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EL NIÑO EFFECTS ON AVIAN ECOLOGY: LESSONS LEARNED FROM THE SOUTHEASTERN PACIFIC

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Resumen. – Efectos de El Niño sobre ecología de aves: lecciones aprendidas en el Pacífico suroriental. – A través de una revisión de la literatura proveniente del borde suroriental de la cuenca del Pacífico, intento identificar qué aspectos de El Niño determinan la disponibilidad de recursos (alimento y hábitat) que a su vez afectan la ecología de las aves. La evidencia muestra que El Niño afecta a las aves marinas esencialmente al reducir su base alimentaria. Las aves marinas comedoras de peces y de peces + calamares generalmente decrecen en abundancia poblacional, posiblemente como resultado combinado de la mortalidad de adultos (hambruna) y de la falla reproductiva. Las aves marinas omnívoras sobreviven los períodos El Niño sin declinaciones importantes, mientras que aquellas que incluyen desechos pesqueros en sus dietas muestran cambios mínimos o inclusive incrementan sus poblaciones durante tales períodos. Las aves acuáticas parecen beneficiarse de la precipitación que acompaña a El Niño, la cual agranda sus hábitat (cuerpos acuáticos). El hábitat incrementado provee mayores oportunidades para instalar nidos adecuados y para obtener alimento suficiente. Finalmente, las aves terrestres son afectadas por las precipitaciones asociadas a El Niño, las que desencadenan la productividad primaria (biomasa aérea de plantas y banco de semillas), la cual a su vez permite incrementos en artrópodos y mamíferos. Las aves granívoras reaccionan rápidamente a los incrementos en semillas, mientras que las insectívoras responden de manera similar a la abundancia de artrópodos. Las aves carnívoras toman algo más de tiempo en reaccionar a los incrementos en poblaciones de mamíferos. Mis conclusiones son que: (a) La escasez de alimento puede ser un factor clave para las poblaciones de aves, pero sus efectos dependen de la amplitud de dieta, alternancia de presas, y parámetros de historia de vida; (b) Los patrones de productividad predecibles (estacionales) pueden determinar la distribución y abundancia de aves residentes, mientras que las variaciones impuestas por ocurrencias impredecibles de El Niño y La Niña pueden determinar la presencia y abundancia de aves migratorias; (c) La dicotomía El Niño versus La Niña u otros años "normales" puede ser artificial; (d) Los estudios de largo plazo son necesarios para entender la conexión entre el clima y las aves.

Abstract. – Through a literature review from the southeastern fringe of the Pacific Basin, I attempt to identify what aspects of El Niño determine the availability of resources (food and habitat) that in turn affect avian ecology. The evidence shows that El Niño affects seabirds essentially by reducing their food base. Fish- and fish + squid-eating seabirds generally decrease their population abundance, likely as a combined result of adult mortality (famine) and reproductive failure. Omnivorous seabirds negotiate El Niño periods without important declines, while those including fishery wastes in their diets show minimal changes or even increase their populations during such periods. Waterbirds seem to benefit from precipitation that accompanies El Niño, which enlarges their habitats (waterbodies). Increased habitat affords more opportunities for installing adequate nests and obtaining enough food. Finally, landbirds are affected by El Niño-driven precipitation, which fires up primary productivity (aboveground plant biomass and seed crop), which in turn fuels arthropod and mammal increases. Granivorous birds react promptly to peaks in seed output, while insectivores respond similarly to arthropod abundance. Carnivorous birds take somewhat longer to react to increases in mammal populations. I conclude that (a) Food shortage may be an important key factor for bird populations, but its effects depend on diet breadth, prey switching, and life history parameters; (b) Predictable (seasonal) patterns of productivity may determine distribution and abundance of resident birds, but variations imposed by unpredictable occurrences of El Niño and La Niña may determine the presence and abundance of migratory birds; (c) The dichotomy El Niño versus La Niña or other "normal" years may be artificial; (d) Long-term monitoring is needed to understand the connection between climate and birds. *Accepted 9 December 2003.*

Key words: El Niño, La Niña, effects, seabirds, waterbirds, landbirds, food resources.

