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George Wittemyer, *et al.*
Science **321**, 123 (2008);
DOI: 10.1126/science.1158900

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28. I thank B. Boyle, K. Cranston, D. Hearn, M. McMahon, B. O'Meara, and T. Wheeler for critical discussions; three anonymous reviewers for critical comments; D. Boss for computing

support; and NSF and the University of Arizona B105 Institute for financial support.

Supporting Online Material

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20 December 2007; accepted 31 March 2008
10.1126/science.1154449

Accelerated Human Population Growth at Protected Area Edges

George Wittemyer,*† Paul Elsen, William T. Bean, A. Coleman O. Burton, Justin S. Brashares*†

Protected areas (PAs) have long been criticized as creations of and for an elite few, where associated costs, but few benefits, are borne by marginalized rural communities. Contrary to predictions of this argument, we found that average human population growth rates on the borders of 306 PAs in 45 countries in Africa and Latin America were nearly double average rural growth, suggesting that PAs attract, rather than repel, human settlement. Higher population growth on PA edges is evident across ecoregions, countries, and continents and is correlated positively with international donor investment in national conservation programs and an index of park-related funding. These findings provide insight on the value of PAs for local people, but also highlight a looming threat to PA effectiveness and biodiversity conservation.

The past three decades have seen a 500% increase in land designated as protected areas (PAs) for nature conservation (1). Many see this explosion of land protection as negatively impacting the livelihoods of local communities through a loss of rights, exclusion from natural resources, and displacement from traditional lands (2–4). As a result, emigration from protected lands may be expected to reduce human population growth at PA edges over time relative to neighboring unprotected lands, if we assume that higher intrinsic growth rates (often linked to increased poverty levels) are not associated with PA proximity. However, PA creation may benefit rural inhabitants by providing access to road networks, employment, foreign aid, increasingly scarce ecosystem services (e.g., firewood, bushmeat, and clean water), and areas of safety during strife (5) (Table 1). If PAs are perceived locally to provide opportunities otherwise scarce in rural areas, we might expect immigration to drive high rates of population growth along PA borders as suggested by a number of recent case studies (6, 7). To investigate this question, we quantified rates of population growth around 306 PAs in 45 countries of Africa and Latin America (Fig. 1).

Department of Environmental Science, Policy, and Management, University of California at Berkeley, Berkeley, CA 94720, USA.

*These authors contributed equally to this work.

†To whom correspondence should be addressed. E-mail: georgew@nature.berkeley.edu (G.W.); brashares@nature.berkeley.edu (J.S.B.)

Using spatially explicit population data for Africa and Latin America from each decade between 1960 and 2000 (8, 9), we calculated average annual rates of population growth within a 10-km buffer of 306 rural (10) International Union for Conservation of Nature (IUCN) category I and II PAs and nature World Heritage Sites (1) (Fig. 1 and table S1). We then compared the mean rates of growth in buffers to national rural population growth rates as measured by the United Nations in the countries in which the PAs were located (11). Our results show average annual growth rates were higher in PA buffers than in rural areas of the same country for 245 of the 306 PAs and in 38 of 45 countries (Figs. 1 and 2). Results were similar across continents, although strongest in Latin America, with buffers around 149 of 164 PAs and in 14 of 16 countries demonstrating greater average growth rates as compared with 96 of 142 PAs and 24 of 29 countries in Africa (Fig. 1). Comparisons of growth rates in PA buffers to alternative estimates of

average rural population growth produced similar results (10).

Our comparison of population growth around the borders of PAs with average rural rates for the same country (11) may present a false picture of human settlement if parks are preferentially placed in areas of high ecological productivity. In such a scenario, humans may settle in the same general region as PAs simply because the land there is better for agriculture or natural resource extraction rather than for reasons related to the PA itself (12). To account for this possibility, we refined our analysis by restricting our comparison of population growth rates in the buffers of PAs to those areas with the same ecological characteristics, defined using the Global Ecoregions Database (13). Results of this comparison show that, similar to our countrywide comparisons, human population growth around PAs is significantly higher than that observed in matched ecoregions (Wilcoxon test: $Z = -291.5$, $n = 69$, $P = 0.04$).

