, during cold conditions a diverse range of animal species have been observed to huddle with their con-specifics in order to maintain a stable body temperature [1].

The strength of social bonds that an individual has with other group members is thought to affect individual fitness [2,3]. However, empirical evidence on the link between sociality and fitness is extremely scarce in the literature. In primates, individuals that share stronger and more stable social relationships tend to have greater infant survival [4,5], a longer life expectancy [6] and sire more offspring [7]. In dolphins, horses and marmots reproductive success has also been linked to the strength of an individual's social relationships [8-10]. No data are currently available on whether sociality affects fitness in response to sudden, extreme changes in ecological conditions that can affect animal survival. These changes can occur naturally but are also increasingly linked to human activity, de-forestation and global warming; all factors forcing animals to inhabit unfavourable habitats [11-13].

We report the death of 30 wild Barbary macaques living in Morocco, during the 2008-2009 winter. This was an exceptionally harsh winter (ESM Table 1), with 20-90cm of snow covering the home range of our two study groups continuously from late November 2008 to early March 2009. These deaths were considered to be due to starvation as snow coverage significantly reduced the monkeys' access to food sources.

We used data collected during the six months preceding the death of our study animals to analyse whether and how ecological and social factors affected the monkeys' survival. We considered an individual's time spent feeding, the number and quality of their social relationships, sex, and rank as potential predictors of survival. We predicted that individuals that were more likely to survive the cold winter were: 1) those that spent more time feeding as they would be in better physical conditions, in terms of fat reserves, and more effective at fulfilling the energetic requirements of thermoregulation [1]; 2) those with a higher number, and on average higher quality of social relationships, as they would gain the social benefits of feeding tolerance [14,15] and behavioural thermoregulation (i.e. huddling: [1,16]); 3) females, due to their smaller body mass and energetic demands compared to males [17]; 4) high ranking individuals, who tend to get preferential access to food [18].

**Methods**

Data presented here were collected between August 2008 and January 2009 on two groups of wild Barbary macaque living in the Middle Atlas Mountains of Morocco. The 30 individuals that died, between December 2008 and January 2009, represented 65% of the animals in the two study groups. Only 17 monkeys survived the 2008-2009 winter, i.e. remained in the group or migrated to a neighbouring group. Detailed methods are provided in the ESM.

We used *ad libitum*, focal and instantaneous scan sampling techniques [19] to collect data on the five factors analysed as potential predictors of survival: feeding time, number and quality (i.e. composite sociality index: [4]) of social relationships, sex, and rank. We used two binary logistic regressions to test which factors (ESM Table 2) best predicted the probability that an animal would survive the winter. We entered group ID as a control variable in both regressions as group size is known to affect foraging competition [20]. First, we used a ‘full-model’ approach, by entering all variables together in a single regression, to test their relative effect on survival. Second, we used a backward stepwise regression (based on the -2 log likelihood value and chi-square statistics for each variable: [21]) to determine which variables best predicted the probability that an individual would survive the winter. All analyses were performed in IBM SPSS Statistics v20.

## Results

Using the ‘full model’ approach (Table 1) we found that feeding time had a positive and significant effect on survival. The number of social relationships an individual held was positively, but marginally non-significantly correlated with survival. Social relationship quality, sex, rank, and group ID had no significant effects.

A backward stepwise regression gave us a model (Table 2) with the amount of time spent feeding, the number of social relationships and group ID as the most important predictors of survival. Individuals that spent more time feeding or had more social relationships were more likely to survive (Figure 1). An increase in one social relationship gave a 0.48 increase in the log-odds of survival. A one percent increase in time spent feeding gave a 0.13 increase in the log-odds of survival. Time spent feeding and number of social relationships were themselves negatively correlated (Spearmans rho: $r_s$=-0.46, p<0.001).

## Discussion

We showed that an animal’s degree of sociality and the time spent feeding affect their chances of survival following extreme environmental conditions. To our knowledge, this is the first study to show that sociality can affect fitness in response to an unpredictable, short-term environmental event, such as the exceptionally harsh winter experienced by our study animals. This is important, as the scarce evidence on the link between sociality and fitness has so far focused on long-term fitness benefits (e.g. life-time reproductive success: [4-10]). Taken together our study and previous research on this topic support the hypothesis that the capacity to establish and maintain social relationships may have independently evolved in different taxa, any time ecological conditions gave fitness benefits to individuals with a stronger network of relationships [3,22,23]. It is important to note that due to the opportunistic nature of this study (i.e. we observed an extremely rare and unexpected event), interpretation of our results is difficult as our hypotheses were based on post-hoc predictions.

