EXTENDED PDF FORMAT
SPONSORED BY
Travel Grants Available
AACR Annual Meeting 2014
Application Deadline:
January 31st
>Apply Now
R&D
http://www.rndsystems.com

Tracking the Long-Term Decline and Recovery of an Isolated Population

Ronald L. Westemeier *et al.*

Science **282**, 1695 (1998);
DOI: 10.1126/science.282.5394.1695

This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by clicking here.

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines here.

The following resources related to this article are available online at www.sciencemag.org (this information is current as of February 7, 2014):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:
http://www.sciencemag.org/content/282/5394/1695.full.html

This article **cites 20 articles**, 1 of which can be accessed free:
http://www.sciencemag.org/content/282/5394/1695.full.html#ref-list-1

This article has been **cited by** 243 article(s) on the ISI Web of Science

This article has been **cited by** 27 articles hosted by HighWire Press; see:
http://www.sciencemag.org/content/282/5394/1695.full.html#related-urls

This article appears in the following **subject collections:**
Ecology
http://www.sciencemag.org/cgi/collection/ecology

Downloaded from www.sciencemag.org on February 7, 2014

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. Copyright 1998 by the American Association for the Advancement of Science; all rights reserved. The title *Science* is a registered trademark of AAAS.

(Fig. 2). Age and stratigraphy: Upper Jurassic, Yixian Formation.
17. Description: Fertile axes vary in size (Fig. 2A). Main axis is 85 mm long from leaf axis and 3 mm wide basally, tapering to 1 mm wide distally. The lateral fertile axis originates from a leaf axil, 86 mm long and 1 mm wide basally, tapering to 0.3 mm wide distally. Fruits are attached by pedicels that are 0.75 to 1.5 mm long by 0.25 to 0.6 mm wide. Fruits are larger basally, 7 to 9 mm long by 2 to 3 mm wide, each containing three (two to four) seeds. Finger-like prominences extend about 1 mm from apex of fruits (Fig. 2B). The fruits are positioned at acute angles to the axis. The main axis has 18 fruits and 11 peg-like bases of pedicels (that bore deciduous reproductive organs) about 0.5 mm long. The lateral axis has 30 fruits and four peg-like remnants of the pedicels that bore deciduous reproductive organs, and smaller fruits, 5 to 6 mm long by 1.5 to 2 mm wide. The fruits are crowded at the axis apex where fruit size decreases. Fruits near the apex are 3 mm long by 2 mm wide, each with two seeds. One other fruiting axis (SZ0917, not figured) contains 17 fruits crowded into 35 mm of the fragmentary axis. Seeds fill fruits and have an oblique orientation. They appear to be attached to the adaxial side of the fruit. Seeds may overlap within fruits or may be distinctly separated by oblique bands of tissue. Cuticles of the seed coats are thin. Epidermal cells are rectangular-polygonal, about 25 to 45 μm by 12 to 20 μm. Anticlinal cell walls are sinuous and cutinized, about 2.5 to 3.5 μm thick (Fig. 2C). Periclinal cell walls are somewhat unevenly cutinized.
18. P. K. Endress, *Plant Syst. Evol.* **152**, 1 (1986).
19. E. M Friis and W. L. Crepet, in *The Origins of Angiosperms and Their Biological Consequences*, E. M. Friis, W. G. Chaloner, P. R. Crane, Eds. (Cambridge Univ. Press, Cambridge, 1987), pp. 145–179.
20. P. R. Crane, *Int. J. Plant Sci.* **157** (suppl.), S50 (1996).
21. S. Y. Duan, *Sci. China Ser. D* **41**, 14 (1998).
22. Z. Y. Cao, S. Q. Wu, P. A. Zhang, J. R. Li, *Chin. Sci. Bull.* **43**, 230 (1998).
23. V. A. Krassilov, *Palaeontogr. Abt. B* **181**, 1 (1982).
24. _____, *Angiosperm Origins: Morphological and Ecological Aspects* (PENSOFT, Sofia, Bulgaria, 1997).
25. A. Cronguist, *An Integrated System of Classification of Flowering Plants* (Columbia Univ. Press, New York, 1981).
26. L. J. Hickey and D. W. Taylor, in *Flowering Plant Origin, Evolution and Phylogeny*, D. W. Taylor and L. J. Hickey, Eds. (Chapman & Hall, New York, 1996), pp. 176–231.
27. P. K. Endress, *Diversity and Evolutionary Biology of Tropical Flowers* (Cambridge Univ. Press, Cambridge, 1994).
28. D. W. Taylor and G. Kirchner, in (*26*), pp. 116–140.
29. D. W. Taylor and L. J. Hickey, *Plant Syst. Evol.* **180**, 137 (1992).
30. D. L. Dilcher, in *Monogr. Syst. Bot. Mo. Bot. Gard.* **53**, 187 (1995).
31. _____, *La importanica del origen de las angiospermas y como formaron el mundo alrededor de ellas*, VI Congreso Latinoamericano de Botanica, Mar Del Plata, Argentina (Royal Botanic Gardens, Kew, UK, 1996), pp. 29–48.
32. P. R. Crane, *Ann. Mo. Bot. Gard.* **72**, 716 (1985).
33. J. A. Doyle and M. Donoghue, *Bot. Rev.* **52**, 1 (1986).
34. T. N. Taylor and E. L. Taylor, *The Biology and Evolution of Fossil Plants* (Prentice-Hall, Englewood Cliffs, NJ, 1993).
35. E. M Friis and P. K. Endress, *Prog. Bot.* **57**, 253 (1996).
36. E. M. Friis, P. R. Crane, K. R. Pedersen, in *Evolution and Diversification of Land Plants*, K. Iwatsuki and P. H. Raven, Eds. (Springer-Verlag, Tokyo, 1997), pp. 121–156.
37. W. L. Crepet, K. C. Nixon, E. M. Friis, J. V. Freudenstein, *Proc. Natl. Acad. Sci. U.S.A.* **89**, 8986 (1992).
38. K. C. Nixon and W. L. Crepet, *Am. J. Bot.* **80**, 616 (1993).
39. P. S. Herendeen, W. L. Crepet, K. C. Nixon, *Plant Syst. Evol.* **189**, 29 (1994).
40. J. A. Keller, P. S. Herendeen, P. R. Crane, *Am. J. Bot.* **83**, 528 (1996).
41. M. A. Gandolfo, K. C. Nixon, W. L. Crepet, *ibid.* **85**, 964 (1998).
42. A. Takhtajan, in *Biogeographical Evolution of the Malay Archipelago*, T. C. Whitmore, Ed. (Oxford Univ. Press, New York, 1987), pp. 26–31.
43. D. I. Axelrod, *Science* **130**, 203 (1959).
44. D. Burger, *Rev. Palaeobot. Palynol.* **65**, 153 (1990).
45. J. A. Doyle, in *Proceedings of the 27th International Geological Congress, Palaeontology 2, USSR Academy of Sciences, Moscow, August 4–14* (VNU Science Press, Utrecht, Netherlands, 1984), pp. 23–33.
46. G. Sun, S. X. Guo, S. L. Zheng, T. Y. Piao, X. K. Sun, *Sci. China Ser. B* **36**, 253 (1993).
47. G. Sun and D. L. Dilcher, *Palaeobotanist* **45**, 393 (1996).
48. V. A. Vakhrameev, *Jurassic and Cretaceous Floras and Climates of the Earth* (Cambridge Univ. Press, Cambridge, 1991).
49. Supported by the National Natural Science Foundation of China (projects 39370055 and 39770059), the Academy of Sciences, China (project KZ952-S1-426), and the Becker/Dilcher Endowment for Paleobotany of the University of Florida Foundation. We thank Z. P. Zhang for his help in fossil collecting, and S. W. Mei, Y. Q. Mao, Z. Y. Song, S. W. Zhao, J. Y. Chen, C. Jaramillo, and T. Lott for their assistance with the preparation of the fossil material and this manuscript.