It also is conceivable that the observed high rates of human population growth in PA buffers are caused by the displacement of people living within PAs to their edges (3). In such a scenario, population growth within parks should decline over time as people move outwards toward PA edges. However, contrary to this expectation, population growth rates were positive, not negative, inside 85% of the PAs we surveyed with the remaining 15% showing no change. This finding makes clear that “leakage” from within parks does not explain our result, as population growth was positive not only at PA borders but also within PAs.

A number of social and economic factors may explain accelerated population growth on PA edges (Table 1). We suggest that this pattern is explained by immigration, but if PAs are located in relatively

Table 1. Potential attractants and deterrents of PAs as settlement sites.

| Attractants | Deterrents |
|--|---|
| Foreign aid and integrated conservation and development projects (e.g., schools and clinics) | Land-use restrictions |
| Employment (e.g., staff positions and tourism) | Wildlife conflict (e.g., livestock and crop depredation) |
| Enhanced ecosystem services (e.g., wood, food, water, and traditional medicine) | Conflict with park staff, government, or rural militias |
| Market access (e.g., road infrastructure) | Cultural degradation and increased cost of living associated with tourism |
| Security (e.g., guards and government staff) | Isolation and/or remoteness from urban centers |

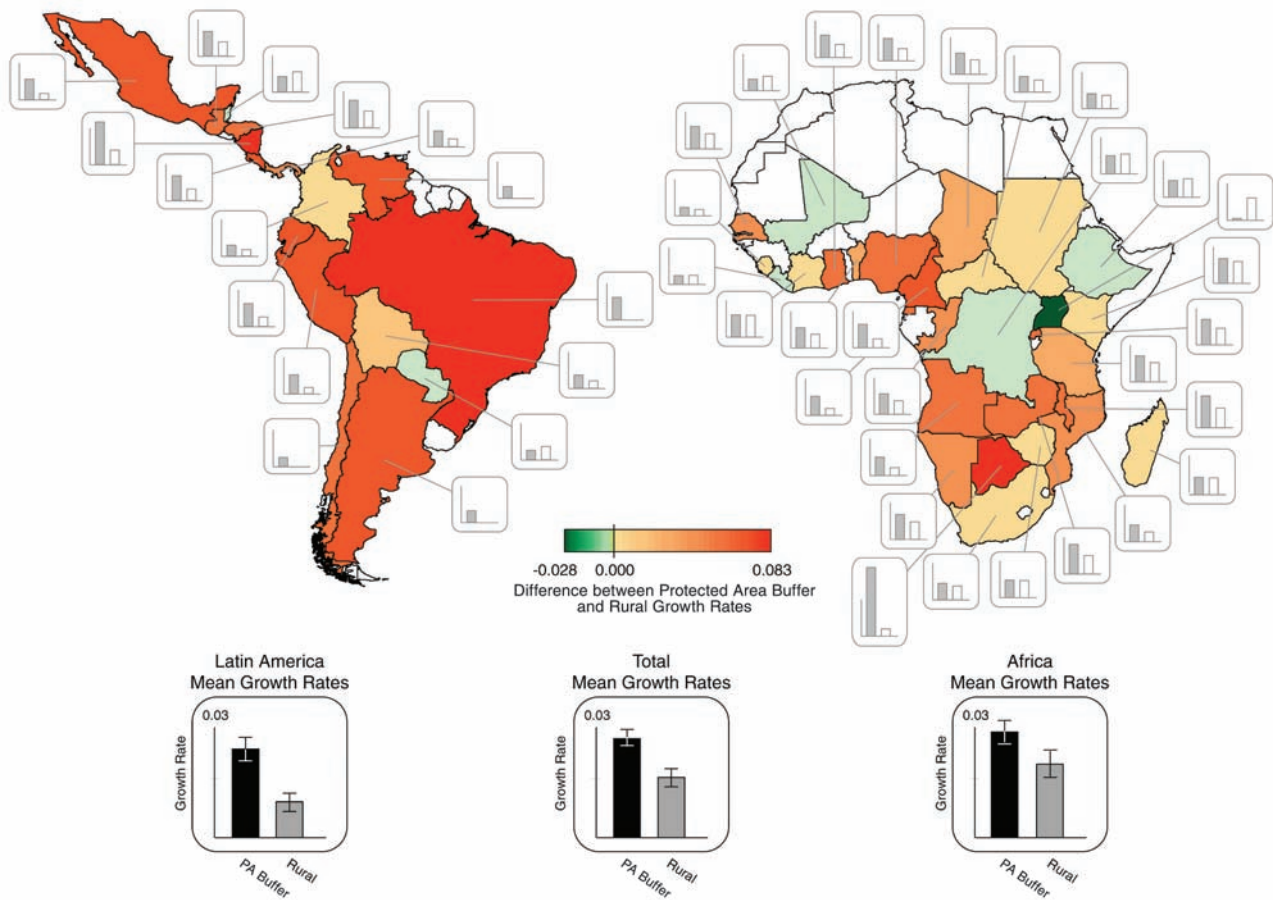


Fig. 1. Across Africa and Latin America, human population growth rates in 10-km buffers surrounding PAs (black bars) nearly doubled those of national rural growth rates (gray bars), exceeding them by an average of ~1% per annum. Error bars show standard errors of the means. Buffer growth rates topped the national rural growth rate in approximately 85% of the 45 countries for which PAs were assessed (colors are scaled by the

difference between buffer and rural growth rates). The smaller histograms compare average buffer (gray) and rural (white) population growth rates for each country. Growth rates in PA buffers were unrelated to PA (29) size (Spearman's rank correlation: $r_s = -0.05$, $n = 284$, $P = 0.40$); country size ($r_s = -0.21$, $n = 45$, $P = 0.16$); or the proportion of area under protection in a country ($r_s = 0.23$, $n = 45$, $P = 0.12$).

impoverished regions of a country or if PAs promote impoverishment, the recognized link between poverty and intrinsic population growth may better explain the patterns we observe. To evaluate this alternative explanation, we examined published data on infant mortality rates (14), a widely recognized correlate of poverty, in areas adjacent to and more distant from PAs in 34 of the 45 countries included in our study (data from 11 countries were not available). We found that rates of infant mortality did not differ between PA edges and other rural areas in these countries (Wilcoxon test: $Z = -20$, $n = 34$, $P = 0.36$), which suggests that poverty rates are not higher near PAs. This result and observations that population growth around PAs sometimes exceeded maximum human reproductive rates support our contention that immigration drives the patterns we report.

