

A review of bird responses to El Niño–Southern Oscillation conditions in the Neotropics

Marcus C. England

Cotinga 13 (2000): 83–88

El Fenómeno Climático de El Niño (ENSO), un calentamiento de las aguas del Océano Pacífico, provoca trastornos en las condiciones climáticas en todo el planeta. Estas condiciones tienen efectos radicales en la productividad primaria tanto en ecosistemas marinos como terrestres, con consecuentes efectos sobre los niveles tróficos superiores. Así, consideramos necesaria una revisión de estos efectos en la avifauna Neotropical. Una productividad reducida en los ecosistemas marinos usualmente tiene efectos negativos en aves marinas pelágicas, aunque existen varias excepciones. La falta de estudios es evidente para las aves terrestres, para las cuales se han registrado distintos resultados, incluyendo aumentos y disminuciones en la fecundidad, cambios en los patrones de vagabundeo, y tasas de mortalidad diferentes de los años normales. Sin embargo, no es posible generalizar para todos los grupos.

Introduction

Birds have the potential to respond rapidly to environmental changes because of their mobility⁵⁸. The El Niño–Southern Oscillation (ENSO) phenomenon is perhaps the most important of climatic anomalies, being responsible for well-documented catastrophic effects on the primary productivity of marine ecosystems⁴⁴. Primary productivity is an important determinant of community dynamics and ecosystem structure and is greatly influenced by such factors as nutrients, light, temperature, and species composition—all of which are strongly affected by large-scale climatic disturbances such as El Niño⁴⁴.

In most years the eastern Pacific Ocean is characterised by cool sea-surface temperatures (SSTs) (22–24°C), while a deep pool of warm water (29–30°C) in the west is associated with intense rainfall over the tropical regions. The cooler SSTs in the eastern region are the result of cold water upwelling from below as trade winds push the surface water west. Every 3–7 years a series of prolonged westerly winds replace the normal weak easterly winds. The suppression of cold water upwelling and subsequent warming of the entire ocean surface results in a shift in the major precipitation regions of the tropics with catastrophic flooding over the west coast of South America, disruption of normal climate patterns at high latitudes, weakened summer monsoons in south Asia, and severe drought in Australia and Indonesia^{6,36,44,45,62}. The cause of this change from the normal state is uncertain, but ENSO is believed to act as a hemispheric energy balancing mechanism²⁰. The term Southern Oscillation refers to the flip in pressure differential between the normally low-pressure Indonesian equatorial region and the high-pressure South Pacific tropical region⁴⁴.

The ENSO event of 1997—possibly the most powerful of the century⁶²—may have caused nest-

ing failures in many species of seabirds²¹ (F. Ortiz-Crespo pers. comm.) and increased mortality or changed migration timing in Neotropical migrants^{22,51} (P. Whan, D. L. Kaplan & T. Thomson pers. comms.). Despite the apparent effects of weather anomalies on birds, few researchers have attempted to generalise the consequences of ENSO events on the avifauna. A review by Hall *et al.*²² only covers terrestrial species and most work is biased toward Nearctic species despite the fact that El Niño is a tropical Pacific Ocean phenomenon²². A review of the effects of ENSO on Neotropical birds is therefore presented here.

Seabirds

The drastic effects of El Niño on seabird species are well documented in the literature; however, the opposing effects exhibited in many species render them resistant to generalisation across taxa. The strong effect of anomalous sea temperatures on primary productivity and resulting changes in the distribution of many fish species correlate with increased mortality and reduced nesting success in many pelagic birds⁸. Changes in ocean ecosystems also appear to modify dispersal patterns and cause the appearance of species in new localities.

Reproductive attempts by Blue-footed Booby *Sula nebouxii* in the Galápagos Islands failed and breeding colonies were deserted after SSTs warmed in January 1987 during an ENSO event, while Masked Booby *S. dactylatra* and Red-footed Booby *S. sula* were either unaffected or simply delayed breeding for several months². Failure of *S. nebouxii* to raise young was associated with reduced availability of their main prey item, which apparently differs from that of *S. sula* and *S. dactylatra*. A gradient in SSTs and ENSOs impact on seabirds was also noted as populations nesting in the cooler south were affected less than those in the warmer north².