6 August 1998; accepted 22 September 1998

Tracking the Long-Term Decline and Recovery of an Isolated Population

Ronald L. Westemeier,* Jeffrey D. Brawn,† Scott A. Simpson, Terry L. Esker, Roger W. Jansen, Jeffery W. Walk, Eric L. Kershner, Juan L. Bouzat, Ken N. Paige

Effects of small population size and reduced genetic variation on the viability of wild animal populations remain controversial. During a 35-year study of a remnant population of greater prairie chickens, population size decreased from 2000 individuals in 1962 to fewer than 50 by 1994. Concurrently, both fitness, as measured by fertility and hatching rates of eggs, and genetic diversity declined significantly. Conservation measures initiated in 1992 with translocations of birds from large, genetically diverse populations restored egg viability. Thus, sufficient genetic resources appear to be critical for maintaining populations of greater prairie chickens.

The conservation implications of small population size are controversial (*1–4*). A significant loss in genetic variation may decrease fitness or limit the long-term capacity of a population to respond to environmental challenges (*5*). Alternatively, chance environmental and demographic events may pose a more immediate threat to small populations (*1, 2*). Conservation strategies can be different depending on the relative importance of these factors (*1, 3, 6*), but fundamental questions persist because there are few data on long-term changes in the demography and genetics of wild populations.

Here we report the results of a long-term study on a remnant population of greater prairie chickens (*Tympanuchus cupido pinnatus*) in southeastern Illinois (*7*). Over the 35-year period of this study, we documented concurrent declines in population size and fitness as well as an overall reduction in genetic diversity. In addition, we report on a conservation strategy initiated in 1992, whereby translocations of individuals from large, genetically diverse populations increased fitness.

