

ity of change) of how bioturbation changes following extinction depend on the order in which species are lost, because extinction risk is frequently correlated with life-history traits that determine the intensity of bioturbation. This finding is important because it argues that the particular cause of extinction ultimately governs the ecosystem-level consequences of biodiversity loss. Therefore, if we are to predict the ecological impacts of extinction and if we hope to protect coastal environments from human activities that disrupt the ecological functions species perform, we will need to better understand why species are at risk and how this risk covaries with their functional traits.

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Supporting Online Material

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 Materials and Methods
 Equations S1 and S2

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Bushmeat Hunting, Wildlife Declines, and Fish Supply in West Africa

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The multibillion-dollar trade in bushmeat is among the most immediate threats to the persistence of tropical vertebrates, but our understanding of its underlying drivers and effects on human welfare is limited by a lack of empirical data. We used 30 years of data from Ghana to link mammal declines to the bushmeat trade and to spatial and temporal changes in the availability of fish. We show that years of poor fish supply coincided with increased hunting in nature reserves and sharp declines in biomass of 41 wildlife species. Local market data provide evidence of a direct link between fish supply and subsequent bushmeat demand in villages and show bushmeat's role as a dietary staple in the region. Our results emphasize the urgent need to develop cheap protein alternatives to bushmeat and to improve fisheries management by foreign and domestic fleets to avert extinctions of tropical wildlife.

The trade in bushmeat for human consumption is a key contributor to local economies throughout the developing world (1, 2), but it is also among the greatest threats to the persistence of tropical wildlife (1–4). Efforts to manage the bushmeat trade are built on the premise that bushmeat consumption is driven by protein limitation. Thus, it is assumed that increases in livestock and agricultural production will reduce human reliance on wild sources of food (5–7). Although it makes intuitive and economic sense that consumption of wild meat would be linked to the availability of alternative sources of protein, there is little empirical evidence to support this assumption, particularly at large geo-

graphic scales (1, 5–7). Furthermore, contrary to predictions of the “protein limitation” hypothesis, unsustainable consumption of wildlife remains a problem even in many relatively prosperous countries (1). Identifying bushmeat's value as a dietary staple versus a nonessential good is vital for targeting conservation interventions and, equally important, for predicting the impacts of wildlife declines on human livelihoods.

We evaluated the protein limitation hypothesis by comparing annual rates of decline for 41 species of wild carnivores, primates, and herbivores (table S1) in six nature reserves in Ghana with supply of fish in the region from 1970 to 1998. As is the

case across the tropics, wild terrestrial mammals are used as a secondary source of animal protein in Ghana, and they comprise the chief commodities in a regional bushmeat trade estimated conservatively at 400,000 tons per year (8). Marine and freshwater fish are the primary source of animal protein consumed in West Africa, and the fisheries sector directly and indirectly accounts for up to one quarter of the workforce in the region (9, 10). From 1965 to 1998, the supply of harvested fish in Ghana (Fig. 1A) ranged from 230,000 to 480,000 tons annually and varied by as much as 24% between consecutive years (11). Here, we test a prediction of the protein limitation hypothesis that years with low fish supply will show larger declines in biomass of terrestrial mammals, suggesting a transfer of harvest pressure and consumption between these resources. We also test for evidence of a mechanism underpinning such a transfer by examining (i) rates of hunting in nature reserves, (ii) sales and price data from local markets, and (iii) spatial trends in correlations of fish supply and wildlife declines.

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In support of the prediction that annual standing biomass of large mammals would be linked positively with the annual supply of marine and freshwater fish, we found that changes in annual biomass of terrestrial mammals from 1970 to 1998 were closely related to annual per capita fish supply. Years with a lower-than-average supply of fish had higher-than-average declines in mammal biomass, and vice versa (Fig. 1B) (12). In contrast, fish supply and wildlife declines were unrelated to other potential explanatory factors, including annual rainfall, land and water temperatures, political cycles, oil prices, and gross national product ($P \geq 0.19$ for each term in multiple-regression models) (13). This correlative support for the protein limitation hypothesis is further supported by three additional analyses.