INTRODUCTION

There is a large and disperse body of literature reporting that El Niño affects different aspects of avian ecology, ranging from individual to population and community aspects. Most of the evidence is anecdotal, qualitative or correlational at the most, with few attempts to relate emerging patterns to underlying causes (see recent reviews by England 2000, Jaksic 2001, Jaksic *et al.* ms.). A pioneer exception was the publication of the proceedings of the "Symposium on birds and the El Niño Southern Oscillation" (Schreiber & Schreiber 1988), which concentrated on El Niño 1982. That symposium was meant to encourage ornithologists to carry out long-term studies that could shed light on the interactions between global atmospheric cycles, oceanographic phenomena, and avian populations. But ornithologists did not follow the advice. Most of the blame may be placed on the fact that the following El Niño's were much weaker and less spectacular than that of 1982. Indeed, those of 1986 and 1991 practically failed to elicit interest from ornithologists. Only with the advent of the strong El Niño of 1997 there was a renewed effort on trying to understand this phenomenon with regard to birds (Jaksic *et al.* ms.). Here, I intend to provide a short synthesis on the putative effects of El Niño on birds, through a review of accumulated evidence. I attempt to disentangle what aspects of El Niño determine the availability of food and habitat resources that in turn affect avian ecology in the southeastern Pacific.

METHODS

I concentrated my literature search in the southeastern fringe of the Pacific Basin, an area with which I am more familiar and where most of the known effects of El Niño on birds come from. I searched the primary literature for quantitative, or at least categorical, data on bird abundance, mortality and reproduction, in connection with fluctuations in prey and habitat resources. The literature sources and specific methods used may be found in Jaksic *et al.* (ms.) I recognized three functional bird types: seabirds, waterbirds, and landbirds, regardless of systematic affinities. With regard to seabirds, I analyzed semi-quantitative information in 10 studies on the effects of El Niño on abundance and reproduction of seabird populations in four areas of the South Pacific Ocean (Jaksic *et al.* ms.). I characterized the diet of 41 seabird species. By summing abundance and reproductive effects, either negative or positive or neutral, one arrives at a single total effect of El Niño for each of the 41 seabird species. For waterbirds, the amount of information available was so limited that there was no need to use screening or summary procedures. For landbirds, I further divided this category among granivorous, insectivorous and carnivorous birds, and obtained as much quantitative information as feasible. Most of these data are unpublished results from this author.

RESULTS

Seabirds

There is an extensive body of literature on these birds. I chose not to cite specific papers in this section, because a detailed analysis of such literature is being published elsewhere (Jaksic *et al.* ms.). Below is a summary of my findings.

Effects on migration, abundance & distribution of seabirds. Massive migrations of resident seabirds away from equatorial waters occur during El Niño events. Distributions of seabirds shift with movements of their preferred water types: During El Niño events, cool-water species become less abundant, and warm-water species more abundant. Species normally not present appear in extra-tropical areas.

Effects on mortality & reproduction of seabirds. Mortality of guano birds as a result of El Niño is well known. During El Niño, large numbers of dead and dying birds are observed throughout the eastern Pacific. The absence of, or the decrease in, adults attempting to nest during El Niño results in a lower reproductive output for eastern Pacific seabirds. Species show smaller clutch size, reduced chick size and lower survival.

Effects of food web structure & rainfall regime on seabirds. Migration and mortality of seabird populations could be associated with alterations of the marine food web, while changes in reproduction could be related to increased rainfall. Changes in the marine food web involve a replacement of primary producers – from dinoflagellates to diatoms –, and of primary consumers – from copepods to chaetognaths –. This in turn produces the migration to deeper water of the main secondary consumers – anchovies and sardines –, the preferred prey of seabirds. Hence follow massive migrations and die-offs of seabirds. Concurrent changes such as a higher plant cover due to increased rainfall, and flooding of seabird reproductive grounds due to increased sea level, are also important causes of reproductive failures.

Effects of fisheries on seabirds. Due to their dependence on anchovies, which usually disappear during El Niño, seabirds are highly sensible to the occurrence of this event. Overfishing has led to a dramatic reduction in catches of anchovies. Because of this, the fishery switched to sardines in Peru and to horse mackerel in Chile. The recovery rate of seabirds after El Niño events has been getting increasingly slower. A possible explanation for this phenomenon is that the anchovy fishery took up the superabundance of food on which the seabirds depended.

Trophic ecological effects on seabirds. Seabird diets consist mainly of three prey types: Fishes, crustaceans, and mollusks. The problem of finding enough food to survive and reproduce is solved in three ways. Coastal or inshore seabirds, such as gulls and terns, gather to feed in areas where prey are abundant or where they are forced to the surface. Diving seabirds, including penguins and alcids, exploit a greater range of depths to obtain food. Pelagic species, such as albatrosses and shearwaters, soar over vast expanses of the ocean in search of widely dispersed surface prey. During periods of reduced food availability, such as El Niño years, seabirds may be forced to switch their diet. Seabirds with a restricted dietary range and with no chances to effect prey switching, suffer important reproductive failures. Seabirds with a broad dietary range and with abilities to perform prey switching, may display no changes in reproduction and survival.

