REFERENCES AND NOTES

1. L. Buck, R. Axel, *Cell* **65**, 175–187 (1991).
2. L. B. Buck, C. Bargmann, in *Principles of Neuroscience*, E. Kandel, J. Schwartz, T. Jessell, S. Siegelbaum, A. J. Hudspeth, Eds. (McGraw-Hill, New York, 2012), pp. 712–742.
3. X. Zhang, S. Firestein, *Nat. Neurosci.* **5**, 124–133 (2002).
4. P. A. Godfrey, B. Malnic, L. B. Buck, *Proc. Natl. Acad. Sci. U.S.A.* **101**, 2156–2161 (2004).
5. Y. Niimura, M. Nei, *Gene* **346**, 13–21 (2005).
6. K. J. Ressler, S. L. Sullivan, L. B. Buck, *Cell* **73**, 597–609 (1993).
7. R. Vassar, J. Ngai, R. Axel, *Cell* **74**, 309–318 (1993).
8. K. Miyamichi, S. Serizawa, H. M. Kimura, H. Sakano, *J. Neurosci.* **25**, 3586–3592 (2005).
9. A. Chess, I. Simon, H. Cedar, R. Axel, *Cell* **78**, 823–834 (1994).
10. B. Malnic, J. Hirono, T. Sato, L. B. Buck, *Cell* **96**, 713–723 (1999).
11. S. Serizawa *et al*., *Science* **302**, 2088–2094 (2003).
12. S. Serizawa, K. Miyamichi, H. Sakano, *Trends Genet.* **20**, 648–653 (2004).
13. B. M. Shykind *et al*., *Cell* **117**, 801–815 (2004).
14. J. W. Lewcock, R. R. Reed, *Proc. Natl. Acad. Sci. U.S.A.* **101**, 1069–1074 (2004).
15. R. P. Dalton, D. B. Lyons, S. Lomvardas, *Cell* **155**, 321–332 (2013).
16. M. Q. Nguyen, Z. Zhou, C. A. Marks, N. J. Ryba, L. Belluscio, *Cell* **131**, 1009–1017 (2007).
17. R. P. Dalton, S. Lomvardas, *Annu. Rev. Neurosci.* **38**, 331–349 (2015).
18. D. J. Nicolay, J. R. Doucette, A. J. Nazarali, *Cell. Mol. Neurobiol.* **26**, 801–819 (2006).
19. D. J. Rodriguez-Gil *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **112**, 5821–5826 (2015).
20. S. Islam *et al*., *Genome Res.* **21**, 1160–1167 (2011).
21. D. R. Bentley *et al*., *Nature* **456**, 53–59 (2008).
22. D. Kim *et al*., *Genome Biol.* **14**, R36 (2013).
23. C. Trapnell *et al*., *Nat. Biotechnol.* **28**, 511–515 (2010).
24. C. Trapnell *et al*., *Nat. Biotechnol.* **32**, 381–386 (2014).
25. J. W. Hinds, P. L. Hinds, *J. Comp. Neurol.* **169**, 15–40 (1976).
26. M. L. Collins *et al*., *Nucleic Acids Res.* **25**, 2979–2984 (1997).
27. H. Tian, M. Ma, *Mol. Cell. Neurosci.* **38**, 484–488 (2008).

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/350/6265/1251/suppl/DC1
Materials and Methods
Figs. S1 to S5
Tables S1 to S7
References (*28*–*35*)

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PROTECTED AREAS

Protected areas and global conservation of migratory birds

Claire A. Runge,[1,2]* James E. M. Watson,[1,3] Stuart H. M. Butchart,[4] Jeffrey O. Hanson,[5] Hugh P. Possingham,[5,6] Richard A. Fuller[5]

Migratory species depend on a suite of interconnected sites. Threats to unprotected links in these chains of sites are driving rapid population declines of migrants around the world, yet the extent to which different parts of the annual cycle are protected remains unknown. We show that just 9% of 1451 migratory birds are adequately covered by protected areas across all stages of their annual cycle, in comparison with 45% of nonmigratory birds. This discrepancy is driven by protected area placement that does not cover the full annual cycle of migratory species, indicating that global efforts toward coordinated conservation planning for migrants are yet to bear fruit. Better-targeted investment and enhanced coordination among countries are needed to conserve migratory species throughout their migratory cycle.