F. Ortiz-Crespo (pers. comm.) reported massive mortality of *S. nebovixii* along the northern side of the Gulf of Guayaquil, Ecuador, in 1997 and many pairs failed to raise young in the same area. Also in Ecuador, Magnificent Frigatebird *Fregata magnificens* courtship commenced in July, two months earlier than usual, and nesting success of the Grey-headed Gull *Larus cirrocephalus* was extremely low. The majority of over 500 *L. cirrocephalus* pairs failed to raise any young and dead small chicks were commonly found on the ground with starvation suspected as the cause. Just 50 first-year birds were seen by October²¹.

Fluctuations in food resources have been linked to altered growth patterns in pelagic seabirds^{8,41}. A study comparing nestling growth rate of the endangered Dark-rumped Petrel *Pterodroma phaeopygia* during and outside ENSO conditions on the Galápagos Islands discovered that chick growth rates were retarded during the 1983 nesting season^{8,9,60}. Chicks in non-ENSO years reached adult mass six weeks after hatching, while chicks in ENSO years reached adult mass ten weeks after hatching. Total length of the nestling period was significantly longer during ENSO years. At fledging, no differences were found in adult dimensions including wing, tarsus, tail and bill lengths, and mass. Although food resources were not measured directly, it was suggested that delayed fledging of young is a result of restraints on tissue maturation due to a decline in ingested energy when parents are restricted in their ability to find food.

Availability of preferred nesting sites can limit breeding success or opportunities in some species of pelagic seabirds⁷. Preferences for certain vegetative characteristics for nesting may exclude use of much of an area despite any superficial homogeneity. In Red-tailed Tropicbird *Phaethon rubricauda*, the 1982–83 ENSO had the immediate effect of disrupting the reproductive cycle. Slow chick growth rates were noted in July 1982 and by autumn many nests had failed^{7,55}. In 1984, changes in the vegetative structure on Christmas Island, as a result of El Niño conditions, permitted an increase in breeding pairs (from 40 in 1980 to 77 in 1984). Similar results were noted in March–April 1997 as the heaviest rains to fall in Ecuador since the 1982–1983 ENSO event contributed to the best breeding season for Gull-billed Tern *Gelochelidon nilotica* since 1986²¹.

Standardised censuses over many years could act as sensitive indicators of the effects of changing ocean productivity and food availability on pelagic taxa. Seabird assemblages dominated by storm-petrels *Oceanodroma*, gadfly petrels *Pterodroma* and shearwaters *Puffinus* were censused in the eastern equatorial Pacific from 1984–1989 by Ribic *et al.*⁴⁷. Although seabird assemblage characteristics varied from year to year, the most significant

changes were during El Niño years. Decreases in richness of both genera and species were recorded, particularly those of medium abundance. Common genera and species were unaffected.

El Niño conditions and associated changes in food abundance and weather appear to correlate with extensive vagrancy in many seabirds. For example, during the 1997 El Niño, two common species along the Peruvian coast—Peruvian Booby *Sula variegata* and Guanay Cormorant *Phalacrocorax bougainvillii*—extended their ranges north into Ecuador, extralimital records of Inca Tern *Larosterna inca* were reported in Colombia and the first record of South American Tern *Sterna hirundinacea* in Ecuador was made²¹. According to Haase²¹, in typical ENSO years, Humboldt Current species are noted in Ecuador; however this did not happen in 1997. A Black Tern *Chlidonias niger* during the 1982–1983 ENSO was only the second record for the Galápagos Islands, while records of Laughing Gull *Larus atricilla* and Sooty Shearwater *Puffinus griseus* in the Galápagos are primarily associated with El Niño events¹⁰.

Terrestrial birds

El Niño effects on terrestrial birds are difficult to assess as it is impossible to prove that El Niño itself has caused specific changes in the observed weather and most evidence is anecdotal. Although severe storms resulting from El Niño can directly cause bird mortality, the influence of weather on food resources is probably the primary agent affecting Neotropical birds³¹. On land, primary productivity is tightly correlated with precipitation^{12,30,33,38,39,42–44,52}. Increased rainfall can cause an upsurge in terrestrial productivity and longer breeding seasons^{18,22,31} or reduced temperatures can depress food availability and, consequently, adult survival and fecundity^{31,35}.