With regard to my own analyses of ten studies reporting data on 41 seabird species, a summary follows (see Table 1 and Fig. 1). The

TABLE 1. Dietary composition and similarity (clusters, see text for explanation) of seabird species in four localities of the southeastern Pacific Ocean affected by El Niño 1982-83. Main prey: 1 = Zooplankton, 2 = Fish larvae, 3 = Sandworms, 4 = Crustaceans, 5 = Octopi, 6 = Squid, 7 = Eel, 8 = Fish, 9 = Seabirds, 10 = Turtles, 11 = Sealion wastes, 12 = Fishery wastes.

Seabirds and clusters	1	2	3	4	5	6	7	8	9	10	11	12
Cluster 1												
Waved Albatross (*Diomedea irrorata*)				X		X		X				
Dark-rumped Petrel (*Pterodroma phaeopygia*)				X		X		X				
Wedge-rumped Storm-petrel (*Oceanites tethys*)				X		X		X				
Great Frigatebird (*Fregata minor*)				X		X		X				X
Frigatebird (*Fregata* sp.)				X		X		X				X
Swallow-tailed Gull (*Creagrus furcatus*)						X		X				
Red-tailed Tropicbird (*Phaethon rubricauda*)						X		X				
Red-footed Booby (*Sula sula*)						X		X				
Red-billed Tropicbird (*Phaethon aethereus*)						X		X				
Peruvian Booby (*Sula variegata*)						X		X				
Lesser Frigatebird (*Fregata ariel*)						X		X				
Humboldt Penguin (*Spheniscus humboldti*)						X		X				
Band-rumped Storm-petrel (*Oceanodroma castro*)						X		X				
Cluster 2												
Pelican (*Pelecanus* sp.)								X				
Masked Booby (*Sula dactylatra*)								X				
Guanay Cormorant (*Phalacrocorax bougainvillii*)								X				
Cormorant (*Phalacrocorax* sp.)								X				
Brown Pelican (*Pelecanus occidentalis*)								X				
Brown Noddy (*Anous stolidus*)								X				
Blue-footed Booby (*Sula nebouxii*)								X				
Black Noddy (*Anous tenuirostris*)								X				
White-throated Storm-petrel (*Nesofregetta albigularis*)								X				
White Tern (*Gygis alba*)								X				
Red-legged Cormorant (*Phalacrocorax gaimardi*)								X				
Peruvian Pelican (*Pelecanus occidentalis thagus*)								X				
Cluster 3												
Brown Booby (*Sula leucogaster*)		X				X		X				
Audubon's Shearwater (*Puffinus lherminieri*)		X		X		X		X				
Sooty Tern (*Sterna fuscata*)		X						X				
Christmas Shearwater (*Puffinus nativitatis*)		X						X				
Wedge-tailed Shearwater (*Puffinus pacificus*)		X						X				
Cluster 4												
Inca Tern (*Larosterna inca*)				X				X				
Galapagos Penguin (*Spheniscus mendiculus*)				X				X				
Gray-backed Tern (*Sterna lunata*)		X		X				X				
Storm-Petrel (*Oceanites* sp.)				X				X				X
Gull (*Larus* sp.)				X	X			X				X
White-vented Storm-petrel (*Oceanites gracilis*)				X				X				
Cluster 5 (singular species)												
Flightless Cormorant (*Nannopterum harrisi*)					X		X	X				

TABLE 1. Continuation.

Seabirds and clusters	1	2	3	4	5	6	7	8	9	10	11	12
Magnificent Frigatebird (*Fregata magnificens*)				X		X		X	X	X	X	X
Lava Gull (*Larus fuliginosus*)			X					X			X	X
Phoenix Petrel (*Pterodroma alba*)		X		X	X							
Northern Phalarope (*Lobipes lobatus*)	X	X		X								

most numerous trophic or dietary group (cluster 1) was composed of seabirds feeding on fishes and squid. A second group (cluster 2) was made up of seabirds feeding strictly on fishes. A third group (cluster 3) was composed of seabirds that fed on fishes and fish larvae, and a fourth group (cluster 4) by seabirds feeding on crustaceans and fishery wastes. The remaining five species showed diverse and peculiar diets sharing low similarity. By averaging species information for each dietary group one finds that the five