Greater prairie chickens are grassland-dependent birds still found in areas of suitable habitat ranging from northwestern Minnesota south to northeastern Oklahoma, and from southeastern Illinois west to northeastern Colorado (*8*). Leks (or booming grounds) are used as arenas for territorial display and breeding by two or more males (*9*). Loss of habitat suitable for successful nesting and brood rearing is the single most important factor leading to declines, isolation, and extirpations throughout the species' range in the midwestern United States (*10*). The eastern subspecies *Tympanuchus cupido cupido*, also known as the heath hen, has been extinct since 1931 (*11*) and Attwater's prairie chicken *Tympanuchus cupido attwateri*, which is restricted to Texas, is near extinction (*12, 13*).

In Illinois, native prairie habitat for prairie chickens originally covered >60% of the state (Fig. 1), but fewer than 931 ha (<0.01%) of the original 8.5×10^6 ha of high-grade prairie remain (*14*). There were possibly several million prairie chickens statewide in the mid-19th century (*15*); by 1962 an estimated 2000 birds

R. L. Westemeier, Illinois Natural History Survey, Effingham, IL 62401, USA. J. D. Brawn, Illinois Natural History Survey, Champaign, IL 61820, USA. S. A. Simpson and T. L. Esker, Illinois Department of Natural Resources, Newton, IL 62448, USA. R. W. Jansen, Douglas-Hart Nature Center, Mattoon, IL 61938, USA. J. W. Walk and E. L. Kershner, University of Illinois, Department of Natural Resources and Environmental Sciences, Urbana, IL 61801, USA. J. L. Bouzat and K. N. Paige, University of Illinois, Department of Ecology, Ethology, and Evolution, Urbana, IL 61801, USA.

*To whom correspondence should be addressed.
†To whom e-mail should be addressed at j-brawn@uiuc.edu

were reported in 179 localized groups occupying about 1500 km^2 in 15 counties in southern Illinois(*16*). Although early efforts (1963–1973) to preserve prairie chickens in Illinois showed marked success on restored grassland habitat (*17*), by 1994 an estimated 46 birds remained on about 33 km^2 in two small populations (*18–20*). These remnant populations were geographically isolated from larger, more contiguous populations about 640 km to the west (*8*). Estimated size of the focal population in Jasper County, Illinois, fluctuated from 84 males in 1963 to about 40 in the mid-1960s and then increased markedly to a high of 206 males counted on 13 leks in 1972 (*21*). By spring 1994, only five or six Illinois males remained on one unstable lek (Fig. 2). The drop to near extirpation occurred despite an increase in local availability of managed grassland habitat between 1963 and 1994 (*22*).

Fertility (fertile incubated eggs per total eggs) and success (hatched eggs per total eggs in fully incubated clutches) rates of eggs are key fitness traits in birds (*23*). These traits also fluctuated over time but decreased significantly in the focal population between 1963 and 1991 (Fig. 2) (*24*). The overall fertility rate (based on 3357 eggs) for 278 clutches was 93% and was sustained at >90% through 1980. Fertility rates declined in the subsequent 12 years with a low of 74% in 1990. In the 1960s, rates of egg success ranged from 91% to 100%, but by 1981 and in all but three of the next 10 breeding seasons, success rates lower than 80% were observed. The decreasing trend was significant even without the extremely low egg success of 38% observed in 1990 ($\phi = 3.35$; $P < 0.001$) (Fig. 2). About 50% of the nests observed before 1981 had partial hatching failure, but only 10% had four or more eggs failing. After 1980, 70% of successful nests contained at least one unhatched egg and failure of four or more eggs per nest was increasingly common (43%). Even two fewer chicks per brood may decrease recruitment rates of prairie chickens (*13*).

Rates of egg success observed in the focal population after 1980 were markedly lower than the 93% rate observed in the same county during the 1930s (*25*), when statewide abundance was estimated at 25,000 birds (*26*). Other data from larger prairie chicken populations to the west, northwest, and north, many during the years covered by our study, reveal an overall average egg success rate of 94% ($n = 216$ successful clutches) with a range among 18 studies of 80% to100% (*25, 27, 28*). Clearly, egg success experienced by the isolated Illinois population after 1980 was unusually low for the species (*29*).

Estimated genetic variation within Illinois' focal population was markedly lower than that within samples from larger populations in Kansas, Nebraska, and Minnesota (*30*). When sampled (1992–1994), all three of these populations numbered in the thousands, but Illinois' focal population probably did not exceed 250 birds when sampled during 1974–1993. The Illinois population had the lowest estimated mean heterozygosity and about two-thirds the allelic diversity observed in the larger populations (*31*). All alleles detected in the Illinois population (for 1974–1993) were present in one or more of the larger populations. Several alleles common to the large populations were not detected in the Illinois population but were known to be present before the 1970s (*30*).

