

attentional processing [18]. These studies typically measure cognitive modulation of activity in extra-foveal representations, and it remains to be seen if foveal superior colliculus will exhibit similar cognitive properties. The magnified foveal representation will, at the very least, likely play a substantial role in attention, given recent work showing selective attention within foveal vision [19] and the known interactions between microsaccades and covert selection [11]. Investigating all the implications of such a fundamental shift in the understanding of how the superior colliculus represents visual space will take many years of work.

Moving the eyes to leverage high-acuity foveal vision is inherent to how humans explore and perceive visual environments. Chen *et al.* [3] shift the superior colliculus narrative by showing it is a key player in active foveal perception. Regrettably, over the past few decades few studies have attempted to investigate this fundamental aspect of vision. This is in large part due to the difficulty imposed by fixational eye movements, but another factor has been the shift to model organisms, such as the mouse, that do not possess a fovea. Hopefully, the recent advancement in stimulus presentation [20] and the intriguing results from Chen *et al.* [3] will reinvigorate the field to study a critical part of human experience, foveal vision.

REFERENCES

- Perry, V.H., and Cowey, A. (1985). The ganglion cell and cone distributions in the monkey's retina: Implications for central magnification factors. *Vis. Res.* 25, 1795–1810.
- Hafed, Z.M. (2011). Mechanisms for generating and compensating for the smallest possible saccades. *Eur. J. Neurosci.* 33, 2101–2113.
- Chen, C.-Y., Hoffman, K.-P., Distler, C., and Hafed, Z.M. (2019). The foveal visual representation of the primate superior colliculus. *Curr. Biol.* 29, 2109–2119.
- Cowey, A., and Perry, V.H. (1980). The projection of the fovea to the superior colliculus in rhesus monkeys. *Neuroscience* 5, 53–61.
- Donders, F.C. (1872). Ueber angeborene und erworbene Association. *Graefes Arch. Clin. Exp. Ophthalmol.* 18, 153–164.
- Robinson, D.A. (1972). Eye movements evoked by collicular stimulation in the alert monkey. *Vis. Res.* 12, 1795–1808.
- Ottens, F.P., Van Gisbergen, J.A., and Eggemont, J.J. (1986). Visuomotor fields of the superior colliculus: a quantitative model. *Vis. Res.* 26, 857–873.
- Hafed, Z.M., Goffart, L., and Krauzlis, R.J. (2009). A neural mechanism for microsaccade generation in the primate superior colliculus. *Science* 323, 940–943.
- Ko, H.-k., Poletti, M., and Rucci, M. (2010). Microsaccades precisely relocate gaze in a high visual acuity task. *Nat. Neurosci.* 13, 1549–1553.
- Arcaro, M.J., Pinsk, M.A., and Kastner, S. (2015). The anatomical and functional organization of the human visual pulvinar. *J. Neurosci.* 35, 9848–9871.
- Hafed, Z.M., Chen, C.-Y., and Tian, X. (2015). Vision, perception, and attention through the lens of microsaccades: mechanisms and implications. *Front. Syst. Neurosci.* 9, 167.
- Hafed, Z.M. (2013). Alteration of visual perception prior to microsaccades. *Neuron* 77, 775–786.
- Chen, C.-Y., Ignashchenkova, A., Thier, P., and Hafed, Z.M. (2015). Neuronal response gain enhancement prior to microsaccades. *Curr. Biol.* 25, 2065–2074.
- Lee, J., and Groh, J.M. (2014). Different stimuli, different spatial codes: a visual map and an auditory rate code for oculomotor space in the primate superior colliculus. *PLoS One* 9, e85017.
- Drager, U., and Hubel, D.H. (1975). Responses to visual stimulation and relationship between visual, auditory, and somatosensory inputs in mouse superior colliculus. *J. Neurophysiol.* 38, 690–713.
- Meredith, M.A., and Stein, B.E. (1986). Visual, auditory, and somatosensory convergence on cells in superior colliculus results in multisensory integration. *J. Neurophysiol.* 56, 640–662.
- Crapse, T.B., Lau, H., and Basso, M.A. (2018). A role for the superior colliculus in decision criteria. *Neuron* 97, 181–194.
- Herman, J.P., Katz, L.N., and Krauzlis, R.J. (2018). Midbrain activity can explain perceptual decisions during an attention task. *Nat. Neurosci.* 21, 1651–1655.
- Poletti, M., Rucci, M., and Carrasco, M. (2017). Selective attention within the foveola. *Nat. Neurosci.* 20, 1413–1417.
- Santini, F., Redner, G., Iovin, R., and Rucci, M. (2007). EyeRIS: A general-purpose system for eye-movement-contingent display control. *Behav. Res. Meth.* 39, 350–364.