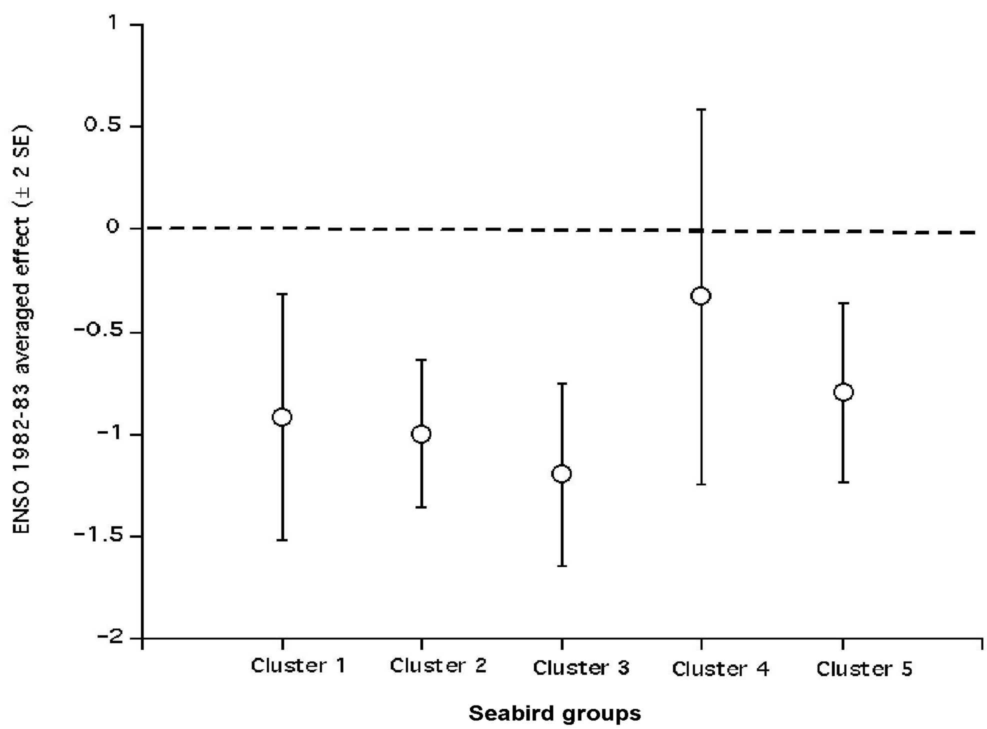

FIG. 1. Averaged effects of El Niño 1982–1983 on seabird species of the southeastern Pacific Ocean. Cluster 1 is composed of 13 seabird species feeding on fishes, squid, crustaceans and sea lion's wastes. Cluster 2 is formed by 12 species feeding strictly on fishes. Cluster 3 is composed of five species that feed on fishes, fish larvae, squid and crustaceans. Cluster 4 is formed by six species feeding on fishes, crustaceans, fish-larvae, octopi, fishery and sea lion wastes. Cluster 5 is composed of five species with diverse and peculiar diets.

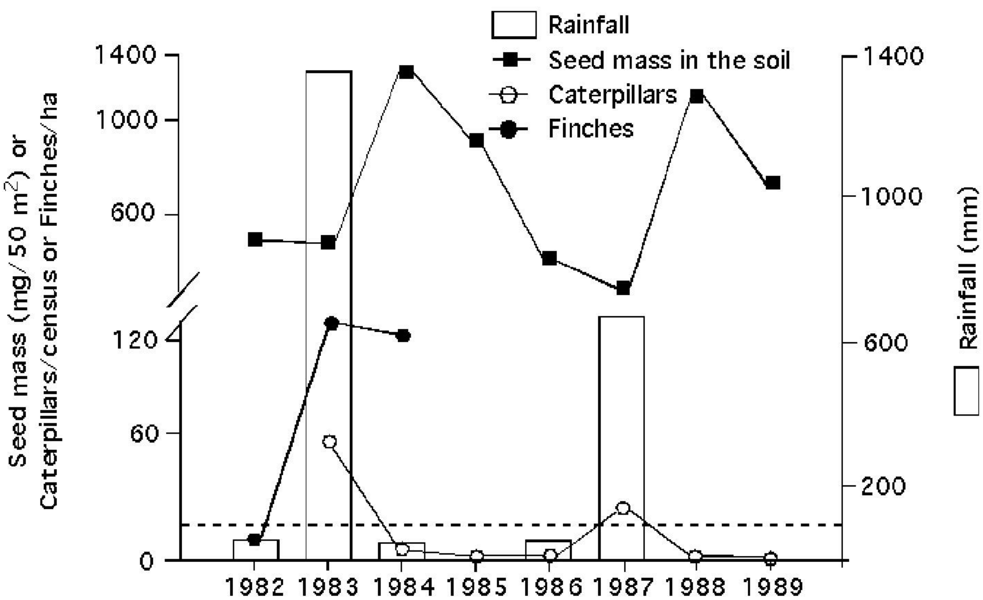

FIG. 2. Yearly course of finch abundance (1982–1989), total seed biomass (1982–1984) and caterpillar abundance (1983–1989), together with rainfall (1982–1989) in Daphne Island, Galapagos Archipelago. Mean annual rainfall is shown as dashed line. El Niño events occurred in 1983 and 1987.