Few data are available to allow many broad-scale and rigorous tests of the role of political, economic, and ecological drivers of human settlement around PAs. Nevertheless, limited data for a subset of 126 of our focal PAs (15) show that the difference between PA buffer growth and rural growth was positively correlated with the

density of PA staff (employees per hectare) (Spearman's rank correlation: $r_s = 0.19$, $n = 126$, $P = 0.03$). Because staff levels are shown to be positively linked with PA budgets and tourism rates (16), PA staff density may serve as an index of a PA's enforcement activity or its economic solvency. As such, the positive correlation we observe indicates population growth rates in buffers are likely influenced by increased economic or occupational opportunities, rather than suppressed through exclusion from natural resources found within PAs. In practice, the mechanisms driving population changes around PAs are likely context-specific, and data collection at local scales is critical for understanding the relation between local people and PAs.

Our observation of high population growth along PA borders in Africa and Latin America may not be surprising considering the significant park-focused integrated conservation and rural development investment made by international donor agencies (7, 17, 18). For example, from 1991 to 2006, the Global Environment Facility (GEF) and its funding partners alone distributed on the order of \$2 billion to support PAs in Africa

and Latin America (19). In fact, for countries included in our study, the amount the GEF spent on biodiversity projects (20) during this period was positively correlated with the rates at which PA buffer growth exceeded rural growth [Spearman's rank correlation: $r_s = 0.38$, $n = 36$, $P = 0.02$; (fig. S1)]. This correlation could simply show that GEF invests most heavily in countries where population growth around PAs is highest, but we think it more likely that international investment contributes to the settlement patterns we observe. We also found a positive correlation between per capita Gross Domestic Product (GDP) and the rates at which PA buffer growth exceeded rural growth in the 45 developing countries included in our analysis ($r_s = 0.38$, $n = 45$, $P = 0.01$). If GDP is a reliable indicator of a country's investment in PA development, population growth around PAs may reflect a demographic response to both national and international funding.