Conservation: Monitoring Elephant Poaching to Prevent a Population Crash

Samuel K. Wasser* and Kathleen S. Gobush

Department of Biology, University of Washington, Seattle, WA 98195, USA

*Correspondence: wassers@uw.edu

<https://doi.org/10.1016/j.cub.2019.06.009>

African elephants are under threat, especially from poaching for illegal ivory trade. New monitoring data show a dramatic increase in elephant poaching in northern Botswana, where the largest remaining population of African elephants resides.

Many plant and animal species have evolved a dependency on the natural services African elephants provide. As the world's largest land mammal with immense resource needs, elephants maintain habitat diversity and disperse seeds of trees important for carbon capture [1–4]. They also provide considerable economic contributions

through ecotourism [5]. Nevertheless, between 1979 and 2015, poaching for ivory reduced Africa's elephant population from an estimated 1.3 million to around 400,000 individuals. One can only imagine how such losses impacted this highly intelligent and socially complex species, let alone their ecological communities. Today, nearly half of



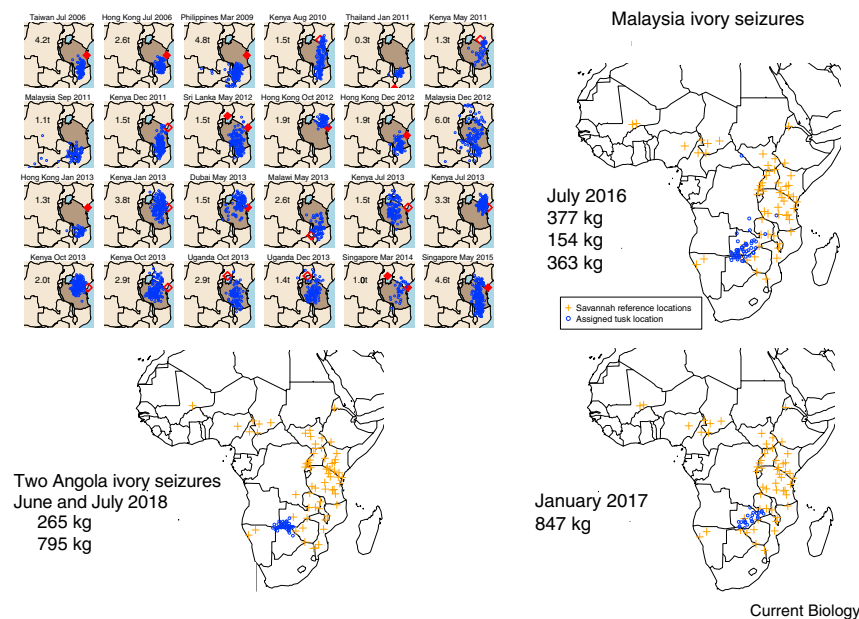


Figure 1. Genetic evidence indicates that Africa's largest poaching hotspot may be shifting south to the KAZA.

Geographic origins of large ivory seizures made across Africa and Asia (top left) between 2006 and 2015, in Angola 2018 (bottom left), and in Malaysia 2016–2017 (right). Blue circles represent the genetically assigned origin of each tusk in the seizure. Crosses illustrate the locations of reference DNA samples used to assign origin to each tusk. The location, date and size of each seizure are also shown. Seizures in top left are zoomed in to show eastern Africa, with Tanzania colored dark brown as a point of reference and a diamond showing where the ivory was exported out of Africa. Data from [1,2], methods are described in [1].