groups were negatively affected by El Niño, but to different extents (Fig. 1). The most affected group was cluster 3 composed by seabirds with a diet based mainly on fish and fish larvae. Slightly less affected were species in clusters 1 and 2, feeding chiefly on fishes and squid. Less affected were species in cluster 5, which fed on a variety of different prey. Finally, there was a group little affected (cluster 4) and even with positive effects for some species, which had in common consumption of crustaceans as well as fishery wastes. In sum, my analyses show that seabirds with a narrow diet are the most affected by El Niño, while species with a broader diet are less affected. In addition, it appears that the inclusion of fishery wastes in the diet alleviates the shortage of food. Seabirds with the ability to switch and use this food type are practically not affected by El Niño.

Waterbirds

For waterbirds, the amount of information available was very limited, and thus I cited below all that was relevant.

Habitat & food effects on waterbirds. The distribution and area of wetlands are highly variable and depend importantly on climate conditions, especially rainfall. Vilina & Cofre (2000) analyzed the seasonal abundance four grebe species in a central Chilean wetland. They found a positive correlation between spring abundance of these species and total rainfall the previous year. Rain fell chiefly during the winter and spring of El Niño year; grebe populations increased during the summer, and peaked in the spring following El Niño. Vilina *et al.* (2002) analyzed the relationship between El Niño, rainfall, and changes in abundance, breeding and local distribution of the Black-necked Swan (*Cygnus melanocorypha*) in a central

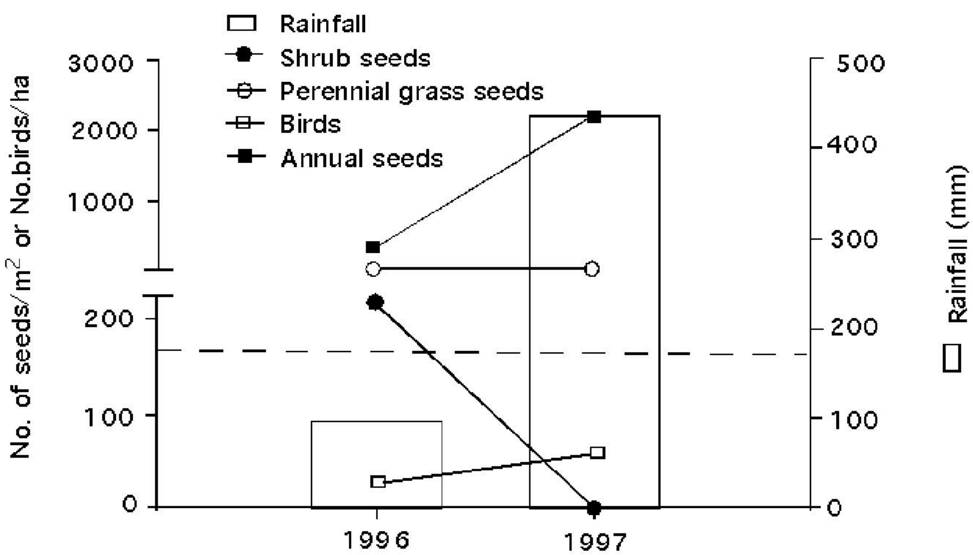

FIG. 3. Yearly course of bird abundance, seed abundance of different types, together with rainfall (1996–1997), in Auco, northern Chile. Mean annual rainfall is shown as dashed line. An El Niño event occurred in 1997.

Chilean wetland. During and after El Niño event, swans increased in abundance, breeding success, and time of permanence. Schlatter *et al.* (2002) showed that Black-necked Swan populations in a wetland of southern Chile more than doubled during La Niña period. They hypothesized that due to migrations from northern wetlands, populations in the south peaked during dry years associated with La Niña. In sum, waterbirds benefit from precipitation that accompanies El Niño, which enlarges the water surface of marshes, coastal lagoons, and other water bodies. Apparently, increased habitat affords more opportunities for installing adequate nests and obtaining sufficient food.

Landbirds

Although there is not a lot of literature on these birds, I preferred not to cite specific papers in this section, because of my detailed analysis being published elsewhere (Jaksic *et al.* ms.). Below is a summary of my findings.

Contrasting effects on landbirds. Landbirds are affected by El Niño in two contrasting ways: Negatively, because when El Niño arrives, excessive precipitation may result in nesting failure and increased chick mortality due to nest flooding, thus lowering reproductive success. On the other hand, El Niño-driven precipitation fires up primary productivity (plant biomass and seed crop), which in turn fuels insect and mammal increases, thus positively affecting bird populations.