The poor reproductive performance and inevitable extirpation of the Illinois population led local managers to initiate a translocation program in August 1992. Objectives were to increase numbers and enhance the genetic diversity and fitness within the focal population. Between 1992 and 1996, 271 greater prairie chickens (144 females and 127 males) were transplanted from large populations in Minnesota, Kansas, and Nebraska. Radiotelemetry data and observations of banded birds on leks indicated that, after each release, 25% to 67% of the transplanted prairie chickens survived and integrated per year into the breeding population (*20*). Although four radio telemetry–tagged hens from Minnesota nested in 1993, recruitment of young was not verified until 1994, when the mixed population of Illinois, Minnesota, and Kansas birds bred. From the low count of five or six Illinois males (plus two Minnesota males) in 1994 on one unstable lek, the spring count in 1996 had increased to 70 males of mixed origin on six leks (Fig. 2).

Eggs in 14 successful nests located in 1993, 1994, and 1997 revealed significant increases from the previous decade (1982–1991) in mean rates of fertility (91% to 99%; Mann-Whitney tests, $Z = 2.32$, $P < 0.05$) and hatching (76% to

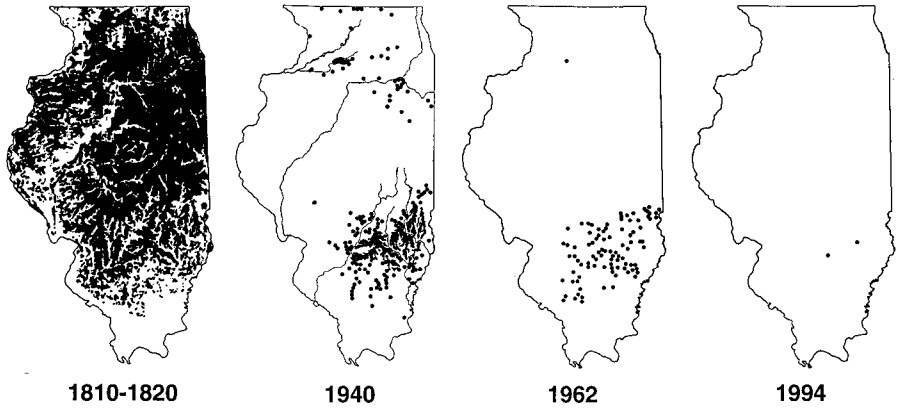

Fig. 1. Illinois prairies during 1810–1820 and distributions of greater prairie chickens in 1940 (*25*), 1962, and 1994. Prairie distributions for 1810–1820 were derived from R. C. Anderson. [Reprinted from R. C. Anderson, *Transactions of the Illinois State Academy of Science* **63,** 214 (1970), with permission.]

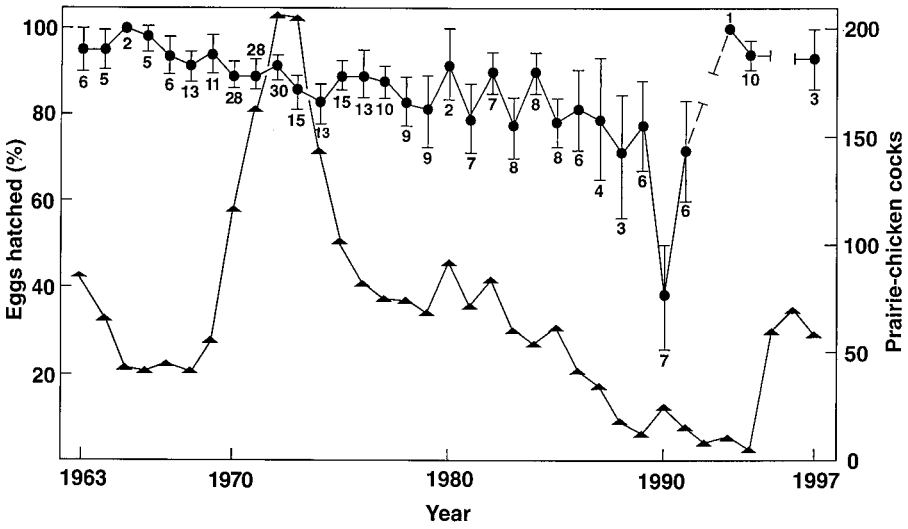

Fig. 2. Annual means for success of greater prairie chicken eggs in 304 fully incubated clutches (circles) and counts of males (triangles) on booming grounds in spring, Jasper County, Illinois, 1963–1997. Translocations of nonresident birds began in August 1992. Test statistics (*24*) for the period 1963–1991 are as follows: egg success rates, $\phi = 4.28$ ($P < 0.001$); male counts, $\phi = 1.88$ ($P = 0.0301$). Bars indicate ± 1 SE and adjacent numbers indicate numbers of nests. For egg fertility rates (not shown), $\phi = 2.18$ ($P = 0.0146$).