Full accounts are difficult to obtain, but even by conservative estimates, the 306 PAs included in our study have received millions of dollars from international development and conservation organizations since their creation (16). This fund-

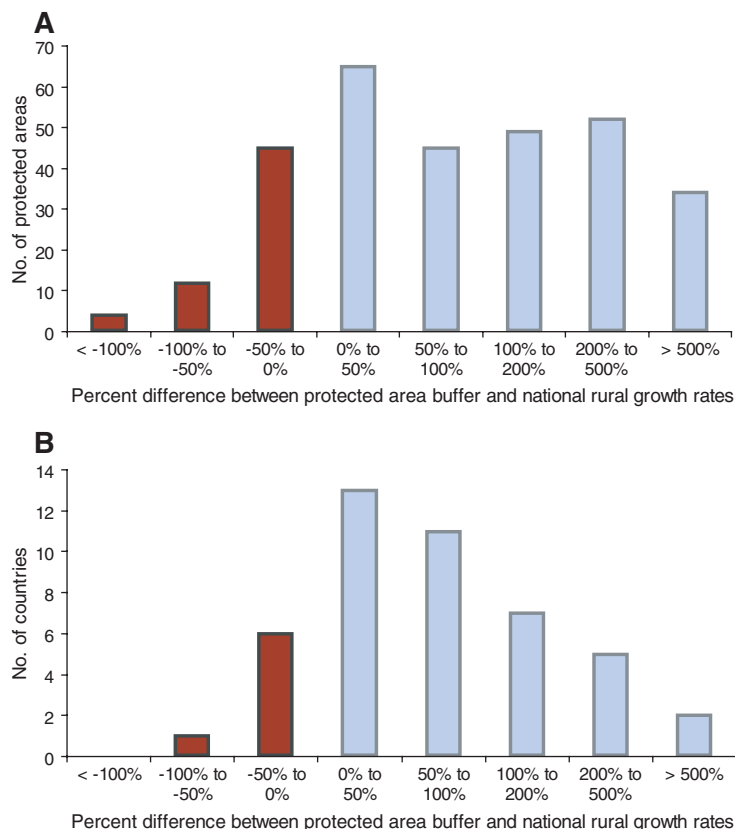


Fig. 2. Population growth rates within 10 km of 306 rural PAs in 45 countries in Africa and Latin America (29) were significantly higher than national rural averages (11) when tested by (A) PA (Wilcoxon test: $Z = -1.58 \times 10^4$, $n = 284$, $P < 0.001$) or (B) country ($Z = -270$, $n = 36$, $P < 0.001$).

ing includes development and capacity-building projects for people living in PA buffers where it directly and indirectly benefits communities through the creation of jobs, roads, clinics, sanitation systems, and schools (19, 21). In some cases, such park-centered financial infusion far exceeds international funds targeted for development in communities distant from PAs. As such, the perceived benefits of park-related development, along with access to increasingly scarce ecosystem services, may be expected to drive immigration and settlement of people on PA edges, a concern that has been a long-standing topic of debate in the development and conservation communities (6, 7). If we assume that patterns of human settlement reflect the will and prosperity of local people, our results suggest local populations in Africa and Latin America perceive benefits from living in proximity to PAs.