Climatic extremes during El Niño events are believed to be significant causes of microevolutionary changes in animal and plant populations on the Galápagos Islands, changes which have been observed closely in Darwin's Finches *Geospiza* spp.¹⁹. Several species reportedly underwent significant evolutionary changes over a short time during an ENSO event, especially positive selection for small bill sizes as large seeds became scarce¹⁹. Rainfall during the 1982–1983 event was 10 times greater than previously recorded and according to Hall *et al.*²² affected nesting success of Medium Ground Finch *Geospiza fortis* and Cactus Finch *G. scandens* as arthropod and seed levels increased. The population levels of both species increased by over 400%. Increased food availability also appeared to reduce maturation time of young and age of first breeding. Similar effects were also noted in Large Cactus Finch *G. conirostris*, although fledging success fell due to nest

abandonment by females during heavy rain and increased predation by owls and mockingbirds *Mimus*. The authors of that study believed that ENSO conditions may have important consequences for life history traits in these species, as a substantial proportion of an individual's lifetime reproductive output may accrue during El Niño years.

The dry season in Panama during the 1982–1983 ENSO began 6–8 weeks earlier than usual²². Weight declines and degradation of pectoral muscles were evident in resident birds and habitat selection patterns changed. In dry areas mist-net capture rates were the lowest ever recorded in eight years—22% and 35% below average—while a wetter area elsewhere had the highest capture rates ever recorded in a dry season (52% above the mean)²⁶. Similar results were found when Lindsey *et al.*³¹ examined the effects of a 1991–1992 ENSO drought in Hawaii on capture rates, fat scores, and the number of active nests of six Hawaiian forest bird species. Overall capture rates in 1992 were 60% lower than 1993 and 62% lower than 1991. Fat scores decreased for four species, and nesting attempts decreased in two species by more than than 90%.

In a study of Turquoise-browed Motmot *Eumotoca superciliosa* breeding biology on the Yucatán Peninsula, Scott & Martin⁵⁶ recorded unusual breeding behaviour during the 1983 ENSO year. Increased rainfall across the region allowed vegetation to remain green during the normal dry season, resulting in early breeding of motmots by a few weeks. More and smaller clutches were laid in 1983 than in 1980 or 1982.

Neotropical migrants

Lack²⁹ and Richardson⁵¹ review the effects of weather on Neotropical migrants. Because of the importance of weather anomalies in any analysis of the effects of El Niño on birds, the effects of adverse weather conditions on the migratory avifauna are discussed in brief here. It is plausible that many effects of weather on migrants may also be applicable to Neotropical resident species, such as the effects of weather on food abundance, energy reserves, and availability of optimal habitat.

It is unknown how migration timing in the tropics may be affected by El Niño conditions as even the basics of timing during normal years have not been studied⁵¹. The progression of fronts that birds in the Nearctic use to facilitate timing is absent in subtropical and tropical regions. However, there is evidence that birds in the tropics use wind changes as a cue^{48,50,51}. According to Richardson⁵¹, variations in numbers of birds aloft from day to day are correlated with daily weather. For example, most migration occurs with following winds, while rain may decrease migration^{11,13,15,34,37,46,51} or even cause

birds to change direction^{1,14,25,27,28,49,51}. When a cold front moves over the northern part of the Gulf, trans-Gulf migrants encounter clouds, rain, and opposing winds that may cause considerable mortality^{5,16,24,32,61}.

Mean annual rainfall influences the overall abundance of wintering Neotropical migrants. The effects of drought, fire, and insect outbreaks⁵³ are often interrelated. In the Caribbean there is evidence that drier areas have lower numbers of individual birds^{4,53,59,64}. Some individuals may die of water stress, effects of water scarcity on food availability and habitat suitability^{17,53,57}. Insect outbreaks may have the obvious benefit of increasing food availability, but may have the negative impact of excessive tree mortality decreasing overall habitat suitability for some species. Subsequent pesticide applications can also have deleterious effects. Fire also changes landscapes, and may have adverse effects on some species while enhancing habitat for others^{53,63}.