94%; $Z = 2.80$, $P < 0.01$) (Fig. 2). Identities were known for eight of the hens associated with these 14 nests because they were radio telemetry–tagged transplanted birds (Table 1). During 1993 and 1994, three hatches involved two Minnesota hens, five hatches involved Kansas hens, and three hatches were by hens of unknown origin; males could have been of Illinois (one definite in 1993), Minnesota, or Kansas origin (*20*). In spring 1994, five Illinois males and two Minnesota males were in situ territory holders and may have predominated in matings with Minnesota hens and newly introduced hens from Kansas. We lack nest data for 1995 and 1996; the three successful clutches found in 1997 were likely derived from birds of mixed origin. Unfortunately, we knew of no successful clutches from Illinois × Illinois crosses that might have served as controls during the 1993, 1994, and 1997 breeding seasons.

We know of no major environmental or climatic changes from previous years on the focal population's breeding grounds that could account for increased egg viability in 1993, 1994, and 1997. In Illinois, May is a critical month for incubation of most prairie chicken clutches and for hatching of the earliest clutches. Excessive rainfall and flooding, or too little rain, have been correlated with decreased reproductive success of prairie chickens (*12*). In 1963–1991, egg success correlated inversely with precipitation in May ($r = -0.36$; $n = 29$; $P < 0.05$). In May 1993, 1994, and 1997, respective rainfall amounts were 85%, 49%, and 91% of normal (*32*), and rates of egg success for those years were the highest in 25 years. Rainfall amounts were similarly favorable during much of the 1970s and 1980s when egg success was declining. Other factors (*33*) that might have suppressed egg fertility and success were still present on the breeding grounds when egg viability was restored. Therefore, egg success likely increased after the transplant because of factors intrinsic to the breeding birds.

Greater prairie chickens in Illinois illustrate the challenge of conserving small populations. From 1962 to the present, intensive management was carried out with the goal of increasing population size. Marked increases occurred from 1968 to 1972. The quality and quantity of managed habitat were enhanced and both nest parasites and predators were controlled (*22*). Yet, despite these efforts and successes, overall population size and fitness decreased. A key demographic event in the 1970s may have doomed the viability of the focal population. Before that time, the population was surrounded by other, albeit smaller, populations within 8 km; during the 1960s gene flow among those populations was likely (Fig. 1). The satellite populations subsequently disappeared and, by 1980, nearly all breeding by greater prairie chickens in the region was on or within 0.8 km of managed grasslands. Once isolated, the focal population lost viability and a conservation strategy designed to enhance genetic variation became necessary.

The demographic performance of the focal population is also a unique example of the general scenario predicted by "extinction vortex" models (*34*). These models predict that demographic and genetic effects reinforce each other in small populations to increase the probability of local extinction. We believe that the near-complete loss of suitable grasslands and satellite populations in the region drove the greater prairie chicken toward this scenario. Small population size and isolation then led to low genetic diversity and decreased fitness. The declining numbers and fitness were not unlike those of the now extinct heath hen (*34*). Attwater's prairie chicken also showed a similar decline in numbers, with egg success of 93% in 1937 but as low as 50% by 1985 (*13*), and two of the three remaining populations showed reduced genetic variability (*35*). Without intervention, our focal population likely would not have recovered genetic variation sufficient to offset adverse effects on vital demographic traits. We predict that periodic translocations will be necessary to maintain the focal population unless significantly more habitat becomes available. Isolated relict populations, such as greater prairie chickens in Illinois, cannot be conserved indefinitely with inadequate habitat and small size.

Table 1. Clutch size, egg fertility, and egg success for nests involving resident prairie chickens and nonresidents translocated to Jasper County, Illinois, by year, state of origin, and known or possible parentage combinations in 1993, 1994, and 1997. N = number of nests.

Year	State of origin		Clutch size			Egg fertility				Egg success			
						Total		Mean		Total		Mean	
	Hens	Cocks	N	Mean	SE	N	Eggs	%	SE	N	Eggs	%	SE
1993*	MN	IL	3	17.0	0.6	2	33	97.0	3.1	1	17	100.0	0.0
1994*	MN	IL, MN, or KS	2	14.5	0.5	2	29	100.0	0.0	2	29	100.0	0.0
1994*	KS	IL, MN, or KS	5	13.0	1.0	5	64	98.5	1.7	5	65	87.7	5.5
1994†	IL, MN, or KS	IL, MN, or KS	3	12.7	1.0	2	24	100.0	0.0	3	38	97.4	2.4
1997†	IL, MN, KS, or NE	IL, MN, KS, or NE	3	14.3	0.7	2	28	100.0	0.0	3	43	93.3	6.7
All			16	14.1	0.5	13	179	98.9	0.8	14	192	93.8	3.0

*Origin of hens verified by radio telemetry tagging, with individual frequencies. †Nests found indicidentally; origin of hens and cocks unknown.