Africa's elephants live in the Kavango Zambezi Transfrontier Conservation Area (KAZA) spanning Botswana, Zimbabwe, Namibia, Zambia and Angola [6]. It was just a matter of time before major criminal poaching organizations began to exploit this population. A new paper in this issue of *Current Biology* by Scott Schlossberg and colleagues [7] indicates that such exploitation may have already begun.

Schlossberg and colleagues [7] meticulously document a substantial rise in poaching in northern Botswana between 2014 and 2018. Signs of poaching include: a six-fold increase in fresh elephant carcasses and a significant increase in the carcass ratio (total carcass count divided by the sum of live and dead elephants). All fresh and recent carcasses inspected showed clear signs of being poached. Schlossberg and colleagues [7] identified five poaching hotspots characterized by a recent increase in the number and clustering of carcasses and a decrease in live elephants. Equally important, they systematically explore numerous plausible alternative explanations for the observed mortality

patterns (e.g. drought, food shortage, crowding and human elephant conflict), none of which are supported by the data. Schlossberg and colleagues [7] raise concern that the extensive signs of poaching they observed could indicate an impending population crash. Botswana may argue that won't happen to them, but that view is contradicted by a long history of elephant strongholds quickly collapsing in countries across the continent [7,8]. More recently, elephant populations in Zimbabwe, Gabon and Mozambique shrank by more than 70% since 2001, 2004 and 2009, respectively [6]. South Africa similarly believed they could protect their rhinos from poaching, but the high value of black-market rhino horn led to brutal losses over the last decade despite sophisticated anti-poaching efforts [9].

Elephant poaching has become dominated by large transnational criminal organizations with the potential to wipe out populations in record time. Such criminal activity is not easy to contain once entrenched [10,11]. Yet, given effective monitoring reported on a timely

basis, such as that provided by Schlossberg and colleagues [7], poaching is one threat of many that we can reduce as long as decision makers and the public listen and act without delay.

Poaching trends are best monitored over time by population surveys, including: carcass ratios based on the number of live versus dead animals; the proportion of illegally killed elephants among observed carcasses; and the number, size and origins of transnational ivory seizures. When all three metrics converge, as is now happening in KAZA, it is careless to ignore them. A 19-country survey of savannah elephants in 2015 [12] found the highest carcass ratios occurring in Cameroon, southeast Zambia and southeast Angola, the latter two of which neighbor northern Botswana [12]. The proportion of illegally killed elephants increased in southern Africa during 2017 and 2018 and now exceeds that of East Africa [13]. At a single Botswanan site, the proportion of illegally killed elephants increased by approximately 60% in 2018 and is at unsustainable levels (>0.60) in three nearby Zambian sites [13]. Analyses of recent large ivory seizures suggest that the largest poaching hotspot in Africa may be shifting south from East Africa [1] to northern Botswana and neighboring countries (Figure 1). Why does this confluence of evidence appear to have little impact on many southern African decision makers?

Decades of divisive debate over whether ivory sales will increase or decrease poaching-related elephant declines has too often obstructed swift action despite numerous reports of intensive poaching and associated population reductions [14]. One side of the debate argues that ivory trade anywhere is a threat to elephants everywhere. Essentially, sanctioned sales from any single nation creates opportunities to disguise illegal ivory as legal, increasing incentives to poach and traffic such contraband. The other side argues that an open (legal) market can replace a black market, with proceeds ploughed back into local conservation. Sound science can help bridge this political and economic divide by providing the highest certainty that poaching is accelerating and urgent action is needed. Sadly, time and again, this debate has sidelined sound science

to the detriment of relevant decision making [14].