There are data that suggest—without certainty—that ENSO events result in lower breeding populations of Neotropical migrants²². In a census of migrants in several areas of the Great Smoky Mountains²² in 1982 (before an ENSO event) and 1983 (after ENSO) migrants decreased in 1983 while permanent residents exhibited only random differences in numbers. In the mountains of West Virginia, a study involving censuses every five years discovered abnormally low populations of Neotropical migrants in 1958 and 1973. Those years were later recognised as summers following ENSO events²². According to Hall *et al.*²², permanent resident species in North America or those that winter in the south-east USA appear unaffected, providing further evidence that ENSO's effects are most likely to occur on the wintering grounds.

As stated above, weight declines and degradation of pectoral muscles have been found in Neotropical resident birds subjected to El Niño-related weather anomalies²². Hall *et al.*²² considered that the same stresses should occur in wintering migrants, possibly resulting in increased mortality. On migration, weather strongly affects food availability and energy requirements of migratory birds, sometimes resulting in starvation in adverse conditions⁵¹. Energy reserves are important to spring migrants in high latitudes as they must often arrive early in relation to seasonal progression for sufficient time to breed successfully. These reserves must often sustain them for days or weeks^{3,23,54}.

Weather patterns greatly affect the seasonal movements of migratory birds and unusual weather patterns have—unsurprisingly—spawned many records of vagrant birds during ENSO years. For example, anomalous weather conditions due to El Niño may have contributed to a 1992 incursion of seven species of vagrant wood warbler (Parulidae)

and vireos (Vireonidae) in California⁴⁰. On the Galápagos archipelago, unusually heavy rains and high winds during October 1982–July 1983 contributed to the occurrence of several unexpected species in that period. An Eared Dove *Zenaida auriculata*, as many as three Rose-breasted Grosbeaks *Phaeucticus ludovicianus*, and a single Eastern Kingbird *Tyrannus tyrannus* were all first records for the islands. Other species that have occurred only, or principally, during ENSO events are Blackpoll Warbler *Dendroica striata*, Cedar Waxwing *Bombicilla cedrorum*, Purple Gallinule *Porphyrio martinica* and Common Nighthawk *Chordeiles minor*. Conditions associated with ENSO may disrupt migration routes or wintering ranges and contribute to the dislocation of such species.

Conclusions

In a study using Breeding Bird Survey data to assess responses of many species to spatial and temporal changes in environmental conditions, Taper *et al.*⁵⁸ concluded that bird species respond to these changes in a very individualistic fashion. Two similar species may respond to the same changes in a very different way, as each species has its own unique niche and is affected differently by a combination of biotic and abiotic factors. These differences among species are evident in the data presented here. The implication is that generalisations across and even within taxa are difficult to make as evident in the varying responses of closely related seabirds to the same environmental perturbations. Many of the data presented here demonstrate some type of negative effect on the bird species illustrated, e.g. increased mortality or decreased fecundity. It is probably true that drastic weather changes typically have a negative effect as birds are forced to respond to less than optimal environmental conditions for foraging, raising young, or migrating. However, in many regions increased food supplies due to these conditions may have a positive effect on fecundity and survival—as exhibited in the four-fold increase in two species of finch on the Galápagos Islands. The only consistent trend obvious from my perusal of the literature is that changes in food abundance due to anomalous weather conditions have some effect—positive or negative—on many species of bird. It appears that ‘this is one of those subjects... forever doomed to the netherworld of correlation, rather than being approachable by manipulation’ (T. C. Grubb, pers. comm.).

We are only now beginning to understand the basics of the El Niño phenomenon. As predictions of its occurrence become more timely, future researchers should be able to prepare adequate tests of its effects on organisms. Particularly interesting would be studies on wide-ranging species whose populations may be subjected to different

environmental conditions in different geographic regions. Also a review of past long-term census and fecundity studies should be undertaken to discover patterns that would have been overlooked before the El Niño’s importance was recognised a short time ago. Biologists must be aware that ENSO conditions can drastically affect both marine and terrestrial species and must be accounted for in their studies^{22,31,55}.