References and Notes

1. R. Lande, *Science* **241**, 1455 (1988).
2. T. M. Caro and M. K. Laurenson, *ibid.* **263**, 485 (1994).
3. G. Caughley, *J. Anim. Ecol.* **63**, 215 (1994).
4. R. Lande, *Conserv. Biol.* **9**, 782 (1995).
5. L. F. Keller, P. Arcese, J. N. M. Smith, W. M. Hochachka, S. C. Stearns, *Nature* **372**, 356 (1994); R. Frankham and K. Ralls, *ibid.* **392**, 441 (1998); I. Saccheri *et al.*, *ibid.*, p. 491.
6. P. W. Hedrick, R. C. Lacy, F. W. Allendorf, M. E. Soule, *Conserv. Biol.* **10**, 1312 (1996).
7. R. L. Westemeier, J. E. Buhnerkempe, J. D. Brawn, *Wilson Bull.* **110**, 190 (1998).
8. P. A. Johnsgard, *The Grouse of the World* (Univ. of Nebraska Press, Lincoln, NE, 1983), pp. 316–340.
9. F. and F. Hamerstrom, *Technical Bulletin No. 64* (Department of Natural Resources, Madison, WI, 1973).
10. M. A. Wisdom and L. S. Mills, *J. Wildl. Manage.* **61**, 302 (1997).
11. A. O. Gross, *Mass. Audubon Soc. Bull.* **15**, 12 (1932).
12. M. E. Morrow, R. S. Adamcik, J. D. Friday, L. B. McKinney, *Wildl. Soc. Bull.* **24**, 593 (1996).
13. M. J. Peterson and N. J. Silvy, *Conserv. Biol.* **10**, 1264 (1996).
14. J. White, *Illinois Natural Areas Inventory Technical Report. Vol. 1: Survey Methods and Results* (Illinois Natural Areas Inventory, Urbana, IL, 1978).
15. Illinois State Historical Society, *Fourth Annual Illinois History Symposium*, Springfield, IL, 2–3 December 1983 (Illinois State Historical Society, Springfield, IL, 1985).
16. G. C. Sanderson and W. R. Edwards, *Trans. Ill. State Acad. Sci.* **59**, 326 (1966).
17. *The Prairie Chicken in Minnesota*, University of Minnesota, Crookston, MN, 28 April 1973 (University of Minnesota, Crookston, MN, 1973).
18. R. L. Westemeier, S. A. Simpson, D. A. Cooper, *Wilson Bull.* **103**, 717 (1991).
19. Our field study focused on Jasper County, near Newton, Illinois, where grasslands were restored on scattered sanctuaries developed by The Prairie Chicken Foundation of Illinois, The Nature Conservancy, and the Illinois Department of Natural Resources. Studies of lesser scope were conducted near Kinmundy in Marion County and annual spring surveys of prairie chickens were conducted in up to 23 areas of south-central Illinois. We used standard methods (*9*) to census prairie chickens during 1963–1997.
20. R. L. Westemeier and R. W. Jansen, *Illinois Natural History Survey Reports No. 332* (Champaign, IL, 1995).
21. Hens observed on leks are not used for annual estimates of abundance because they represent a lesser and more variable proportion of their actual numbers than is typical for males (*9*).
22. R. L. Westemeier, *Illinois Natural History Survey Reports No. 343* (Champaign, IL, 1997).
23. A. J. van Noordwijk and W. Scharloo, *Evolution* **35**, 674 (1981); F. W. Allendorf and R. F. Leary, in *Conservation Biology, The Science of Scarcity and Diversity*, M. E. Soule, Ed. (Sinauer Associates, Sunderland, MA, 1986).
24. From 1963 to 1991 this study involved the systematic efforts of 29 teams of 2 to 15 researchers and field assistants who searched on foot a cumulative total of nearly 4050 ha for nests of grassland birds; prairie chickens were the key species. Of 1125 prairie chicken nests examined, 1003 were from the focal population in Jasper County. A smaller sample of 99 nests was found in and near a study area in Marion County, 64 km of the primary study area. In 1993, 1994, and 1997, 23 additional nests