Although PAs may be positive for localized rural development in Africa and Latin America, human populations around PAs frequently have significant, negative impacts on biodiversity (22). The scale of human settlement around PAs is a strong predictor of illegal timber and mineral extraction (23), bushmeat hunting (24), fire frequency (25), and, more generally, species extinction (24) within PAs. We examined such impacts directly by comparing population growth rates in PA buffers with published rates of deforestation in the area surrounding 55 forest PAs included in

our study (26). Rates of deforestation were highest around PAs where human population growth was greatest (Fig. 3). This finding links population growth around PAs to habitat loss and suggests settlement around PAs may create a ring of disturbance that isolates PAs from surrounding habitats. Although population growth along PA edges clearly has impacted tropical forest habitats, our analyses across all habitat types indicate PAs in grassland and dry forest ecosystems may be the most at risk as buffers in these regions contain particularly high population growth rates (fig. S2). If PAs are expected to serve as refuges for the “last of the wild” (27), the patterns we document here are cause for concern.

If humans are drawn to PAs for the economic opportunities they provide, international funding for conservation may, ironically, exacerbate the same anthropogenic threats to biodiversity it aims to alleviate. By no means should this possibility rationalize reduced funding for PAs and the communities around them. Instead, it suggests that international and local funding must go in part toward developing spatially dynamic PA systems that account for patterns of human settlement and needs of local communities. Creation of large multi-use buffer areas surrounding core habitats and corridors (possibly with mixed-use buffers of their own) between PAs may facilitate effective protection of biodiversity while supporting potentially heavy human settlement on PA borders.

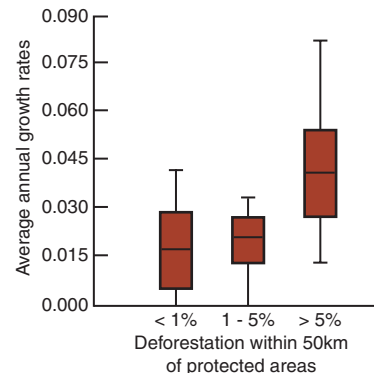


Fig. 3. Deforestation measured within a 50-km buffer of 55 forested PAs in Africa and Latin America (26) was greatest where annual rates of human population growth in PA buffers were highest (Kruskal-Wallis test: $H_2 = 16.48$, $P < 0.001$). Box plots show the median (horizontal line), interquartile range (box), and range of the data (whiskers). The two lower deforestation categories showed no difference with regard to population growth rates (rank-sum difference test: $P = 0.27$). Population growth in buffers where deforestation was greater than 5% was significantly higher than in the two lower deforestation categories, both independently and combined (rank-sum difference tests: $P < 0.001$).

Additionally, approaches that pair PA-based conservation with economic development targeted at areas more distant from PAs may aid rural communities while simultaneously reducing human pressure on PAs (28). Such advanced landscape planning, in concert with effective PA management, may maintain and increase the benefits of PAs for rural people while also ensuring those benefits do not result in unsustainably heavy use of the flora, fauna, and processes PAs endeavor to sustain.

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30. Supported by NSF OISE-0502340 and the J. S. McDonnell Foundation (G.W.), the Hellman Fund (J.S.B.) and the University of California at Berkeley. We thank A. Balmford, A. Bruner, P. Coppolillo, C. Golden, C. Kremen, R. Kuriyan, J. Scharlemann, A. R. E. Sinclair, C. Stoner, two anonymous reviewers, and the Geospatial Imaging and Informatics Facility (GIIF), Museum of Vertebrate Zoology (MVZ), and Department of Environmental Science, Policy, and Management (ESPM) at the University of California at Berkeley. The authors declare no competing financial interests.

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9 April 2008; accepted 4 June 2008
10.1126/science.1158900

Robust, Tunable Biological Oscillations from Interlinked Positive and Negative Feedback Loops

Tony Yu-Chen Tsai,^{1*} Yoon Sup Choi,^{1,2*} Wenzhe Ma,^{3,4} Joseph R. Pomeroy,⁵ Chao Tang,^{3,4} James E. Ferrell Jr.^{1†}

A simple negative feedback loop of interacting genes or proteins has the potential to generate sustained oscillations. However, many biological oscillators also have a positive feedback loop, raising the question of what advantages the extra loop imparts. Through computational studies, we show that it is generally difficult to adjust a negative feedback oscillator's frequency without compromising its amplitude, whereas with positive-plus-negative feedback, one can achieve a widely tunable frequency and near-constant amplitude. This tunability makes the latter design suitable for biological rhythms like heartbeats and cell cycles that need to provide a constant output over a range of frequencies. Positive-plus-negative oscillators also appear to be more robust and easier to evolve, rationalizing why they are found in contexts where an adjustable frequency is unimportant.