First, our working hypothesis suggests that the observed link between fish supply and wildlife decline occurs because bushmeat hunting and consumption increased when fish became scarce. In support of this suggestion, we found that annual counts of hunters observed by wildlife rangers in five nature reserves in Ghana (13) were related negatively to per capita fish supply from 1976 to 1992 (Fig. 2A). Annual counts of hunters were also closely related to annual rates of wildlife decline in these same nature reserves ($R = 0.76, n = 17, P < 0.01$). Thus, hunters were more common in reserves in years when fish supply was low, and these

increases in hunters were linked to accelerated declines of wildlife.

Second, if annual variation in fish supply and bushmeat hunting are linked causally, we would expect that the availability of bushmeat in local markets would be related negatively to the supply of fish (5). In support of this prediction, we found that monthly supply of fish in 12 local markets in northern, central, and eastern Ghana from 1999 to 2003 (13) was related negatively to the volume of bushmeat sold in these markets (Fig. 2B). In addition, the price of fish sold in markets was closely and negatively related to local fish supply ($R = 0.73, n = 52, P < 0.01$) and positively related to the volume of bushmeat sold ($R = 0.48, n = 52, P < 0.01$). The strong negative correlation between fish price and quantity sold, combined with the positive correlation between fish price and bushmeat sales, is consistent with the idea that variation in fish supply drove bushmeat sales. Comparing monthly fish price in markets with the bushmeat sales in the following month yielded even stronger correlations, again suggesting that bushmeat sales were driven by fish availability and price more so than the reverse case (fig. S1). These results show a substitution of wildlife for fish at the local scale. Taken together with the observation of increased bushmeat hunting during periods of fish scarcity, these results also support our suggestion of a causal, macroscale link between fish supply and wildlife declines (Fig. 1).

Third, more than half of Ghana's human population of 20 million resides within 100 km of the coast, where the majority of employment and dietary protein are derived from fishing (10). Poor fish harvests result in reduced income and food for coastal communities and reduce the availability of fish throughout the region (9, 14). The widespread loss of jobs and income associated with poor fish harvests also may lead some portion of households to rely on bushmeat hunting both for income and sustenance. If fish supply and bushmeat consumption are linked causally, it follows that the transfer of harvest pressure between aquatic and terrestrial resources would be most evident in

Fig. 1. Year-to-year change in estimated biomass of 41 large mammal species was linked closely to annual harvest of marine and freshwater fish in Ghana ($R = 0.73, n = 28$ years, $P < 0.001$). (A) Time series plots of annual fish supply and change in estimated mammal biomass. (B) Conventional plot of data shown in (A). The trend line describes the equation $y = 0.0058x + 0.81$. Values of annual fish supply [from (11)] represent landings plus imports and minus exports. Biomass of large mammals was calculated for each year by multiplying the number of animals observed in ~700 walking counts of 10 to 15 km each (17) by species-specific body weights. The products of these calculations were then summed across all species.