We found a significant positive effect of the amount of time spent feeding on an individual's probability of survival. Individuals that spent more time feeding were more likely to fulfil their energetic requirements for thermoregulation in the cold [1]; congruent with optimal foraging theory [24] and the positive relationship between increased energy intake and survival observed in animals [25,26]. Previous studies testing the relationship between inclusive fitness and sociality [4-10] have used measures of relationship quality, rather than the number of social relationships, to analyse the strength of an individual's social network. In our study, we tested the effect of both measures of sociality. We provide evidence that it is the quantity and not the quality of these relationships that predicts an animal's survival. We predicted that individuals with a higher degree of sociality would be more likely to survive as they would gain the social benefits of feeding tolerance. In support of this prediction we found that both the number of social relationships and time spent feeding were positively correlated with survival. These variables were themselves negatively correlated. This suggests that the increased feeding tolerance resulting from a larger network of social relationships favours more efficient foraging, enabling individuals to devote less time and energy to foraging (and potential associated aggression) and thus improves their chances of survival. These findings are consistent with evidence that social bonds promote foraging tolerance [14,15] which, in turn, can impact on an individual's time budget and survival [23,27].

We also predicted that having more and higher quality social relationships would impact on an individual's ability to thermoregulate via huddling. During the night, Japanese macaques have been observed to huddle more frequently with kin and familiar social partners [28], and as temperatures get colder, the size of their huddling clusters increase [14]. We did not collected data on the time individuals spent in contact with their conspecifics at night, so we could not directly test the link between survival and the amount of time an individual spent huddling at night [28]. However, our results suggest that individuals with more social relationships may have had more opportunities to gain access to these huddling groups, making it easier for them to preserve energy in cold periods. Finally, the absence of a relationship between rank or sex with survival suggests that females and high ranking individuals did not significantly benefit from, respectively, their reduced energetic demands or increased social power [17,18].

Global climate change poses a serious and imminent threat to our planet's biodiversity [29,30], particularly to those species which are unable to migrate to more favourable climates. If animals are forced to live in habitats for which they have limited physiological and behavioural adaptive responses, as is the case of the Barbary macaque [31], this may disrupt their behaviour and have negative consequences for their reproduction and survival. A harsh winter can pose similar ecological pressure on animals as a human induced change in their habitat (e.g. a new ecological barrier due to logging). Our findings highlight that sociality affects how animals respond to short-term changes and that social factors should be taken into account when assessing the viability of a population and for effective conservation plans.

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**Figure 1 –** Mean±SD time spent feeding (left) and number of social relationships held (right) by survivors (white bars) and non-survivors (grey bars)

**Table 1 –** Logistic regression results using the full model approach (N=47)

| **Variable** | **Co-efficient ± SE** | ***Wald* ($X^2$)** | ***P*** |
|---|---|---|---|
| Feeding time | 0.11 ± 0.05 | 4.36 | 0.04 |
| Number of social relationships | 0.42 ± 0.23 | 3.28 | 0.07 |
| Quality of social relationships | 0.11 ± 1.18 | 0.01 | 0.93 |
| Sex | -0.18 ± 1.23 | 0.02 | 0.88 |
| Rank | 0.04 ± 0.08 | 0.30 | 0.58 |
| Group ID | 1.86 ± 2.14 | 0.76 | 0.39 |

**Table 2 –** Logistic regression results using the best model approach (N=47)

| **Variable** | **Co-efficient ± SE** | ***Wald ($X^2$)*** | ***P*** |
|---|---|---|---|
| Feeding time | 0.13 ± 0.05 | 7.31 | 0.01 |
| Number of social relationships | 0.48 ± 0.19 | 6.52 | 0.01 |
| Group ID | 2.37 ± 1.30 | 3.34 | 0.07 |

**Short title:** Coping with the cold