were found in Jasper County, 17 of which involved radio telemetry–tagged hens from Minnesota and Kansas. To determine clutch size, fertility, and egg success, we used only nests with eggs or egg shells in good condition at the time of discovery and not those known to be partially or fully depredated. Searches were timed so that about 90% of nests were hatched, depredated, or abandoned upon discovery; about 10% were still active when found. Although researcher disturbance of 47 active nests was suspect in biasing egg success rates, a separate study of this possibility was inconclusive (*7*). Hence, we tested rates of egg success with and without the disturbed clutches. When only undisturbed nests were used the test statistic was still highly significant ($\phi = 2.95$; $P = 0.0016$). Fertility and egg success were calculated by dividing the number of fertile (germinal discs or embryos evident but eggs not always hatched or fully incubated) or hatched eggs by the total number of eggs in unparasitized, fully incubated clutches. We excluded 38 successful nests parasitized by ring-necked pheasants (*Phasianus colchicus*) in calculating egg success to avoid bias of low success in parasitized nests [R. L. Westemeier, J. E. Buhnerkempe, W. R. Edwards, J. D. Brawn, S. A. Simpson, *J. Wildl. Manage.* **62**, 854 (1998)]. All tests (1963–1991 data) in Fig. 2 and for egg fertility were based on a nonparametric test for trend developed by E. L. Lehmann [*Nonparametrics—Statistical Methods Based on Ranks* (McGraw-Hill, New York, 1975)] using the normal approximation in all cases.

25. R. E. Yeatter, *Ill. Nat. Hist. Surv. Bull.* **22**, 377 (1943).
26. J. Lockart, *Ill. Dep. Conserv. Tech. Bull.* (1968).
27. A. O. Gross, *Wis. Conserv. Comm. Bull.* (1930); F. N. Hamerstrom Jr., *Wilson Bull.* **51**, 105 (1939); C. W. Schwartz, *Univ. Mo. Stud.* **20**, 1 (1945); W. B. Grange, *Wis. Conserv. Dep. Publ.* **328** (1948); M. F. Baker, *Univ. Kans. Mus. Nat. Hist. Biol. Surv. Kans.* **5** (1953); F. L. Arthaud, thesis, University of Missouri (1968); N. J. Silvy, thesis, Kansas State University (1968); R. D. Drobney, thesis, University of Missouri (1973); L. H. Sisson, *The Sharp-Tailed Grouse in Nebraska, a Research Study* (Nebraska Game and Parks Commission, Lincoln, 1976); W. D. Svedarsky, dissertation, University of North Dakota (1979); L. A. Rice and A. V. Carter, *Completion Report No. 84-11* (South Dakota Department of Game, Fish, and Parks, Pierre, SD, 1982); G. J. Horak, *Kansas Fish and Game Commission Wildlife Bulletin No. 3* (1985); J. A. Newell, thesis, Montana State University (1987); D. P. Jones, thesis, University of Missouri (1988); J. E. Toepfer, dissertation, Montana State University (1988).
28. L. L. McDaniel, unpublished material.
29. Our nest data were highly representative of the focal population because, on average during 1963–1991, total nests found represented 46% (range, 28% to 76%) and 77% (range, 39% to 188%) of the number of males and hens, respectively, censused on booming grounds in Jasper County.
30. J. L. Bouzat, H. A. Lewin, K. N. Paige, *Am. Nat.* **152**, 1 (1998); J. L. Bouzat *et al., Conserv. Biol.* **10**, 836 (1998).
31. Estimates of genetic variability were based on highly polymorphic type II markers (microsatellites), which are more sensitive for detecting potential changes in genetic diversity. The relatively small reduction in Illinois average heterozygosity (about 9%) results from the large numbers of alleles detected at the microsatellite loci. Estimates of genetic diversity based on type I markers (that is, markers associated with coding sequences of structural genes) would likely reveal a more drastic decline in average heterozygosity. The observed declines of fitness components in the Illinois population should not be attributed to the particular loci analyzed (which are noncoding and presumably neutral DNA sequences). The effects of inbreeding are probably more directly related to the expression of lethal recessive alleles at structural genes. Our results also indicate that allelic diversity is more drastically affected than heterozygosity, as is expected following population bottlenecks (M. Nei, T. Maruyama, R. Chakraborty, *Evolution* **29**, 1 1975). Declines in fitness in the Illinois population probably result from a drastic decrease in heterozygosity at structural genes and the random extinction of critical alleles through the population bottleneck.
32. Illinois State Water Survey, *Ill. Agric. Stat. Serv.* (1993); *ibid.* (1994); *ibid.* (1997).
33. Factors other than inbreeding can cause fertility and hatchability problems. Other possible factors included competing species that may transmit disease (pheasants and waterfowl), pollutants (oil and pesticides), and human disturbances. However, egg success was declining about one decade before there was a large abundance of pheasants in the mid-1980s, researcher disturbance of active nests (mostly the mid-1980s to 1991) (*7*), a large increase in oil production (1983), and pesticides used for no-till farming. Similarly, waterfowl, mostly mallards (*Anas platyrhynchos*), did not feed or nest with prairie chickens until the late 1970s. Also, hatch rates of northern bobwhites (*Colinus virginianus*), pheasants, and other sympatric species in the study area have not declined.
34. M. E. Gilpin and M. E. Soule, in *Conservation Biology: The Science of Scarcity and Diversity*, M. E. Soule, Ed. (Sinauer Associates, Sunderland, MA, 1986), pp. 19–34.
35. A. O. Gross, *Mem. Boston Soc. Nat. Hist.* **6**, 491 (1928).
36. E. A. Osterndorff, thesis, Texas A&M University (1995).
37. We thank the many field assistants who made this report possible and especially project assistants D. R. Vance and J. E. Buhnerkempe; R. J. Ellis led the project during 1963–1965. We appreciate technical reviews of the manuscript by K. M. Giesen, C. A. Phillips, and P. W. Brown and editing and figure graphics by T. E. Rice. J. E. Toepfer provided guidance in all phases of translocation efforts and, with P. S. Beringer, helped in securing birds from Minnesota for translocation to Illinois. Illinois wild turkeys were traded for Minnesota prairie chickens with the assistance of the Illinois Department of Natural Resources–Division of Wildlife Resources. Various other wildlife staff in Minnesota, North Dakota, Kansas, and Nebraska supported translocation of prairie chickens. L. L. McDaniel provided unpublished egg success data from the Valentine National Wildlife Refuge, Nebraska. This is a contribution in part of Federal Aid Wildlife Restoration Project W-66-R, with the Illinois Department of Natural Resources–Division of Natural Heritage, U. S. Fish & Wildlife Service, Illinois Natural History Survey, The Nature Conservancy, Illinois Nature Preserves Commission, Illinois Endangered Species Protection Board, and the University of Illinois at Urbana–Champaign; cooperating. Funding for translocations of prairie chickens was provided by the Illinois Wildlife Preservation Fund and Natural Areas Acquisition Fund. Funding for locating nests in 1997 was provided by the Illinois Council on Food and Agricultural Research (C-FAR).