From the writings of Aristotle (*1*) to the musings of Gilbert White in Georgian England (*2*), migratory birds have fascinated and inspired people for generations. Migrants undertake remarkable journeys, from endurance flights exceeding 10,000 km by bar-tailed godwits (*Limosa lapponica*) (*3*) to the annual relay of arctic terns (*Sterna paradisaea*), which fly the equivalent of the distance to the moon and back three times during their lives (*4*). Migratory species make major contributions to resource fluxes, biomass transfer, nutrient transport, predator-prey interactions, and food-web structure within and among ecosystems (*5*) and play an important role in human culture (*6*). Yet more than half of migratory birds across all major flyways have declined over the past 30 years (*7*).

Threats in any one part of a annual cycle can affect the entire population of a migratory species (*8*), and so environmental management actions for migrants need to be coordinated across habitat types, seasons, and jurisdictions (*8*). Protected area designation is a widely used approach for averting species loss (*9*) because it can reduce habitat loss, habitat degradation, hunting pressure, and disturbance (*10*). Yet the extent to which the distributions of migratory species are covered by protected areas globally is poorly understood. Many previous global and regional species conservation assessments and prioritization analyses either omit parts of the annual cycle or treat all species' distributions as static (*9*–*12*). Here, we explore how protected area coverage of migratory birds varies across their annual cycle and among countries and compare their current levels of protected area coverage against standard conservation targets. Overlaying maps of protected areas (*13*) onto distribution maps of the world's birds, we assessed whether the proportion of each species' distribution covered by protected areas met a target threshold (*9*, *11*). For migratory species, we set targets for each stage of the annual cycle separately for the 1451 migratory birds, with mapped distributions throughout their annual cycle.

We discovered that 91% of migratory bird species have inadequate protected area coverage for at least one part of their annual cycle, despite individual elements of the annual cycle being well protected for some species (Table 1). This is in stark contrast to 55% of nonmigratory species with inadequate protected area coverage across their global distribution. A typical migrant relies on two or three disjoint geographic locations, and the chance that they are all adequately conserved is probabilistically lower than for a single location (supplementary materials). We found that migratory species are less likely to meet protection targets as the number of seasonal areas increases and that the proportion of migratory species meeting targets is consistent with randomly allocated conservation effort (Fig. 1), indicating that despite widespread recognition of the need for an internationally coordinated approach to conservation of migratory species, protection is not yet systematically coordinated across the seasonal ranges of species. Twenty-eight migratory bird species have no coverage in at least one part of their annual cycle, and 18 of these have no protected area coverage of their breeding range. Two species lack any protected area coverage across their entire distribution (Table 1). Disturbingly, less than 3% of threatened migratory bird species have adequate protected area coverage across all parts of their annual cycle (table S1).

Widespread migrants may benefit more from broader-scale policy responses (such as targeting

[1]School of Geography, Planning and Environmental Management, University of Queensland, Brisbane, QLD, 4072, Australia. [2]National Center for Ecological Analysis and Synthesis (NCEAS), University of California, Santa Barbara, Santa Barbara, CA 93101, USA. [3]Global Conservation Program, Wildlife Conservation Society, New York, NY, USA. [4]BirdLife International, Wellbrook Court, Cambridge CB3 ONA, UK. [5]School of Biological Sciences, University of Queensland, Brisbane, QLD 4072, Australia. [6]Department of Life Sciences, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, England, UK.
***Corresponding author. E-mail: claire.runge@uqconnect.edu.au**

Table 1. Protected area coverage of migratory and nonmigratory bird species. Representation targets are based on species' geographic range size, with a target of 100% of a distribution to be covered by protected areas where the geographic range is <1000 km, log-linearly decreasing to 10% where the range size is >250,000 km (*10*, *12*).