Ambiguous effects on granivorous birds. In Daphne Island, Ecuador (Fig. 2), seed abundance peaked with El Niño of 1983, and decreased slightly thereafter. Finches peaked one year after the rainfall and seed peak, subsequently declined, and again peaked with 1-year lag after the high-rainfall year brought by El Niño 1987. In Auco, semiarid Chile (Fig. 3), the increased rainfall brought by El Niño 1997 resulted in an immediate increase in annual grass seeds, in a lack of response in perennial

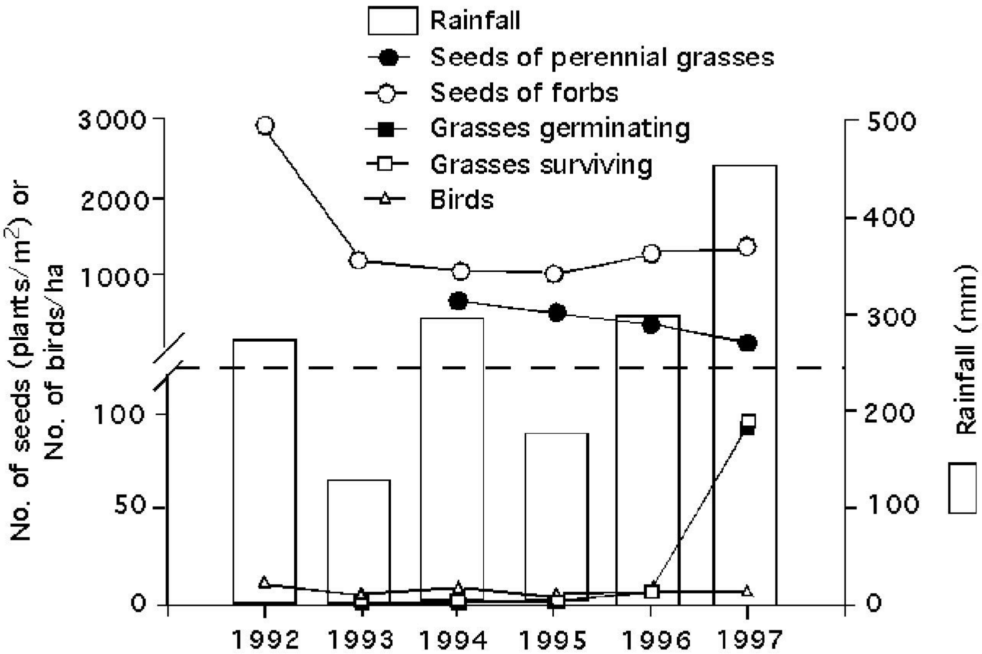

FIG. 4. Yearly course of bird abundance, seed abundance of different types, seed germination and survival, together with rainfall (1993–1997), in Ñacuñan, western Argentina. Mean annual rainfall is shown as dashed line. An El Niño event occurred in 1997.

grass seeds, and in a decrease in shrub seeds. Granivorous birds increased in abundance from 26 to 58/ha – by 123% A similar phenomenon was described in Fray Jorge, semiarid Chile, where the increased rainfall brought by El Niño 1991 resulted in an immediate increase in annual grass seeds, a slower one in perennial grass seeds, a 1-year delayed increase in geophyte seeds, and a decrease in shrub seeds. Unfortunately, no tally was kept of granivorous bird abundance. In Ñacuñan, Monte desert of Argentina (Fig. 4), El Niño 1997 brought increased precipitation. Higher rainfall did not elicit a response from the part of perennial grasses or forbs, but there was a marked increase in seed germination and survivorship. Nevertheless, bird abundance remained flat. In sum, the response of granivorous birds to peaks in seed output is suggestive. Both in Daphne Island and in Auco there was a positive response. In Ñacuñan there was no increase in seed crop to which the birds could respond. The best database, that from Fray Jorge, failed at recording bird abundance and thus did not contribute to make a better case for the coupling between seeds and birds.

Suggestive effects on insectivorous birds. In Daphne Island, Ecuador (Fig. 2), caterpillar abundance was high during El Niño of 1983, and decreased thereafter until El Niño 1987, which resulted in another caterpillar peak. Unfortunately, the tally kept for bird abundance considered only finches, which are chiefly granivorous (but feed caterpillars to their nestlings). In Auco, semiarid Chile (Fig. 5), insect and insectivorous bird populations