With the exception of Angola, the KAZA nations have a history of petitioning for commercial ivory trade. Botswana, Namibia, Zimbabwe and South Africa successfully petitioned CITES to downlist their elephant populations starting in the late 1990s; sanctioned sales of national ivory stocks followed in 2002 and 2008 [14]. Along with Zambia, these countries are petitioning CITES for renewed legal trade at the upcoming 18th Conference of the Parties. Previous attempts by Zambia to downlist their elephants failed due to significant seizures of tusks from its elephants (6.5 tons and 0.7 tons seized in Singapore in 2002 and 2007, respectively) [14]. Their current request again comes in the midst of unsustainable poaching there. In Botswana, the former administration shifted from promoting legal trade and hunting to a total ban on both, along with a shoot-to-kill policy against poachers. The current administration appears to have shifted back by recently lifting the elephant hunting ban ([Botswana lifts hunting ban](#)) under the guise of reducing human–elephant conflict. More likely, resuming elephant hunts is aimed towards reestablishing a high-end trophy hunting industry, servicing elites as opposed to a means to attend to needs of rural communities living near protected areas. Hunting to benefit marginalized communities represents a dangerous and unproven tactic when more durable economic opportunities are needed. Legal hunting could also make monitoring poaching more difficult if carcasses are not carefully tracked. At worst, the added carcasses could make it easier for poachers to carry on undetected. It is difficult to imagine how these countries can take such a turn when so many metrics argue that poaching and the illegal ivory trade continue unabated.

Killing, whether poaching, culling or hunting, is myopic. These reactive tactics are more likely to exacerbate human–elephant conflict, causing long-term negative impacts on both elephants and neighboring human communities. Killing encourages surviving family members to flee danger zones including so-called protected areas. Heavy poaching appears to have repeatedly pushed forest elephants from Congo into Uganda [15],

leading to high rates of hybridization between forest and savannah elephants there [16]. These unidirectional movements also coincided with increased crop raiding [15]. Killing elephant matriarchs for their large tusks compounds the problem. It removes the female leaders along with their knowledge of scarce water during drought [17]. Leaderless herds in unknown habitat are likely to wander more widely, potentially increasing their likelihood of encountering crops. Stress associated with loss of matriarchs also leads to a cascade of other negative effects [18]. Conversely, providing wildlife corridors to encourage movements of elephants across borders, often unnaturally restricted by fences, offers a far better solution to relieve locally high densities. Given access, elephants are known to return to former habitat when conditions become safe again [19]. Facilitating movements across borders is also more likely to promote resilient ecosystems as well as wildlife–human coexistence. This is especially the case when combined with adequate resource management in buffer zones next to protected areas and coordinated multi-national law enforcement efforts to combat poaching and trafficking.

Governments and managers need to listen to and act upon sound science to assure they make wise and holistic management decisions. We can't afford to get this wrong. It's time to move beyond the notion that killing at risk species provides a tool to conserve them. The stakes are too high and political resistance is influenced by too many factors independent of truth. Evidence, like that presented by Schlossberg and colleagues [7], is needed to accurately inform the debate, unite political divisions and create a lasting coexistence between nature and mankind.

DECLARATION OF INTERESTS

K.S. Gobush is an employee of Vulcan Inc. and a member of the IUCN African Elephant Specialist Group. The views and opinions expressed in this article are those of the authors and do not necessarily reflect the official policy or position of either of these two organizations.

REFERENCES

1. Beaune, D., Fruth, B., Bollache, L., Hohmann, G., and Bretagnolle, F. (2013). Doom of

the elephant dependent trees in a Congo tropical forest. *For. Ecol. Mgmt.* 295, 109–117.