Acknowledgements

The original draft of this paper was written at the end of my career as a student at the Ohio State University. At OSU I would like to thank John Condit and Paul Doherty for all of their advice during my years there. I would especially like to thank my advisor, Thomas C. Grubb, for overseeing this project and his helpful comments on the original draft. It was after I arrived at the Lamanai Field Research Center (LFRC) that I rewrote and honed this paper into its final form. At the LFRC I would like to thank directors Mark & Monique Howells for allowing me the time away from my normal research schedule to finish this paper. This is ornithology contribution number 3 of the Lamanai Field Research Center.

References

1. Able, K. P. (1972) Fall migration in coastal Louisiana and the evolution of migration patterns in the Gulf region. *Wilson Bull.* 84: 231–242.
2. Anderson, D. J. (1989) Differential responses of boobies and other seabirds in the Galapagos, North Pacific Ocean to the 1986–87 El Niño–Southern Oscillation Event. *Marine Ecology—Progress Ser.* 52: 209–216.
3. Ankney, C. D. (1977) Feeding and digestive organ size in breeding Lesser Snow Geese. *Auk* 94: 275–282.
4. Askins, R. A., Ewert, D. N. & Norton, R. L. (1992) Abundance of wintering migrants in fragmented and continuous forests in the U.S. Virgin Islands. In Hagen, J. M. & Johnson, D. W. (eds) *Ecology and conservation of Neotropical migrant landbirds*. Washington, DC: Smithsonian Institution Press.
5. Bullis, H. R. (1954) Trans-gulf migration, spring 1952. *Auk* 71: 298–305.
6. Canby, T. Y. (1984) El Niño’s ill wind. *National Geographic* 165: 144–183.
7. Clark, L., Schreiber, R. W. & Schreiber, E. A. (1990) Pre- and post- El Niño Southern Oscillation comparison of nest sites for Red-tailed Tropicbirds breeding in the central Pacific Ocean. *Condor* 92: 886–896.
8. Cruz, J. B. & Cruz, F. (1990) Effect of El Niño–Southern Oscillation conditions on nestling