	Mean of range covered (%)	Number of gap species (defined as zero coverage)	Percentage of species meeting coverage targets	Total number of species
Nonmigrants	18.9	243	44.8	7457
Full migrants	10.2	2	8.8	1451
Part of annual cycle				
Resident	11.3	3	43.7	898
Breeding	14.1	18	34.4	1260
Nonbreeding	10.9	8	39.8	1267
Passage	13.4	2	26.2	530
Any part of cycle		28		

forestry and agriculture planning and practices) than individual site-based interventions (*14*). However, for nearly all bird species worldwide for which site-based conservation is appropriate and needed, key sites—Important Bird and Biodiversity Areas (IBAs)—have been identified, so it is informative to assess protection levels for such sites (*15*). A total of 8283 IBAs has been identified for 885 migratory bird species, either because they congregate in sufficient numbers so that any individual site holds >1% of the global or flyway population of one or more migrant species (43% of sites) or because they support populations of one or more globally or regionally threatened migrant species (55% of sites; the remainder relate to other IBA criteria). The protected area coverage of IBAs for migrants provides a finer resolution metric of the degree to which protected areas adequately cover the key locations for the world's migrants and accounts for some of the variation in abundance of migratory species across their distribution; for example, some migratory species are widely dispersed when breeding but congregate in large numbers in a few particularly important sites when on migration or in their nonbreeding range. We discovered that for only 2.9% of migratory birds are their IBAs fully protected across each of their seasonal areas (table S2). On average, 22% of the IBAs identified for each migratory species are completely covered by protected areas, and an additional 41% are partially covered, which is consistent with nonmigrants (24 and 42%, respectively) (table S2). Most IBAs for migratory species are identified in their breeding distributions (77% of migratory species with an IBA), yet for the majority of those species, the breeding range is the least well-protected stage of the migratory cycle. IBAs along the migratory route from breeding to nonbreeding areas are most likely to be incompletely protected, with only 16% being completely covered.

Our results highlight an urgent need to coordinate the designation of protected areas across the annual cycle (Fig. 2). For example, habitat loss is one of the key threats to the Vulnerable red-spectacled amazon (*Amazona pretrei*), a migratory parrot of Brazil (*16*), yet less than 4% of its distribution occurs within protected areas, with negligible coverage of seasonal breeding and nonbreeding areas (*17*). Similarly, the great knot (*Calidris tenuirostris*), a once abundant migratory shorebird, is now classified as globally Vulnerable (*18*). Just 7% of its distribution is covered by protected areas during migration, where the species congregates in high numbers. Filling the protection gaps for such species throughout their annual cycle is necessary for their conservation.

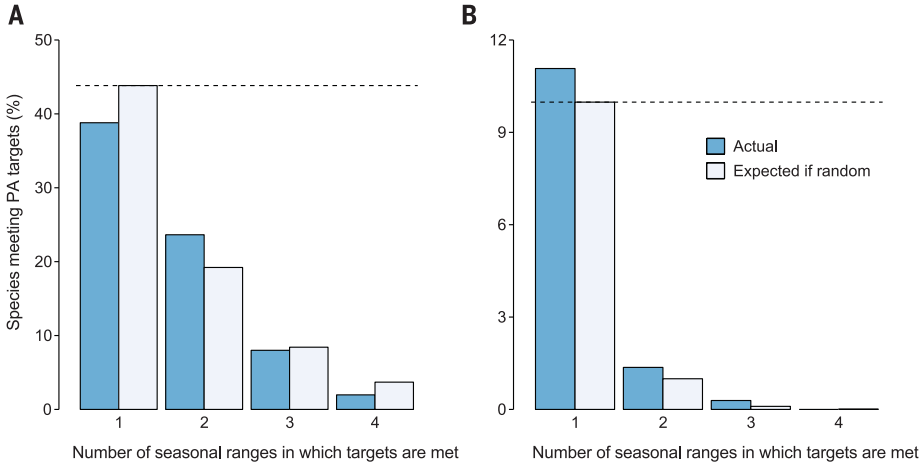

Fig. 1. The shortfall in protected area coverage for migratory species is related to their requirement for protection across each of their seasonal ranges—resident, breeding, nonbreeding, and passage ranges. (**A** and **B**) The proportion of migratory species meeting targets for (A) protected area coverage of their distribution and (B) complete coverage of all key sites (IBAs) identified for them decreases rapidly with the number of seasonal ranges, which is consistent with a random allocation of conservation effort. Dashed lines represent the proportion of species expected to meet targets where conservation is systematically coordinated across the seasonal ranges of species (so that an appropriate proportion of each part of the range is covered by protected areas).

