



## Resting time as an ecological constraint on primate biogeography

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Time constraints can limit an animal's potential to survive in a given habitat and the maximum size of its group. Many studies have, therefore, investigated the ecological correlates of time allocated to travelling, foraging and vigilance. However, animals spend more time inactive than active, and understanding the determinants of this resting time may provide new insights into the habitat-specific time-budgeting problems that animals face. We analysed the environmental constraints that determine the minimum amount of daytime an average primate has to spend resting, using data from a wide range of ecologically different species. However, total resting time consists of two components: enforced resting time (imposed on the animal by ecological constraints) and free resting time (the time available for allocation to ecologically functional activities). We show that the ecologically important enforced resting time is determined by diet and annual temperature as well as by temperature variation. Our tests of the biological significance of this relationship show that enforced resting time distinguishes between locations that are suitable or unsuitable for particular genera. We show that an annual temperature increase of 2–4 °C would greatly increase enforced resting time, leading to serious time-budgeting problems for many species. The effect of changes to enforced resting time on the biogeographical distribution of species is especially strong for folivorous primates. This study shows that resting time is an important component of animal behaviour that can help us understand extinction risk and geographical distribution of taxa.

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Time is an important resource for all animals, and decisions about time allocation have always been at the core of optimal foraging theory (Schoener 1971; Stephens & Krebs 1986). While feeding, travelling and being vigilant have attracted considerable attention as activities that have immediate impact on fitness, resting time has often been viewed as being simply time that is not required for more important behaviours. However, resting reflects not only time waiting to be allocated to something more useful, but also time needed for recuperation, predator avoidance, digestion and thermoregulation (Herbers 1981), and it can be an important variable that affects primate group size (Pollard & Blumstein 2008; Dunbar et al. 2009).

It is, therefore, important to distinguish between at least two separate forms of resting that together constitute total resting time: enforced resting (for digestive and thermoregulatory purposes) and

uncommitted resting time (Dunbar 1996). Only the second is available for conversion into additional feeding, travel or social time when these are required. Enforced resting time may impose significant limits on a species' distribution by making it difficult for animals to allocate sufficient time to other biologically essential activities. This may be especially problematic for diurnal species that are unable to compensate by foraging at night for time lost because of high heat loads during the day.

In principle, enforced resting time is most likely to be influenced by climate and by dietary considerations. Species living in extreme climates may be obliged to seek shelter or simply reduce thermally costly behaviours, either to reduce heat loss at high latitudes or to minimize heat load at lower latitudes (Stelzner 1988; Roberts & Dunbar 1991; Hill 1999). In the tropics, for example, thermal stress resulting from high ambient heat loads and high radiant heat gain over the middle hours of the day results in a significant rise in core body temperature (Taylor 1970; Mount 1979). The vertebrate brain is especially sensitive even to fairly minor changes in tissue temperature (Precht et al. 1973). Although many species have anatomical mechanisms to reduce heat load (e.g. venal retes to dissipate blood heat, enlarged muzzles to increase evaporative cooling), seeking shelter and resting is often the most effective behavioural solution. The other factor influencing enforced resting

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time is likely to be the demands of digestion (which, in turn, will partly reflect diet and food quality). This is most obvious in the case of ruminants, which are forced to spend substantial amounts of time inactive to permit rumination (van Soest 1982; van Hoven & Boomker 1985).

We investigated the extent to which climatic and dietary variables influence demand for enforced resting time in primates, and evaluated the consequences of this for the biogeographical distribution of primates. We used primates for this analysis because they represent a well-studied taxon for which time budget data are available for many species. Furthermore, there is a wide variation in dietary specializations and distribution patterns both between and within different primate genera. This allows us to look at the effects of climate and diet on resting time and, consequently, on the extinction risks that individual species face under climate warming.

## METHODS

### *The Data*

We searched the literature for quantitative data on resting time, diet and group sizes (data summarized per species is provided in the Appendix). Studies were selected if all behavioural and demographic parameters of interest were measured, and if observations had been carried out over at least 8 months and/or data were available for multiple seasons. Data on resting time and diet had to be obtained using either scan sampling or focal animal sampling. The differences between these methods will introduce additional error variance into the analyses (Dunbar 1976; Rhine & Flanigan 1978; Mitlöchner et al. 2001), but this should only act conservatively by reducing significance levels. In the few cases where auto-grooming and time spent vigilant while resting were mentioned (Struhsaker & Leland 1979; Kumar et al. 1995; Kaplin & Moermond 2000), they were included in resting time because most researchers do not analyse these categories separately. These typically represent less than 5% of total resting time. For present purposes, resting time excludes social time. Social interactions are energetically costly and do not constitute rest in any meaningful sense; more importantly, it is not environmentally dictated in the sense defined by our concept of enforced resting time (primate social time is determined mainly by group size: Dunbar 1991; Lehmann et al. 2007b). Some studies, however, did not mention social time within the time budget components. When excluding all cases where there was even the slightest doubt of whether or not resting included social time (reduced data set of 66 species, see Appendix), all results remained very similar.