- growth rate in the Dark-rumped Petrel. *Condor* 92: 160–165.
9. Cruz, F. & Cruz, J. (1985) The effect of El Niño on the breeding of the Dark-rumped Petrel on Cerro Pajas, Floreana. In Robinson, G. & del Pino, E. M. (eds) *El Niño in the Galápagos Islands: the 1982–1983 event*. Quito: Charles Darwin Foundation for the Galápagos Islands.
 10. Curry, R. L. & Stoleson, S. H. (1988) New bird records from the Galápagos associated with the El Niño–Southern Oscillation. *Condor* 90: 505–507.
 11. Curtis, S. G. (1969) Spring migration and weather at Madison, Wisconsin. *Wilson Bull.* 81: 235–245.
 12. Davidson, D. (1977) Species diversity and community organization in desert seed eating ants. *Ecol.* 58: 711–724.
 13. Devlin, J. M. (1954) Effects of weather on nocturnal migration as seen from one observation point in Philadelphia. *Wilson Bull.* 66: 93–101.
 14. Eastwood, E. (1967) *Radar ornithology*. London, UK: Methuen.
 15. Forsyth, B. J. & James, D. (1971) Springtime movements of transient nocturnally migrating landbirds in the Gulf coastal bend region of Texas. *Condor* 73: 193–207.
 16. Gauthreaux, S. A. (1971) A radar and direct visual study of passerine spring migration in southern Louisiana. *Auk* 88: 343–365.
 17. George, T. L., Fowler, A. C., Knight, R. L. & McEwen, L. C. (1992) Impacts of severe drought on grassland birds in western North Dakota. *Ecol. Appl.* 2: 275–284.
 18. Gibbs, H. L. & Grant, P. R. (1987) Ecological consequences of an exceptionally strong El Niño event on Darwin's Finches. *Ecology* 68: 1735–1746.
 19. Grant, B. R. & Grant, P. R. (1993) Evolution of Darwin's finches caused by a rare climatic event. *Proc. Royal Soc. London Ser B: Biol. Sci.* 251 (1331): 111–117.
 20. Gunn, J. (1991) Influences of various forcing variables on global energy balance during the period of intensive instrumental observation, 1958–1987, and their implications for paleoclimate. *Climatic Change* 19: 393–420.
 21. Haase, B. (1997) The impact of El Niño Southern Oscillation (ENSO) on birds: update from Ecuador 1997. *Cotinga* 8: 64–65.
 22. Hall, G. A., Gibbs, H. L., Grant, P. R., Botsford, L. W. & Butcher, G. S. (1988) Effects of El Niño–Southern Oscillation (ENSO) on terrestrial birds. *Proc. International Orn. Congr.* 19: 1759–1775.
 23. Irving, L. (1972) *Arctic life of birds and mammals including man*. New York: Springer Verlag.
 24. James, P. (1956) Destruction of warblers on Padre Island, Texas in May 1951. *Wilson Bull.* 68: 224–227.
 25. Jögi, A. I. (1961) Zug von Wasservögeln und Wetterlage. *Vogelwarte* 22: 306.
 26. Karr, J. R., Robinson, S. K., Blake, J. G. & Bierregaard, R. O. (1990) The avifauna of Barro Colorado Island and the Pipeline Road, Panama. In Gentry, A. (ed.) *Four Neotropical rainforests*. New Haven: Yale University Press.
 27. Lack, D. (1959) Migration across the North Sea studied by radar. Part 1. Survey through the year. *Ibis* 101: 209–234.
 28. Lack, D. (1960) Migration across the North Sea studied by radar. Part 2. The spring departure 1956–1959. *Ibis* 102: 26–57.
 29. Lack, D. (1960) The influence of weather on passerine migration. A review. *Auk* 77: 171–209.
 30. Lieth, H. (1973) Primary productivity in ecosystems: comparative analysis of global patterns. In Lieth, H. (ed.) *Patterns of primary productivity in the biosphere. Benchmark Papers in Ecology*, 8. Stroudsburg: Dowden, Hutchinson & Ross.
 31. Lindsey, G. D., Pratt, T. K., Reynolds, M. H. & Jacobi, J. D. (1997) Response of six species of Hawaiian forest birds to a 1991–1992 El Niño drought. *Wilson Bull.* 109: 339–343.
 32. Lowery, G. H. (1945) Trans-gulf spring migration of birds and the coastal hiatus. *Wilson Bull.* 57: 92–121.
 33. Ludwig, J. (1986) Primary production variability in desert ecosystems. In Whitford, W. (ed.) *Pattern and process in desert ecosystems*. Albuquerque: University of New Mexico Press.
 34. Lyuleeva, D. S. (1973) Features of swallow biology during migration. In Bykhovskii, B. E. (ed.) *Bird migration: ecological and physiological factors*. New York: Halsted-Wiley.
 35. Miskelly, C. M. (1990) Effects of 1982–1983 El Niño event on two endemic landbirds on the Snares Islands, New Zealand. *Emu* 90: 24–27.
 36. Nicholls, N. (1991) The El Niño/Southern Oscillation and Australian vegetation. *Vegetation* 91: 23–36.
 37. Nisbet, I. C. T., Evans, P. R. & Feeny, P. P. (1961) Migration from Morocco into southwest Spain in relation to weather. *Ibis* 103: 349–372.
 38. Noy-Meir, I. (1981) Spatial effects in modeling of arid ecosystems. In Goodall, D. & Perry, R. (eds.) *Arid-land ecosystems: structure, functioning, and management*, 2. Cambridge, UK: Cambridge University Press.
 39. Noy-Meir, I. (1985) Desert ecosystem structure and function. In Evenari, M. (ed.) *Hot deserts and arid shrublands*. Amsterdam: Elsevier.