Because migrants move across international borders, achieving their protection is a shared responsibility. Some countries (such as France and Venezuela) meet targets for protected area coverage for more than 80% of their migratory bird species, whereas others (such as China and India) meet targets for less than 10% (Fig. 2A and database S1). Countries across North Africa and Central Asia stand out as having low protected area coverage of migratory bird distributions. We also discovered wide variation in the proportion of migratory bird species occurring in each country that meet their protection targets overseas—a consequence of the migratory connections linking jurisdictions and continents (Fig. 2B). For instance, Germany meets targets for protected area coverage for more than 98% of migratory bird species occurring within its borders, but less than 13% of Germany's migrants are adequately protected across their global range (Fig. 2). This is not simply a case of wealthy nations losing natural heritage to poor nations. Many Central American countries (with low gross domestic product) meet targets for more than 75% of their migratory species, but these species have lower levels of protected area coverage in Canada and the United States (Fig. 2).

Our analyses focus on coverage of species' distributions and key sites by protected areas and do not account for variation in management effectiveness of protected areas or consider broader-scale conservation actions beyond protected sites. Many protected areas are inadequately managed (*10*), and our results based on coverage thus overestimate true protection. Indeed, achieving effective management of existing protected areas may be just as beneficial as designating new sites. However, even when well managed so as to abate core threats to migratory species such as habitat loss and hunting, protected areas are just one tool for minimizing species loss (*10*), and broader-scale interventions will also be needed to address all threats to migratory species. Many migratory species are widespread and undertake broad-front movements, meaning that entire landscapes need to be managed to conserve them. For instance, intensification and mechanization of grassland management is a key threat to the migratory corncrake (*Crex crex*), which breeds in agricultural meadows across Europe, and effective conservation outcomes for the species will involve both identifying key sites for strict protection during its annual cycle and developing incentives for farmers to implement agricultural practices that benefit the species in important areas outside reserves (*16*). Full knowledge of the spatial distribution of threats, how they can best be abated, and how they affect population dynamics across the annual cycle of each migratory species will allow conservation actions to be prioritized most efficiently (*18*). Alongside identifying key sites for protection, broader policy instruments need to be strengthened or developed in order to conserve migratory species.

Protected areas are usually designated at the national scale, but collaborative international partnerships and concerted intergovernmental coordination and action are crucial to safeguard migratory species (*7*). A number of international agreements [such as the Convention on the Conservation of Migratory Species of Wild Animals (CMS) and the Ramsar Convention on Wetlands] recognize the specific challenges associated with migratory species and attempt to deliver special protection to migrants. Migratory landbirds in particular lack coverage under flyway-based bird conservation instruments (*19*), although this is now being addressed through initiatives such as the African-Eurasian Migratory Landbird Action Plan being developed under the CMS (*20*). However, only 120 nations are parties to the CMS, and there is an urgent need to strengthen other agreements, including those between range states in specific migratory flyways. Internationally coordinated action (particularly within flyways) through these and other mechanisms will require substantially greater international leadership and resourcing.

Although there has been considerable focus through the Convention on Biological Diversity (CBD) Strategic Plan on increasing both the size and representation of the global protected area estate (*21*), with some success (*12*), our results highlight a failure to consider adequately the