10 August 1998; accepted 9 October 1998

Arabidopsis NPH1: A Flavoprotein with the Properties of a Photoreceptor for Phototropism

John M. Christie, Philippe Reymond, Gary K. Powell, Paul Bernasconi, Andrei A. Raibekas, Emmanuel Liscum, Winslow R. Briggs*

The *NPH1* gene of *Arabidopsis thaliana* encodes a 120-kilodalton serine-threonine protein kinase hypothesized to function as a photoreceptor for phototropism. When expressed in insect cells, the NPH1 protein is phosphorylated in response to blue light irradiation. The biochemical and photochemical properties of the photosensitive protein reflect those of the native protein in microsomal membranes. Recombinant NPH1 noncovalently binds flavin mononucleotide, a likely chromophore for light-dependent autophosphorylation. The fluorescence excitation spectrum of the recombinant protein is similar to the action spectrum for phototropism, consistent with the conclusion that NPH1 is an autophosphorylating flavoprotein photoreceptor mediating phototropic responses in higher plants.

Plants rely heavily on the surrounding light environment to regulate normal growth and development. Over the past two decades, considerable progress has been made in characterizing the phytochrome family of photoreceptors that monitor the red and far-red regions of the electromagnetic spectrum (*1*). However, only recently have advances been made that increase our understanding of ultraviolet-A (UV-A)–blue light perception in plants (*2*).

Cryptochromes are UV-A–blue light photoreceptors with homology to microbial DNA photolyases (*2*). Like photolyases, the cryptochromes contain dual light-harvesting chromophores—flavin adenine dinucleotide (FAD) and either a deazaflavin (*3*) or a pterin (*4*)—but exhibit no DNA repair activity (*4, 5*). The two cryptochrome genes of *Arabidopsis*, *CRY1* and *CRY2*, encode homologous proteins (*3, 6*) that appear to overlap in function

J. M. Christie and W. R. Briggs, Department of Plant Biology, Carnegie Institution of Washington, 260 Panama Street, Stanford, CA 94305, USA. P. Reymond, Institut de Biologie et de Physiologie Végétales, Université de Lausanne, 1015 Lausanne, Switzerland. G. K. Powell and P. Bernasconi, Novartis Agribusiness Biotechnology Research Inc., 3054 Cornwallis Road, Research Triangle Park, NC 27709, USA. A. A. Raibekas, Department of Biological Chemistry, University of Michigan, M5416 Medical Science I, Ann Arbor, MI 48109, USA. E. Liscum, Division of Biological Sciences, University of Missouri, Columbia, MO 65211, USA.

*To whom correspondence should be addressed. E-mail: briggs@andrew.stanford.edu