40. Patten, M. A. & Marantz, C. A. (1996) Implications of vagrant southeastern vireos and warblers in California. *Auk* 113: 911–923.
41. Pettit, T. N., Byrd, G. V., Whittow, G. C. & Seki, M. P. (1984) Growth of the Wedge-tailed Shearwater in the Hawaiian Islands. *Auk* 101: 103–109.
42. Polis, G. A. (1991) Desert communities: an overview of patterns and processes. In Polis, G. A. (ed.) *The ecology of desert communities*. Tucson: University of Arizona Press.
43. Polis, G. A., & Farley, R. D. (1979) Characteristics and environmental determinants of natality, growth, and maturity in a natural population of the desert scorpion, *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). *J. Zool.* 187: 517–542.
44. Polis, G. A., Hurd, S. D., Jackson, C. T. & Piñero, F. S. (1997) El Niño effects on the dynamics and control of an arid island ecosystem in the Gulf of California. *Ecol.* 78: 1884–1897.
45. Quinn, W. H., Zopf, D. O., Short, K. S. & Kuo Yang, R. T. W. (1978) Historical trends and statistics of the Southern Oscillation, El Niño, and Indonesian droughts. *Fishery Bull.* 76: 663–678.
46. Rappe, A. (1964) Notes sur le passage nocturne des grives en Belgique. *Gerfaut* 54: 338–361.
47. Ribic, C. A., Ainley, D. G. & Spear, L. (1992) Effects of El Niño and La Niña on seabird assemblages in the equatorial Pacific. *Marine Ecology—Progress Ser.* 80: 109–124.
48. Richardson, W. J. (1974) Spring migration over Puerto Rico and the western Atlantic, a radar study. *Ibis* 116: 172–193.
49. Richardson, W. J. (1975) Bird migration over southeastern Canada, the western Atlantic, and Puerto Rico: a radar study. Ph.D. thesis. Ithaca, NY: Cornell University.
50. Richardson, W. J. (1976) Autumn migration over Puerto Rico and the western Atlantic, a radar study. *Ibis* 118: 309–332.
51. Richardson, W. J. (1978) Timing and amount of bird migration in relation to weather: a review. *Oikos* 30: 224–272.
52. Rosenzweig, M. L. (1968) Net primary productivity of terrestrial communities: predictions from climatological data. *Am. Naturalist* 102: 67–74.
53. Rotenberry, J. T., Cooper, R. J., Wunderle, J. M. & Smith, K. G. (1992) Incorporating effects of natural disturbances in managed ecosystems. In *Status and management of Neotropical migratory birds*. USDA Forest Service Gen. Tech. Rep. RM-229.
54. Ryder, J. P. (1971) Spring bird phenology at Karrak Lake, Northwest Territories. *Can. Field Nat.* 85: 181–183.
55. Schreiber, R. W. & Schreiber, E. A. (1984) Central Pacific seabirds and the El Niño Southern Oscillation: 1982 to 1983 perspectives. *Science* 225: 713–716.
56. Scott, P. E. & Martin, R. F. (1986) Clutch size and fledging success in the Turquoise-browed Motmot. *Auk* 103: 8–13.
57. Smith, K. G. (1982) Drought-induced changes in avian community structure along a montane sere. *Ecol.* 63: 952–961.
58. Taper, M. L., Böhning-Gaese, K. & Brown, J. H. (1995) Individualistic responses of bird species to environmental change. *Oecologia* 101: 478–486.
59. Terborgh, J. W. & Faaborg, J. R. (1980) Factors affecting the distribution and abundance of North American migrants in the eastern Caribbean region. In Keast, A. & Morton, E. S. (eds.) *Migrant birds in the neotropics: ecology, behavior, distribution, and conservation*. Washington, DC: Smithsonian Institution Press.
60. Valle, C. A., Cruz, F., Cruz, J. B., Merlen, G. & Coulter, M. C. (1987) The impact of the El Niño–Southern Oscillation on seabirds in the Galapagos Islands, Ecuador. *J. Geophys. Res.* 92: 14437–14444.
61. Webster, F. S. (1966) South Texas region. *Audubon Field Notes* 20: 525–532.
62. Webster, P. J. & Palmer, T. N. (1997) The past and future of El Niño. *Nature* 390: 562–564.
63. Wright, H. A. & Bailey, A. W. (1982) *Fire ecology*. New York: John Wiley & Sons.
64. Wunderle, J. M. & Waide, R. B. (1992) Distribution of overwintering Nearctic migrants in the Bahamas and Greater Antilles. Report to World Wildlife Fund-US.

Marcus C. England

Lamanai Field Research Center, P.O. Box 63, Orange Walk, Belize. E-mail: lamanai@btl.net.