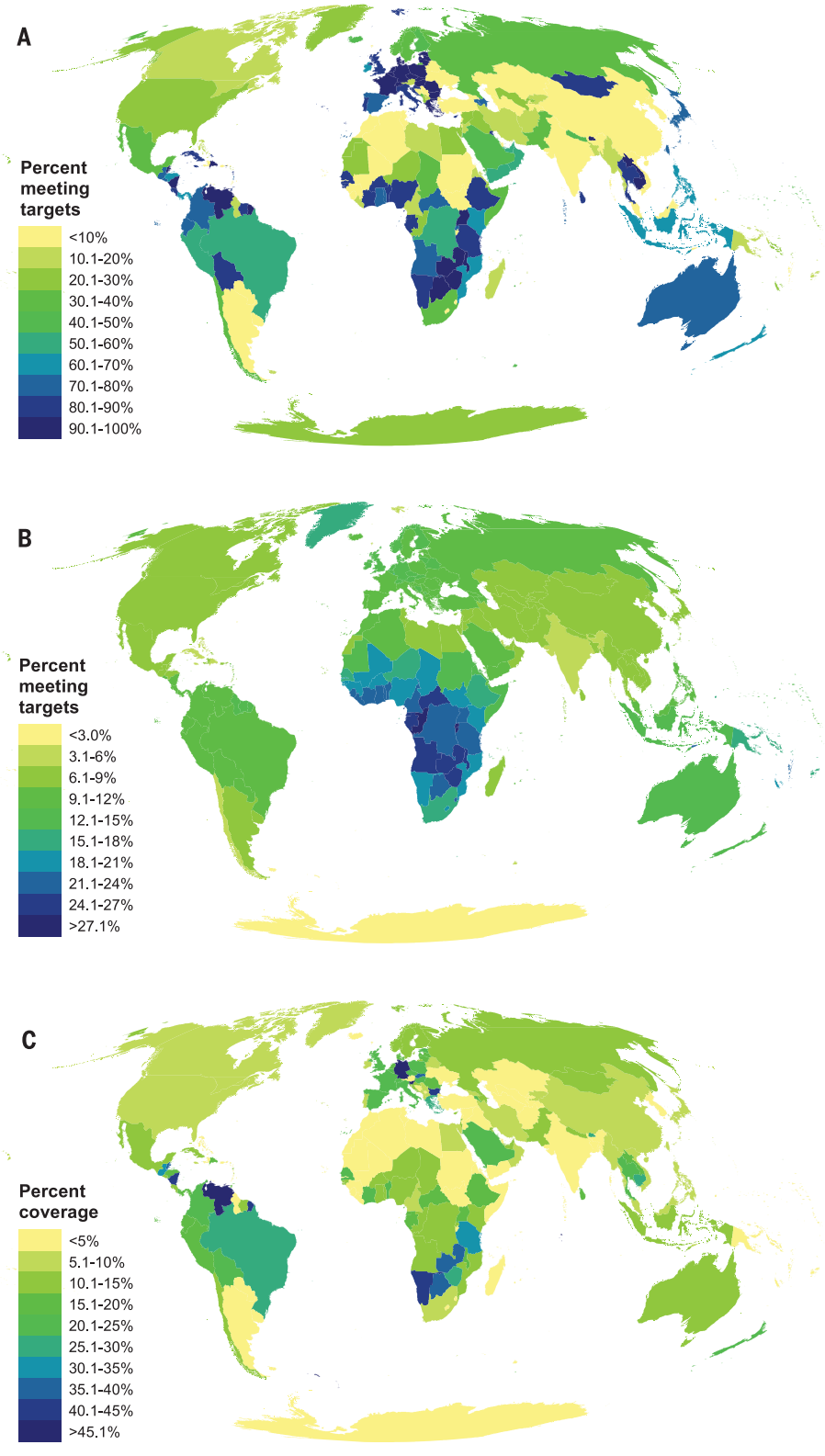

Fig. 2. Global inequity in protected area coverage of migratory birds. (**A** to **C**) The percentage of migratory bird species within each country meeting targets for protected area coverage (A) for each part of their migratory range within that country, (B) for each part of their migratory range globally, and (C) the percentage area covered by protected areas in that country. Targets are scaled by the size of each part of the seasonal distribution. There is a difference in the range of the color ramp between the three maps.

linkages between protected areas. Our data show that migratory species remain very poorly represented in the global protected area system. The CBD's Aichi Targets for 2020 (*21*) will likely drive the greatest expansion of protected areas in history and represent a key opportunity for conserving migrants (*15*). However, safeguarding the world's migratory birds will require better resourcing and use of existing international mechanisms to target new and expanded protected areas, enhance enforcement and management effectiveness, and greatly strengthen coordination between countries.

