

# Costs and benefits of group living are neither simple nor linear

Colin A. Chapman<sup>a,b,1</sup> and Kim Valenta<sup>a</sup>

<sup>a</sup>Department of Anthropology, McGill University, Montreal, QC, Canada H3A 2T7;

and <sup>b</sup>McGill School of Environment, McGill University, Montreal, QC, Canada H3A 2A7

Identifying the ecological and social factors that underlie vertebrate group size and social organization have been central components of behavioral ecology since the field started (1–3).

This interest stems, at least in part, from the enormous variability in group size, both within and among species. For example, in primates group size varies from 2 to over 300 individuals (4). In addition, group size affects many aspects of the lives of social species, such as individual stress levels (5), disease susceptibility (6), reproductive and developmental rates (7), and individual and group behavior (8).

Among the numerous hypotheses proposed to explain this large variation in group size in vertebrates is competition over food resources (3, 9–11). A key relationship used in the development of theoretical models of determinants of group size was individual energy intake as a function of group size (12, 13). The ecological constraints model (4) predicts that the increased nutritional requirements of larger groups necessitate traveling farther to visit more food patches that are depleted more rapidly, and that this relationship is linear (4, 14). The increased energetic costs of living in a large group may be a sensible investment, if larger groups experience decreased predation or increased success in intergroup encounters.

The need to develop theoretical models for predicting group size is illustrated with the case of folivorous monkeys (Fig. 1). The apparent abundance of resources (i.e., leaves) for folivorous primates has led to the suggestion that scramble competition (i.e., one animal simply gets to a food item first; thus, it is not available for other animals in the group) should be limited or absent, and thus not constrain their group size (15). This hypothesis has been supported by numerous between-group comparisons of folivorous primates, which have found no relationship between group size and day range (16, 17). However, if large groups have increased success in intergroup competition, large groups can monopolize better habitats; thus, one would

not expect a nonlinear relationship between group size and day range.

In PNAS, Markham et al. (18) use a remarkable dataset involving the study of five social groups of baboon (*Papio cynocephalus*) over 11 y, which included collecting fecal samples to determine stress hormone levels (glucocorticoids), to test predictions of the ecological constraints model. Their test involved examining the relationships between group size, ranging behavior, and female glucocorticoids. Counter to the typical formulation of the ecological constraints model, the authors found a U-shaped relationship between group size and average daily travel distance, home-range size, evenness of space use, and glucocorticoid levels. Thus, Markham et al. suggest that large and small baboon groups were energetically more stressed, whereas intermediate-sized groups were closer to the optimal energy strategy.

The results of this study have a number of important implications. Particularly, it highlights the complexity of constraints on group size: namely, constraints will vary for groups of different sizes, but the relationship need not be linear. In fact, the shape of this relationship may vary among populations or species. For example, some species have intense intergroup encounters, whereas in other species groups just seem to avoid each other and upon the detection of the approach of a neighboring group just change the direction of travel. Markham et al.'s (18) research suggest that the relationship between group size and average daily travel distance, home-range size, evenness of space use, and glucocorticoid levels would be very different for these two species.

As predicted by the ecological constraints model, Markham et al. (18) suggest that large baboon groups seem to be limited by the fact that they deplete patches more rapidly (i.e., more mouths to feed) and thus are forced to travel further to meet energetic requirements. In contrast, small groups have elevated glucocorticoids because they are frequently



**Fig. 1.** Gelada baboons (*Theropithecus gelada*): one-male units engaged in late-afternoon grooming along the edge of a sleeping cliff at Guassa, Ethiopia. Geladas illustrate the complexity of evaluating group size because they have a multilevel social organization (i.e., social units within a larger social group). Image courtesy of Peter Fashing (Fullerton University, Fullerton, CA).

displaced by larger groups during between-group competition events. A prediction stemming from this finding is that smaller groups will be forced to use habitats of poorer quality. Markham et al. (18) further suggest that groups will often be larger than the optimum because there are greater pressures for small groups, in addition to pressures for dispersing, or solitary individuals to join groups, although there is not great pressure for optimal groups to exclude immigrants (19, 20).

Many forms of human disturbance to baboon habitats will decrease resource availability, which should theoretically favor smaller

Author contributions: C.A.C. and K.V. designed research, performed research, analyzed data, and wrote the paper.

The authors declare no conflict of interest.

See companion article 10.1073/pnas.1517794112.