The mammalian heart rate is normally established by the sino-atrial node. The node generates constant-amplitude action potentials at a tunable frequency of ~50 to 150 action potentials per minute, depending on the body's oxygen demands. The cell cycle oscillator may also require this combination of an adjustable frequency and invariant amplitude. The period of the cell cycle ranges from about 10 min in rapidly dividing embryos to tens of hours in rapidly dividing somatic cells (and longer in slowly dividing somatic cells), but variations in the amplitude

[the peak concentration of active cyclin-dependent kinase-1 (CDK1)] of the oscillations seem neither necessary nor desirable.

Two basic types of circuits have been proposed for biological oscillators: (i) those that contain both positive and negative feedback loops and (ii) those containing only negative feedback (Table 1) (1–6). Both the sino-atrial node oscillator and the cell cycle oscillator fall into the positive-plus-negative feedback class, suggesting that this design might be better suited for generating oscillations with a tunable frequency and constant amplitude.

We tested this idea through computational studies, beginning with an ordinary differential equation model of CDK1 oscillations in the *Xenopus* embryonic cell cycle (7). The model includes a negative feedback loop [active CDK1 brings about its inactivation through the anaphase-promoting complex (APC)] and a pair of positive feedback loops (active CDK1 activates its activator Cdc25 and inactivates its inhibitor Wee1) (Fig. 1A). We specified the strength of the posi-

tive feedback through a parameter r , the ratio of the activities of Cdc25 and Wee1 in interphase versus M phase. Because the rate of cyclin synthesis determines the frequency of CDK1 oscillations in *Xenopus* embryos (7, 8), we varied the cyclin synthesis rate constant k_{synth} in the model and determined how the amplitude and frequency of the oscillations were affected by this variation.

In the negative feedback-only version of the model ($r = 1$ in Fig. 1, B and C), a relatively small range of k_{synth} values yielded oscillations. Plotting the amplitude and frequency of the oscillations on a log-log plot yielded a tight, inverted U-shaped curve (Fig. 1B). The range of frequencies over which the oscillator functioned was small (1.7-fold), and even within this range, the frequency could not be adjusted without compromising the amplitude substantially.

Adding positive feedback markedly changed the amplitude/frequency relation (Fig. 1, B and C). At a biologically realistic feedback strength of $r = 10$ (9–11), the oscillator functioned over a 4900-fold range of frequencies (Fig. 1B, green points). Over much of this range, the frequency of the oscillator was linearly proportional to k_{synth} , and the amplitude was approximately constant (Fig. 1, B and C). Thus, positive feedback provided a highly tunable frequency and robust amplitude.

Something other than the cyclin synthesis rate may tune the frequencies of some cell cycles. We therefore asked whether the negative feedback-only oscillator might operate over a wider range of frequencies if one of the model's other 20 parameters were varied. This was not the case; invariably, the oscillator operated over only a narrow frequency range. Of course if all of the rate constants were multiplied by the same factor (equivalent to scaling the units of time), the oscillator's frequency could be varied without changing the amplitude. However, this type of coordinated regulation is not relevant to any of the biological oscillators that we are familiar with (Table 1).

¹Department of Chemical and Systems Biology, Stanford University School of Medicine, Stanford, CA 94305–5174, USA.

²School of Interdisciplinary Bioscience and Bioengineering, Pohang University of Science and Technology, Pohang, 790–784, Republic of Korea. ³Center for Theoretical Biology, Peking University, Beijing, 100871, China. ⁴California Institute for Quantitative Biosciences, University of California, San Francisco, CA 94143–2540, USA. ⁵Department of Biology, Indiana University, Bloomington, IN 47405, USA.

*These authors contributed equally to this work.

†To whom correspondence should be addressed. E-mail: james.ferrell@stanford.edu