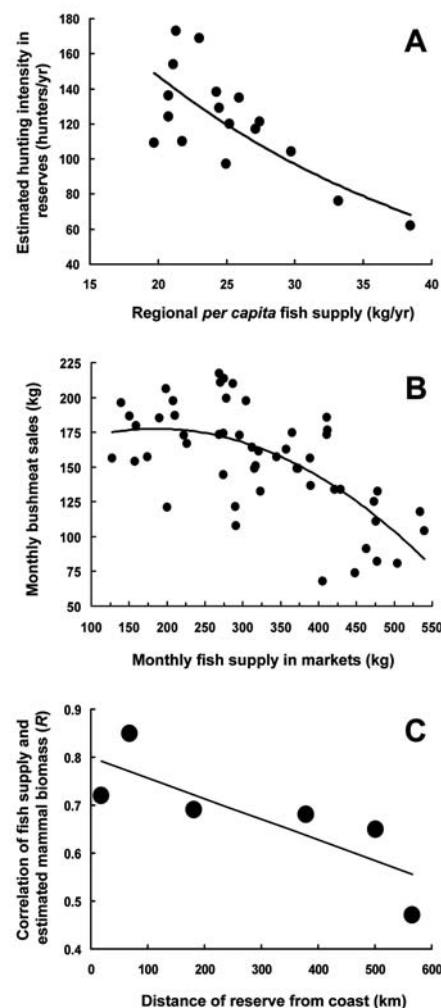
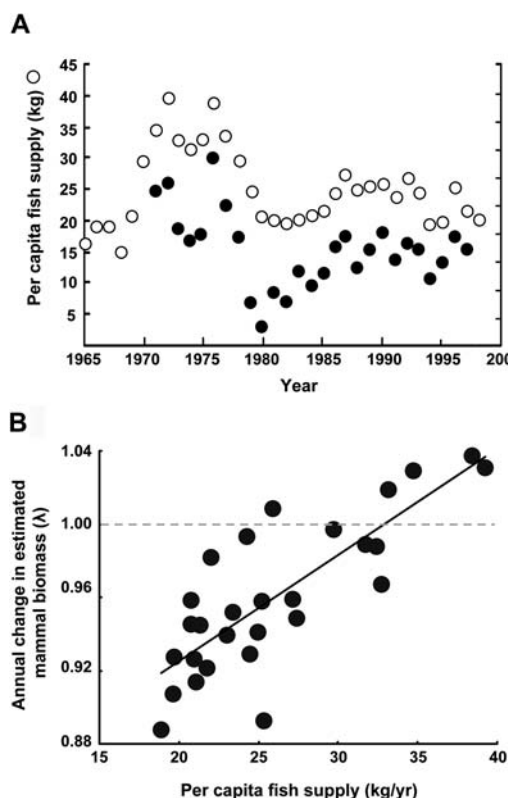


Fig. 2. Links between fish supply and bushmeat hunting and consumption are evident in observations that (A) annual counts of hunters in five terrestrial reserves in Ghana from 1976 to 1992 were related negatively to supply of fish in the region ($R = -0.52, n = 17, P = 0.03$); (B) monthly sales of bushmeat in 12 rural markets in Ghana were related negatively to local fish supply ($R = -0.61, n = 52, P < 0.01$); and (C) fish supply and wildlife declines were related most closely in reserves occurring nearest to the coast ($R = 0.81, n = 6, P = 0.05$).

coastal areas where reliance on fish for both income and animal protein is greatest. We tested this last prediction by repeating the analysis in Fig. 1 separately for each of six nature reserves in Ghana. We found the strongest link between annual variation in marine and freshwater fish supply and annual change in mammal biomass in reserves near the coast and weaker, though still significant, linkages for reserves farther inland (Fig. 2C).

These three lines of evidence indicate that fish supply is linked negatively to the price of fish, the number of wildlife hunters, and the sales and supply of bushmeat in local markets. Our results also show that the substitution of fish for bushmeat occurs most intensively close to the coast, where fish are more important as sources of food and income. All of these findings are consistent with the protein limitation hypothesis and inconsistent with the notion that bushmeat in Ghana is primarily a nonessential good (summarized in fig. S2).

Our results provide clear evidence to suggest that the outcomes of programs aimed at promoting economic development, food security, and the conservation of biological diversity in Ghana, and perhaps elsewhere in Africa, will be closely linked. First, the close correlation between hunting pressure, markets, and long-term trends in wildlife abundance suggests strongly that the persistence of the more than 400 species of terrestrial vertebrates that supply the bushmeat trade in West Africa will depend ultimately on the availability of affordable alternative protein sources for the region's growing human population. Second, our failure to conserve existing wildlife populations as core sources for managed, sustainable harvests could have serious deleterious effects on the stability of the long-term human food supply and the livelihoods of bushmeat hunters and sellers. Our findings and those of others suggest that the harvest of terrestrial wildlife can buffer the impact of environmental or other shocks by providing animal protein and income in times of economic hardship or food scarcity (2, 15, 16). However, marked declines in large

mammal abundance and marine and freshwater fish stocks documented in the region over the past 30 years now suggest that this buffer system can no longer be sustained (14, 17–20).