<sup>1</sup>To whom correspondence should be addressed. Email: Colin.Chapman@McGill.ca.

groups. This is because larger groups deplete patches faster and if habitat disturbance decreases patch availability, it increases the distance between patches and groups must travel further. At some threshold of habitat disturbance, large groups will no longer be viable. This is an important consideration for animals like forest baboons because of the extent of deforestation; between 2000 and 2012, 2.3 million km<sup>2</sup> of forest was lost globally, and in the tropics forest loss increased by 2101 km<sup>2</sup> per year (21). In savanna or woodland habitat, baboons will be similarly impacted because of the cutting of trees for charcoal or conversion to agricultural land. Cropland increased globally by 48,000 km<sup>2</sup> per year between 1999 and 2008 (22). One estimate suggests that 1 billion ha of new agricultural land, primarily in developing countries, will need to be converted to agriculture by 2050 to meet the demands of the growing human population, an area larger than Canada (23). As for cutting of savanna tree for wood or charcoal, sub-Saharan countries still obtain 80% or their fuels for cooking from charcoal and wood, and the percentage of household receiving electricity is very low in many countries (e.g., Uganda = 2%) (24).

The cascading impacts of anthropogenic habitat changes are often hard to identify, but are important to understand

in the construction of informed management and conservation plans. The study by Markham et al. (18) not only adds an exciting twist to theory concerning group size, it suggests that changing group size may be

one of the cascading impacts of human disturbance.

**ACKNOWLEDGMENTS.** C.A.C. was supported by the Canada Research Chair Program, and K.V. received support from Natural Sciences and Engineering Research Council.

- 1 Eisenberg JF, Muckenhirn NA, Rundran R (1972) The relation between ecology and social structure in primates. *Science* 176(4037): 863–874.
- 2 van Schaik CP (1983) Why are diurnal primates living in groups? *Behaviour* 87(1):120–144.
- 3 Wrangham RW (1980) An ecological model of female-bonded primate groups. *Behaviour* 75(1):262–300.
- 4 Chapman CA, Chapman LJ (2000) Determinants of group size in primates: The importance of travel costs. *On the Move: How and Why Animals Travel in Groups*, eds Boinski S, Garber PA (Univ of Chicago Press, Chicago), pp 24–41.
- 5 Pride RE (2005) Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behav Ecol* 16(3):550–560.
- 6 Loehle C (1995) Social barriers to pathogen transmission in wild animal populations. *Ecology* 76(2):326–335.
- 7 Borries C, Larney E, Lu A, Ossi K, Koenig A (2008) Costs of group size: Lower developmental and reproductive rates in larger groups of leaf monkeys. *Behav Ecol* 19(6):1186–1194.
- 8 Koenig A (2002) Competition for resources and its behavioral consequences among female primates. *Int J Primatol* 23(4):759–783.
- 9 Sterck EHM, Watts DP, vanSchaik CP (1997) The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41(5):291–309.
- 10 Elgar MA (1989) Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biol Rev Camb Philos Soc* 64(1):13–33.
- 11 Snaith TV, Chapman CA (2007) Primate group size and socioecological models: Do folivores really play by different rules? *Evol Anthropol* 16(3):94–106.
- 12 Pulliam HR, Caraco T (1984) Living in groups: Is there an optimal group size. *Behavioural Ecology: An Evolutionary Approach*, eds Krebs JR, Davies NB (Sinauer Associates, Sunderland, England), 2nd Ed, pp 122–147.
- 13 Wrangham RW, Gittleman JL, Chapman CA (1993) Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behav Ecol Sociobiol* 32(3):199–209.
- 14 Janson CH, van Schaik CP (1988) Recognizing the many faces of primate food competition: Methods. *Behaviour* 105(1/2):165–186.
- 15 Isbell LA (1991) Contest and scramble competition: Patterns of female aggression and ranging behaviour among primates. *Behav Ecol* 2(2):143–155.
- 16 Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. *Journal of Zoological Society of London* 183(1):1–39.
- 17 Janson CH, Goldsmith ML (1995) Predicting group size in primates: Foraging costs and predation risks. *Behav Ecol* 6(3): 326–336.
- 18 Markham AC, Gesquiere LR, Alberts SC, Altmann J (2015) Optimal group size in a highly social mammal. *Proc Natl Acad Sci USA*, 10.1073/pnas.1517794112.
- 19 Giraldeau L-A, Gillis D (1985) Optimal group size can be stable: A reply to Sibly. *Anim Behav* 33(2):666–667.
- 20 Sibly RM (1983) Optimal group size is unstable. *Anim Behav* 31(3):947–948.
- 21 Hansen MC, et al. (2013) High-resolution global maps of 21st-century forest cover change. *Science* 342(6160):850–853.
- 22 Phalan B, et al. (2013) Crop expansion and conservation priorities in tropical countries. *PLoS One* 8(1):e51759.
- 23 Laurance WF, Sayer J, Cassman KG (2014) Agricultural expansion and its impacts on tropical nature. *Trends Ecol Evol* 29(2):107–116.
- 24 Mohammed YS, Bashir N, Mustafa MW (2015) Overuse of wood-based bioenergy in selected sub-Saharan Africa countries: Review of unconstructive challenges and suggestions. *J Clean Prod* 96(3):501–519.