In addition to climatic and environmental variables, the feeding and travel components of a time budget can also be influenced by social group size (e.g. through competition effects: Janson 1988; Dunbar 1992b; Janson & Goldsmith 1995) and may thus negatively influence the free time available for resting. We therefore included group size in our initial list of independent variables. Most primate species form stable groups that stay together throughout the day. However, a few species live in communities whose membership is stable, but which split up into smaller subgroups (parties) which regularly reunite and reorganize throughout the day (fission–fusion); although individuals hardly ever aggregate as the entire community, they none the less maintain social relationships with all community members (Aureli et al. 2008). In other species, the typical social unit may occasionally join other such units at limited resources, although in these cases social interactions between units are typically minimal. Therefore, we defined ‘group’ as the maximum unit that individuals come together in and ‘party’ as the average size of groups in which individuals are typically found during the day. For species that do not show fission–fusion, the

group is synonymous with party; for species that do (*Cebus apella*, *Ateles* spp., *Brachyteles* spp., *Lagothrix* spp., *Alouatta seniculus*, *Theropithecus gelada*, *Pan* spp.), a party is the typical subgroup the animals are found in, and a group is the community; and for species that form multigroup aggregations (*Colobus angolensis*, *Rhinopithecus bieti*), a party is the typical social unit within the multigroup aggregation (which was defined as the group). We considered parties separately from groups in our analyses. To check the effect of large-scale aggregations in *C. angolensis* and *R. bieti*, we confirmed that treating multiunit aggregations as parties or social units as groups made no difference.

Two sources were used to determine climate conditions at study sites: (1) the authors’ or colleagues’ climate descriptions during the study period; and, if these were not available, (2) Willmott and Matsuura’s climate model (v3.01; <http://climate.geog.udel.edu/~climate/>). Willmott and Matsuura provide a global data set of monthly and annual temperature and rainfall in grids of 0.5° latitude by longitude, based on a combination of the Global Historical Climatology Network (GHCN v2) and weather station records from 1950 to 1999 (Legates & Willmott 1990a, b). From this data set, we calculated the average value of each climate variable for the data points that fell within a radius of 0.5° longitude and latitude to the site. For the populations for which we had average annual temperature ( $N = 52$ ) and/or rainfall ( $N = 101$ ) from the authors for the time of the study, these values were very comparable to those obtained from Willmott and Matsuura’s data set (Spearman correlation: temperature:  $r_s = 0.903$ ,  $P < 0.0001$ ; rainfall:  $r_s = 0.844$ ,  $P < 0.0001$ ).

The following climate variables were investigated: average annual rainfall in mm ( $P_{ann}$ ), mean annual temperature in °C ( $T_{ann}$ ), and variation between calendar months in mean monthly temperature (measured as the standard deviation across the 12 months,  $T_{moSD}$ ) and in mean monthly rainfall (measured as Shannon’s diversity index across the 12 calendar months,  $P_{moSH}$ ). These variables were important components of our individual taxon time budget models (Dunbar 1992a, b; Williamson & Dunbar 1999; Hill & Dunbar 2002; Korstjens et al. 2006; Lehmann et al. 2007a, 2008a, b; Dunbar et al. 2009; Willems & Hill 2009).

Climatic and behavioural variables were first determined separately for each population in our data set, and then averaged across populations of the same species to yield a species-specific ‘typical’ value (see Appendix). Initially, we carried out separate analyses at both the species and the population levels, but since the results were virtually identical we present only the species-level analysis, which avoids the problem of data interdependency.

### *Determinants of Total Resting Time*

We first identified the best-fit multiple regression relationship for total resting time using backward multiple regression analysis (SPSS 16.0.0, SPSS Inc., Chicago, IL, U.S.A.). We confirmed our results using generalized linear models, identifying the best model using the Akaike information criterion (AIC). Starting with a maximally parameterized model, we removed the parameters with the lowest effect size (partial  $\eta^2$ ) in stepwise fashion until the model with the fewest number of variables while maintaining a low AIC was established.

We tested for the effects of phylogeny using the method of phylogenetic generalized least squares, PGLS (Grafen 1989; Martins 1999; Garland & Ives 2000; Lehmann et al. 2007a). PGLS incorporates the expected covariance among species into a statistical model fitted by generalized least squares. Thus, the correlation between error terms is altered so that it reflects the degree of phylogenetic relatedness among species (Shultz et al. 2005). PGLS was implemented in R (Ihaka & Gentleman 1996) using the Analysis of Phylogenetics and Evolution (APE) package (Paradis et al. 2004) and

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