From 1970 to 1998, the biomass of 41 species of mammals in nature reserves in Ghana declined by 76% (Fig. 3), and 16 to 45% of these species became locally extinct (17). Similarly, trawl surveys conducted in the Gulf of Guinea since 1977 and other regional stock assessments estimate that fish biomass in nearshore and offshore waters has declined by at least 50% (Fig. 3). At the same time, a threefold increase in human populations in the region since 1970 has resulted in per capita declines in fish supply, despite steady increases in regional fish harvests (11, 14). These sharp declines in terrestrial wildlife and marine fish suggest that stocks in this region may face imminent collapse (9, 18). The consequences of collapse of either fish or terrestrial wildlife are daunting and may be felt immediately as widespread human poverty and food insecurity in the region (14). Reduced fish stocks have already severely damaged the region's artisanal fisheries sector (14, 21), and recent collapses of mammal populations in some areas of West Africa have been linked to geographic patterns of poverty and malnourishment (8, 17). Agricultural production is a third potentially critical, though poorly understood, factor linking human food supply to biodiversity conservation in the region (16).

One management response to the potential collapse of fish and terrestrial wildlife stocks in West Africa is to build up regional livestock and agriculture sufficiently to alleviate pressure on overexploited wild resources (7). However, such efforts could take decades to implement and face enormous economic, regulatory, and political hurdles. Thus, more immediate plans to enhance the sustainability of wild protein sources are required. One immediate route to increasing production and sustainability of domestic fisheries, and thereby reducing pressure on terrestrial wildlife, is to limit the access of large and heavily subsidized

foreign fleets to fish off West Africa (18–24). Declines of fish stocks in nearshore and offshore waters of West Africa have coincided with more than 10-fold increases in regional fish harvests by foreign and domestic fleets since 1950 (11). The European Union (EU) has consistently had the largest foreign presence off West Africa, with EU fish harvests there increasing by a factor of 20 from 1950 to 2001 (fig. S3). Furthermore, EU financial support of its foreign fleet increased from about \$6 million in 1981 to more than \$350 million in 2001 (fig. S3), with the effect of artificially increasing the profitability of fishing in African waters for EU boats, despite declining fish stocks (22). West African commercial fleets also have expanded considerably since 1950 (fig. S3) and there is no guarantee that reductions of foreign catches would not be taken up by increased domestic fishing. However, even short-term increases in the domestic supply of fish both for commercial export and local consumption may enhance regional economies (14) and ease exploitation of terrestrial wildlife resources. Over the longer term, intensive management to enhance fish stocks and stabilize harvests must become a regional conservation and economic priority.

A second route to increase the sustainability of fish and wildlife harvests could come by enhancing the protection of harvested marine and terrestrial resources. Pirate fishing vessels from foreign ports are abundant in West African waters and illegally extract fish of the highest commercial value while, like many commercial fleets, dumping 70 to 90% of their haul as by-catch (9, 18). Increased policing of exclusive fishing zones and enforcement of existing quotas and tariffs for commercial fleets should reduce exploitation and provide an immediate boost to marine resources available to local fisheries (14, 19). On land, wildlife has persisted at near historic levels in inaccessible and well-protected areas of West Africa's nature reserves (4, 17). Increasing the size, number, and protection of wildlife reserves in the region may not offer a long-term solution to concerns over human livelihoods and protein supply, but it is likely to offer the most immediate prospects for slowing the region's catastrophic wildlife decline.

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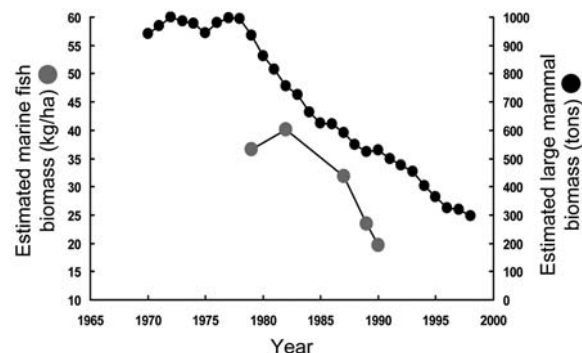


Fig. 3. Estimates of marine fish biomass in the Gulf of Guinea (gray circles) and large mammal biomass in Ghana (black circles). Estimates of fish biomass are from trawl surveys (24, 25). Analyses of fisheries catch data with ecosystem models indicate that fish biomass in coastal West and Northwest Africa has declined by a factor of 13 since 1960 (20). Estimates of mammal biomass are based on abundances of 41 species observed in ~700 wildlife counts per year in six nature reserves (17) (see map, fig. S4).