2. Blake, S., Deem, S.L., Mossimbo, E., Maisels, F., and Walsh, P. (2009). Forest elephants: tree planters of the congo. *Biotropica* 41, 459–468.
3. Boko, M., I. Niang, A. Nyong, C. Vogel, A. Githeko, M. Medany, B. Osman-Elasha, R. Tabo, and P. Yanda. (2007). In *Climate Change: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, chapter 9, Africa, pages 434–467. (Cambridge University Press).
4. Pringle, R.M., Prior, K.M., Palmer, T.M., Young, T.P., and Goheen, J.R. (2016). Large herbivores promote habitat specialization and beta diversity of African savanna trees. *Ecol.* 97, 2640–2657.
5. Naidoo, R., Fisher, B., Manica, A., and Balmford, A. (2016). Estimating economic losses to tourism in Africa from the illegal killing of elephants. *Nat. Commun.* 7, 13379.
6. Thouless, C.R., Dublin, H.T., Blanc, J.J., Skinner, D.P., Daniel, T.E., Taylor, R.D., Maisels, F., Frederick, H.L., and Bouche, P. (2016). African Elephant Status Report 2016: an update from the African Elephant Database, Occasional Paper Series of the IUCN Species Survival Commission, No. 60 IUCN/SSC (Gland, Switzerland: African Elephant Specialist Group, IUCN), pp. vi-309.
7. Schlossberg, S., Chase, M.J., and Sutcliffe, R. (2019). Evidence of a growing elephant poaching problem in Botswana. *Curr. Biol.* 29, 2222–2228.
8. Douglas-Hamilton, I. (1989). Overview of status and trends of the African elephant. In *The Ivory Trade and the Future of the African Elephant: Prepared for the Seventh CITES Conference of the Parties*, S. Cobb, ed. (Lausanne, Oxford (United Kingdom): Ivory Trade Review Group), pp. 1–36.
9. Emslie, R.H., Milliken, T., Talukdar, T., Ellis, S., Adcock, K., and Knight, M.H. (2016). African and Asian rhinoceroses – status, conservation and trade. CoP17 Doc16, Annex 5, Retrieved from. <https://cites.org/sites/default/files/eng/cop/17/WorkingDocs/E-CoP17-68-75>.
10. Wasser, S.K., Brown, L., Mailand, C., Mondol, S., Clark, W., Laurie, C., and Weir, B.S. (2015). Genetic assignment of large seizures of elephant ivory reveals Africa's major poaching hotspots. *Science* 349, 84–87.
11. Wasser, S.K., Torkelson, A., Winters, M., Hoareau, Y., Tucker, S., Otieno, M.Y., Sitam, F.A.T., Buckleton, J., and Weir, B.S. (2018). Combating transnational organized crime by linking multiple large ivory seizures to the same dealer. *Sci. Adv.* 4, eaat0625.
12. Chase, M.J., Schlossberg, S., Griffin, C.R., Bouché, P.J.C., Djene, S.W., Elkan, P.W., Ferreira, S., Grossman, F., Kohi, E.M., Landen, K., et al. (2016). Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ*, e2354.

13. CITES (2019). Report and Addendum on the Monitoring of Illegal Killing of Elephants (MIKE) Addendum: CITES 18th Meeting of the Conference of the Parties, Doc.69.2 and Addendum. CITES, Geneva.
14. Wasser, S.K., Poole, J., Lee, P., Lindsay, K., Dobson, A., Hart, J., Douglas-Hamilton, I., *et al.* (2010). Elephants, ivory and trade. *Science* 327, 1331–1332.
15. Keigwin, M., Wabukawo, V., and Wasser, S.K. (2016). Impacts on transboundary elephant movements between Queen Elizabeth National Park, Uganda and the Park National des Virunga, Democratic Republic of Congo and associated crop raiding. *Pachyderm* 57, 118–121.
16. Mondol, S., Moltke, I., Hart, J., Keigwin, M., Brown, L., Stephens, M., and Wasser, S.K. (2015). New evidence for hybrid zones of forest and savannah elephants in Central and West Africa. *Mol. Ecol.* 24, 6134–6147.
17. Foley, C., Pettorelli, N., and Foley, L. (2008). Severe drought and calf survival in elephants. *Biol. Lett.* <https://doi.org/10.1098/rsbl.2008.0370>.
18. Gobush, K.S., Mutayoba, B.M., and Wasser, S.K. (2008). Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of adult female African elephants. *Cons. Biol.* 22, 1590–1599.
19. Chase, M.J., and Griffin, C.R. (2011). Elephants of south-east Angola in war and peace: their decline, re-colonization and recent status. *Afr. J. Ecol.* 49, 353–361.