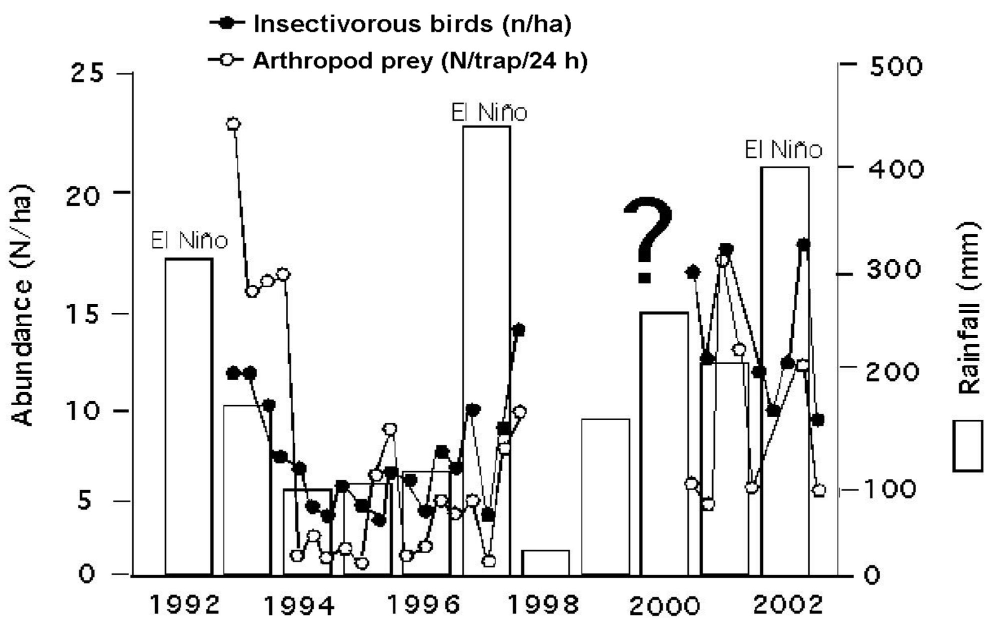

FIG. 5. Seasonal course of the abundance of insectivorous birds and arthropod prey, together with yearly rainfall (1992–2002) in Auco, northern Chile. ? = No animal data are available 1998–2000. During winter and spring 2002 arthropods could not be sampled. Yearly rainfall corresponds to precipitation accumulated from autumn (March) to summer the following year (February). El Niño events occurred in 1992, 1997, 2002.

were declining since the last El Niño of 1991 until the increased rainfall brought by El Niño 1997 resulted in a simultaneous increase in insect and bird abundance. Unfortunately, the monitoring data covering the following three years disappeared, and thus the response of insects and birds to El Niño 2002 was obscured by the lack of preceding background. Nevertheless, a plot of insectivorous bird abundance against insect abundance yielded a good fit to a curve of diminishing returns (Jaksic *et al.* ms). The functional response of insectivorous birds was steep at the start, but tended to saturate quickly, apparently reaching toward an asymptote. In sum, the response of insectivorous birds to peaks in insects is suggestive, but marred by lack of consistent monitoring.

Clear effects on carnivorous birds. In Auco, semiarid Chile (Fig. 6), mammal and carnivorous bird populations were declining since El Niño 1991 until increased rainfall brought by El Niño 1997 resulted in a simultaneous increase in mammal and bird abundances. As I said before, raptor census data covering the following three years disappeared, but still the response of mammals and birds to El Niño 2002 is suggestive enough. Indeed, a plot of carnivorous bird abundance against mammal abundance (Jaksic *et al.* ms.) yielded a good fit to a curve of diminishing returns. Same as with insectivores, the functional response of carnivorous birds was steep at the start, but tended to saturate quickly, clearly reaching an asymptote. In this case, there is no ambiguity in the response of carnivorous birds to their prey resources, although the missing