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Supporting Online Material

www.sciencemag.org/cgi/content/full/306/5699/1180/DC1

Materials and Methods

Figs. S1 to S5

Tables S1 and S2

References

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The Genetic Basis of Singlet Oxygen-Induced Stress Responses of *Arabidopsis thaliana*

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Plants under oxidative stress suffer from damages that have been interpreted as unavoidable consequences of injuries inflicted upon plants by toxic levels of reactive oxygen species (ROS). However, this paradigm needs to be modified. Inactivation of a single gene, *EXECUTER1*, is sufficient to abrogate stress responses of *Arabidopsis thaliana* caused by the release of singlet oxygen: External conditions under which these stress responses are observed and the amounts of ROS that accumulate in plants exposed to these environmental conditions do not directly cause damages. Instead, seedling lethality and growth inhibition of mature plants result from genetic programs that are activated after the release of singlet oxygen has been perceived by the plant.

Abiotic stress conditions limit the ability of plants to use light energy for photosynthesis, often reducing their growth and productivity and causing photooxidative damages (1–3). The emergence of these stress symptoms has been closely associated with the enhanced production of several ROS (4, 5). Because different ROS are generated simultaneously, it is difficult to determine the biological activity and mode of action for each of these ROS separately. In order to address this problem, one would need to find conditions under which only one specific ROS is generated at a given time, within a well-defined subcellular

compartment, and which also triggers a visible stress response that is easy to score.

Recently, we have isolated the conditional *flu* mutant of *Arabidopsis thaliana* that fulfills these requirements (6). The mutant generates singlet oxygen in plastids in a controlled and noninvasive manner. Immediately after the release of singlet oxygen, mature *flu* plants stop growing, whereas seedlings bleach and die (6). Here, we demonstrate that the two stress responses, growth inhibition and seedling lethality, do not result from physicochemical damage caused by singlet oxygen during oxidative stress but are caused by the activation of a genetically determined stress response program.

We set out to identify such a genetic program by identifying second-site mutations that abrogate either one or both of the two stress responses of the *flu* mutant. Three different groups of second-site mutations could be distinguished (7) (fig. S1A). One of these groups contained 15 mutants that

behaved like wild type when kept under nonpermissive light-dark conditions (7) [group III (fig. S1, B to D)]. Allelism tests and mapping revealed that they were allelic, representing a single locus that was named *EXECUTER1*. In contrast to wild-type plants but like *flu*, the *executer1/flu* double mutant accumulated free protochlorophyllide (Pchl_{id}) in the dark (Fig. 1, A to C, and fig. S1B). After transfer to the light, *executer1/flu* generated singlet oxygen in amounts similar to those of *flu* (Fig. 1, F to H) but grew like wild type when kept under nonpermissive light-dark cycles (Fig. 1, A to C). The second stress reaction of *flu* to the release of singlet oxygen is an inhibition of growth. In *flu* plants, the growth rate was reduced immediately after the beginning of reillumination (Fig. 1D). The *executer1/flu* plants, however, grew like wild-type plants (Fig. 1D). Growth inhibition of *flu* plants was particularly striking when plants were transferred to repeated light-dark cycles, whereas *executer1/flu* continued to grow like wild-type plants (Fig. 1E). All three plant lines grew equally well under continuous light (fig. S2).

As a first step toward the functional characterization of *EXECUTER1*, we used a map-based cloning strategy to isolate the *EXECUTER1* gene. *EXECUTER1* was genetically mapped on chromosome IV on a genomic fragment of about 90 kb (Fig. 2A). A contig consisting of 11 cosmid clones that encompassed this chromosomal region was generated (Fig. 2A), and the ability to complement the *executer1* mutation was tested (7). Seedlings of the double mutant transformed with the genomic DNA of the cosmid clone 44 that contained a wild-type copy of *EXECUTER1* died like *flu* seedlings when grown under nonpermissive dark-light conditions, whereas seedlings of plants transformed with genomic DNA of other cosmid clones grew like seedlings of the original *executer1/flu* parental line (Fig. 2B).

The second test was done with mature T2 plants transformed with DNA of cosmid

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