Chromosome Organization: Making Room in a Crowd

Handuo Shi¹ and Kerwyn Casey Huang^{1,2,3,*}

¹Department of Bioengineering, Stanford University, Stanford, CA 94305, USA

²Department of Microbiology and Immunology, Stanford University School of Medicine, Stanford, CA 94305, USA

³Chan Zuckerberg Biohub, San Francisco, CA 94158, USA

*Correspondence: kchuang@stanford.edu
<https://doi.org/10.1016/j.cub.2019.06.002>

Despite their small size and lack of membrane-based DNA encapsulation, prokaryotic cells still organize and scale their nucleoid in specific subcellular regions. Two studies show that the DNA-free regions in prokaryotes are full of large biomolecules, which exclude DNA via entropic forces.

The apparent complexity and diversity of living organisms belies simple and intuitive morphological scaling relationships. During human development, the unique physiology of the brain [1] means that its growth is slower than that of the body, leading to infants having proportionally larger heads than adults [2]. By contrast, most other organs such as the heart scale with body size. Such scaling phenomena also occur within single cells, whose components can occupy distinct physical spaces. For instance, eukaryotic cells enclose most of their genetic material in the nucleus, physically separated from the cytoplasm by two layers of membrane. As these cells increase in size, they robustly regulate their nuclear size to maintain an approximately constant ratio with the overall size of the cell [3]. Unlike eukaryotes, prokaryotic cells lack membrane-based encapsulation of their DNA, which instead co-mingles with other cellular components [4,5]; nonetheless, they can achieve exquisite organization of chromosomal loci [6]. Two new studies by Gray *et al.* [7] in *Cell*

and Wu *et al.* [8] in *Current Biology* demonstrate that bacterial cells are also capable of regulating nucleoid size and positioning, and highlight the consequences of biophysical interactions between the nucleoid and the cytoplasm.

The quest to determine whether organellar sizes scale with cell size dates back more than a century and the initial focus was on nuclei, with the extensive observations of Conklin [3] showing that at each stage of embryonic development, nuclear sizes precisely scale with cell size despite continuous growth and division. Similar scaling phenomena were later identified for other cellular components such as the mitochondria [9] and the Golgi complex [10], leading to the hypothesis that regulation of the relative sizes of all components is optimal for cellular functions. As the largest structure inside prokaryotic cells, the chromosome is a natural focal point for size-scaling studies, although the lack of obvious confinement mechanisms means that the chromosome can in principle diffuse freely across the whole cell. While

prokaryotes lack nucleosomes, they contain many proteins that associate with, and potentially structure, the chromosome [11]. Moreover, the chromosome in at least some bacterial species forms compact, highly self-interacting domains [12], suggesting that bacterial chromosomes may organize in a conceptually similar manner to eukaryotic DNA. Indeed, the nucleoids in *Escherichia coli* cells have been observed to occupy only specific regions of the cell [4,5], implicating the existence of underlying mechanisms that regulate the size and position of bacterial chromosomes. To further investigate the connection between nucleoid size and cell size, Gray *et al.* [7] surveyed these quantities across >40 bacterial and archaeal strains, revealing that each strain robustly maintains a species-specific ratio between nucleoid size and cell size. Wu *et al.* [8] took a complementary approach and studied the position and size of a single chromosome copy in replication-arrested *E. coli* cells, discovering that although longer cells accommodated a larger nucleoid size, the nucleoid was



Update

Current Biology

Volume 29, Issue 15, 5 August 2019, Page 2593

DOI: <https://doi.org/10.1016/j.cub.2019.07.029>

Conservation: Monitoring Elephant Poaching to Prevent a Population Crash

Samuel K. Wasser* and Kathleen S. Gobush

*Correspondence: wassers@uw.edu

<https://doi.org/10.1016/j.cub.2019.07.029>

(Current Biology 29, R627–R630; July 8, 2019)

In the preparation of the manuscript, a referencing error occurred. Two references [7, 8] were supposed to be cited together. Instead, only one of the two references [7] was cited in the correct place, and the second reference [8] was mistakenly cited in the following sentence, where an earlier reference [6] should have been re-cited. These errors have now been corrected online. The authors apologize for the errors.