REFERENCES AND NOTES

1. Aristotle, *Historia Animalium*, J. A. Smith, W. D. Ross, Transls. (Clarendon Press, Oxford, 1910).
2. G. White, *The Natural History and Antiquities of Selborne* (B. White & Son, London, 1789).
3. P. F. Battley *et al.*, *J. Avian Biol.* **43**, 1–12 (2012).
4. C. Egevang *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 2078–2081 (2010).
5. S. Bauer, B. J. Hoye, *Science* **344**, 1242552 (2014).
6. D. S. Wilcove, *No Way Home: The Decline of the World's Great Animal Migrations* (Island Press, Washington, DC, 2010).
7. J. S. Kirby *et al.*, *Bird Conserv. Int.* **18** (suppl. 1), (2008).
8. C. A. Runge, T. G. Martin, H. P. Possingham, S. G. Willis, R. A. Fuller, *Front. Ecol. Environ* **12**, 395–402 (2014).
9. O. Venter *et al.*, *PLOS Biol.* **12**, e1001891 (2014).
10. J. E. M. Watson, N. Dudley, D. B. Segan, M. Hockings, *Nature* **515**, 67–73 (2014).
11. J. E. M. Watson *et al.*, *Conserv. Biol.* **25**, 324–332 (2011).
12. S. H. M. Butchart *et al.*, *Cons. Lett.* **8**, 329–337 (2015).
13. IUCN, UNEP-WCMC, *The World Database on Protected Areas (WDPA)*; accessed 1 February 2013 from www.protectedplanet.net.
14. C. Boyd *et al.*, *Conserv. Lett* **1**, 37–43 (2008).
15. BirdLife International, *Important Bird and Biodiversity Areas: A Global Network for Conserving Nature and Benefiting People* (BirdLife International, Cambridge, UK, 2014).
16. BirdLife International, *IUCN Red List for Birds*; accessed 8 May 2014 from www.birdlife.org.
17. M. Â. Marini, M. Barbet-Massin, J. Martinez, N. P. Prestes, F. Jiguet, *Biol. Conserv.* **143**, 102–112 (2010).
18. V. J. D. Tulloch *et al.*, *Front. Ecol. Environ* **13**, 91–99 (2015).
19. T. Jones, T. Mundkur, "A review of CMS and non-CMS existing administrative/management instruments for migratory birds globally," prepared on behalf of the CMS Working Group on Flyways (UNEP, Bonn, Germany, 2010).
20. Convention on the Conservation of Migratory Species of Wild Animals, "Conservation of migratory landbirds in the African-Eurasian region," paper no. UNEP/CMS/COP11/Doc.23.1.4 (2014).
21. "Conference of the Parties 10 Decision X/2: Strategic plan for biodiversity 2011-2020," tenth meeting of the Conference of the Parties to the Convention on Biological Diversity, Nagoya, Japan (2010).

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/350/6265/1255/suppl/DC1
Materials and Methods
Supplementary Text
Figure S1
Tables S1 to S5
References (*22*–*28*)
Databases S1 to S3

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GENE REGULATION

Single–base pair differences in a shared motif determine differential *Rhodopsin* expression

Jens Rister, Ansa Razzaq, Pamela Boodram, Nisha Desai, Cleopatra Tsanis, Hongtao Chen,* David Jukam,† Claude Desplan‡

The final identity and functional properties of a neuron are specified by terminal differentiation genes, which are controlled by specific motifs in compact regulatory regions. To determine how these sequences integrate inputs from transcription factors that specify cell types, we compared the regulatory mechanism of *Drosophila Rhodopsin* genes that are expressed in subsets of photoreceptors to that of phototransduction genes that are expressed broadly, in all photoreceptors. Both sets of genes share an 11–base pair (bp) activator motif. Broadly expressed genes contain a palindromic version that mediates expression in all photoreceptors. In contrast, each *Rhodopsin* exhibits characteristic single-bp substitutions that break the symmetry of the palindrome and generate activator or repressor motifs critical for restricting expression to photoreceptor subsets. Sensory neuron subtypes can therefore evolve through single-bp changes in short regulatory motifs, allowing the discrimination of a wide spectrum of stimuli.