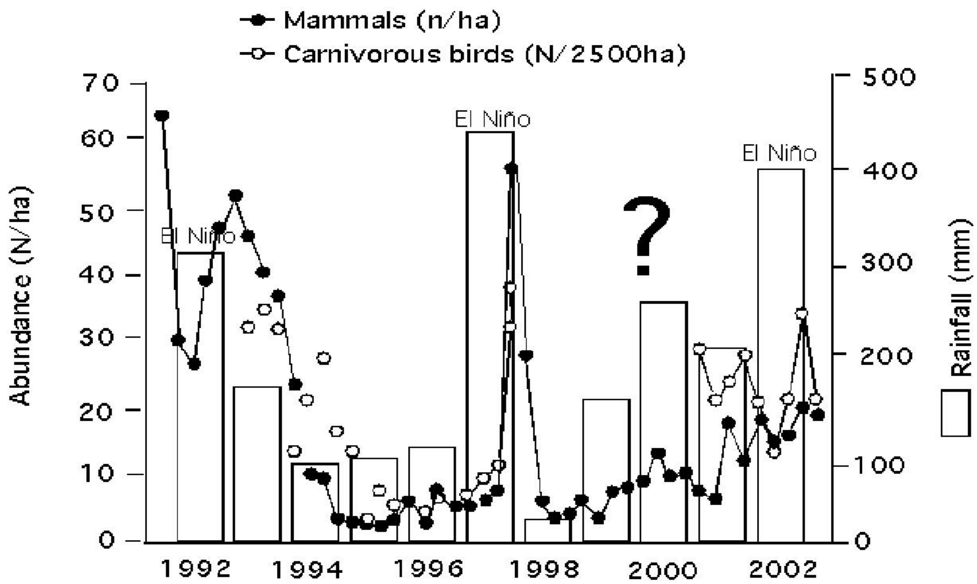

FIG. 6. Seasonal course of the abundance of carnivorous birds and mammal prey, together with yearly rainfall (1992–2002) in Auco, northern Chile. Bird sampling started in winter 1993. ? = No bird data are available 1998–2000. Yearly rainfall corresponds to precipitation accumulated from autumn (March) to summer the following year (February). El Niño events occurred in 1992, 1997, 2002.

three years of data dent an otherwise great picture.

DISCUSSION

There are four major conclusions that may be developed from the findings that I reported (Jaksic *et al.* ms.).

Effects of El Niño depend on bird diet. Based chiefly on information reported for the 1982 and 1997 events, it may be concluded that the primary effects of El Niño on seabirds are related with both lowered primary productivity in the marine food web and with the effects of rain and runoffs on seabird nesting grounds. No specific mechanisms have been proposed to explain the interaction between oceanographic and atmospheric anomalies with seabird population changes. My analyses show that food shortage may be an important cause but that its net effects depend on seabird diet breadth and prey switching. In terms of reproduction, it has been proposed that the rapid changes in primary productivity occurring during and after El Niño events could be an important selective factor for breeding biology and life history patterns of seabirds. Common patterns among species with rapid recoveries after El Niño are: large clutch sizes, high growth rates, and early reproductive ages. Luna-Jorquera *et al.* (2003) showed that seabird assemblages along the Humboldt Current system are dominated by species with these characteristics. It could then be predicted that landbirds showing rapid responses to abrupt increases in primary productivity, should display similar life history aspects in diet breadth, prey switching, clutch size, and age at maturity.

El Niño imposes unpredictability to bird assemblage. The structure of bird assemblages may be determined by basal levels of primary productivity, but also by the predictable (seasonal) and unpredictable (ENSO) fluctuations of that variable. Hurlbert & Haskell (2003) showed that basal levels of primary productivity determine resident species richness, while the range of predictable variation (or seasonality) of this variable determines migrant species richness. The approach of Hurlbert & Haskell could be used in the search of general mechanisms for ENSO effects in both terrestrial and marine bird assemblages. It could be that superimposed on seasonally predictable changes of productivity, the range of variation imposed by unpredictable but rather frequent occurrences of El Niño and La Niña determine geographic distribution and population abundance of the birds living in areas affected by these anomalies.

El Niño and La Niña are extremes of a wide range of variability. The occurrence and magnitude of El Niño are declared after some pre-defined threshold is reached, according to atmospheric or oceanographic indices such as sea surface temperature and southern oscillation index. Nevertheless, physical fluctuations (anomalies) are continuously occurring at different time scales. These anomalies are usually treated as departures from normality, where normal conditions represent either climatic means or non El Niño/La Niña conditions. Thus, normality is not treated as a real phenomenon but as the absence of extreme conditions. However, El Niño/La Niña thresholds encompass a wide range of real physical fluctuations that may have effects on bird assemblage attributes. In addition, there appears to be a weak correlation between the magnitude of El Niño/La Niña events as measured by physical indices, and the magnitude of recorded biological effects. Therefore, physical and biological dynamics do not have a direct coupling, and thus environmental signals may be filtered by terrestrial and marine communities in such a way that they may resist some El Niño/La Niña events regardless of their magnitude.

The need for long-term time series. Finally, it seems obvious that without good baseline data we are doomed to be surprised by the arrival of El Niño every few years. Even when ornithologists are at hand to take advantage of an incoming El Niño, lack of preceding data, and of monitoring afterwards, makes it difficult to understand responses of birds to the successive El Niño, La Niña, and normal years. Indeed, during the last century there were 12 El Niño years and 12 La Niña years, thus leaving about 76 normal years in between (Jaksic 2001). Thus, by heavily concentrating attention on only 12% of the time span (El Niño), and of neglecting another 12% (La Niña), we are essentially ignoring what happens during 76% of the time. This situation may be remedied only as long as data are logged on a continuous basis, that is, as long-term time series.

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