In the visual system, different photoreceptor neurons express specific light-sensing pigments (*1*); however, common downstream factors amplify and convert the response to the visual stimulus into a neuronal signal. For instance, each unit eye (ommatidium) of the *Drosophila* retina contains eight photoreceptors (R1 to R8) that express different light-sensing Rhodopsins (Rhs) that are restricted to specific photoreceptor subsets. Outer photoreceptors R1 to R6 express Rh1. Inner photoreceptors R7 and R8 express either Rh3 in pR7s coupled with Rh5 in pR8s, or Rh4 in yR7s with Rh6 in yR8s (Fig. 1A) (*1*). R1 to R8 all share broadly expressed phototransduction factors (Fig. 1B and fig. S1A) that amplify and convert the response to the visual stimulus into a neuronal signal (*2*).

Here, we examine the cis-regulatory mechanisms that distinguish restricted from broad expression patterns for Rhodopsins and downstream phototransduction factors, respectively. All *Rhs* share the conserved *Rhodopsin* Core Sequence I (RCSI) (*3*, *4*), which resembles the palindromic P3 motif (TAATYNRATTA), an optimal binding site for paired-class homeodomain proteins (*5*). Almost all known broadly expressed phototransduction genes contain a P3 motif in their proximal promoter (Fig. 1B, fig. S1A, and supplementary text). The presence of a conserved P3/RCSI motif within 100 base pairs (bps) of the *Rh* transcription start site (TSS) is significantly associated with enrichment in adult eyes (χ-square test, $P < 0.001$). P3/RCSI is required for activation in photoreceptors because its mutation caused either a loss or a strong reduction in expression of 16 broad or restricted reporters (figs. S1 to S3), with the exception of *Arr1* (fig. S2K). Moreover, expression of 10 out of 15 reporters was lost in mutants for the photoreceptor-specific transcription factor Pph13 (Fig. 1B and figs. S2 and S3), a paired-class homeodomain protein that binds P3 and the *Rh6* RCSI in vitro (*6*, *7*).

Because each *Rh* promoter has a highly conserved RCSI variant (Fig. 1B) (*4*), we tested the sufficiency of P3 and RCSI to determine the significance of the specific differences between perfectly palindromic (P3) and imperfect motifs (RCSI) (Fig. 2). Four copies of the P3 motif (including four neighboring bps for spacing; the contribution of these additional bps was only tested for *Rh4*) from the broadly expressed *ninaC*, *rdgA*, or *trpl* drove broad expression in all photoreceptors (Fig. 2, A and A′, and fig. S4, A and A′), consistent with our previous results (*8*). In sharp contrast, multimerized RCSI motifs drove expression in subsets of photoreceptors. The RCSI of *Rh3* and *Rh6* contains a K_{50} motif, a binding site for K_{50} homeodomain proteins such as the Dve repressor or the Otd activator (Fig. 1B). Expression of $[Rh3\ RCSI]_4$ and $[Rh6\ RCSI]_4$ was biased to inner photoreceptors: $[Rh3\ RCSI]_4$ mediated restricted expression in R8 and R7, with a strong bias toward the pR7 subset, where *Rh3* is normally expressed (Fig. 2, B and B′). This pattern is complementary to the expression of Dve (Fig. 1B) (*9*), which is indeed responsible for the restricted expression as $[Rh3\ RCSI]_4$ drove a broad, P3-like pattern in *dve* mutants (Fig. 2 B″). $[Rh6\ RCSI]_4$ drove restricted expression in R8s and R7s; expression in R1 to R6 was very weak in comparison to P3 motifs,

Center for Developmental Genetics, Department of Biology, New York University, 100 Washington Square East, New York, NY 10003-6688, USA.
*Present address: Joseph Henry Laboratory of Physics, Lewis-Sigler Institute for Integrative Genomics, Princeton University, Princeton, NJ 08544, USA. †Present address: Department of Biology, Stanford University, Stanford, CA 94305, USA.
‡Corresponding author. E-mail: cd38@nyu.edu