Studies in Avian Biology No. 35:1–99

FORAGING DYNAMICS OF SEABIRDS IN THE EASTERN TROPICAL PACIFIC OCEAN

Larry B. Spear, David G. Ainley, and William A. Walker

Abstract. During a 9-yr period, 1983–1991, we studied the feeding ecology of the marine avifauna of the eastern tropical Pacific Ocean (ETP), defined here as pelagic waters from the coast of the Americas to 170° W and within 20° of the Equator. This is one of few studies of the diet of an entire marine avifauna, including resident breeders and non-breeders as well as passage migrants, and is the first such study for the tropical ocean, which comprises 40% of the Earth's surface. During spring and autumn, while participating in cruises to define the dynamics of equatorial marine climate and its effects on the seabird community, we collected 2,076 specimens representing, on the basis of at-sea surveys, the 30 most-abundant ETP avian species (hereafter; ETP avifauna). These samples contained 10,374 prey, which, using fish otoliths and cephalopod beaks, and whole non-cephalopod invertebrates, were identified to the most specific possible taxon.

The prey mass consumed by the ETP avifauna consisted of 82.5% fishes (57% by number), 17.0% cephalopods (27% by number), and 0.3% non-cephalopod invertebrates (16% by number). Fish were the predominant prey of procellariiforms and larids, but pelecaniforms consumed about equal proportions of fish and cephalopods. Based on behavior observed during at-sea surveys, the ETP avifauna sorted into two groups—15 species that generally fed solitarily and 15 species that generally fed in multispecies flocks. Otherwise, the avifauna used a combination of four feeding strategies: (1) association with surface-feeding piscine predators (primarily tuna [*Thunnus* and *Euthynnus* spp.]), (2) nocturnal feeding on diel, vertically migrating mesopelagic prey, (3) scavenging dead cephalopods, and (4) feeding diurnally on non-cephalopod invertebrates (e.g., scyphozoans, mollusks, crustaceans, and insects) and fish eggs. Because of differential use of the four strategies, diets of the two seabird groups differed; the solitary group obtained most of its prey while feeding nocturnally, primarily on mesopelagic fishes (myctophids, bregmacerotids, diretmids, and melamphaids), and flocking species fed primarily on flying fish (exocoetids and hemirhamphids) and ommastrephid squid (*Sthenoteuthis oualaniensis*) caught when feeding diurnally in association with tuna. Many of the smaller species of solitary feeders, particularly storm-petrels, small gadly petrels and terns, supplemented their diets appreciably by feeding diurnally on epipelagic non-cephalopod invertebrates and by scavenging dead cephalopods. Flock-feeding procellariiforms also supplemented their diet by feeding nocturnally on the same mesopelagic fishes taken by the solitary species, as well as by scavenging dead cephalopods. Some spatial and temporal differences in diet were apparent among different species.

An analysis of otolith condition in relation to hour of day that birds were collected showed that procellariiform species caught mesopelagic fishes primarily between 2000 and 2400 H. Selection of these fishes by size indicates that they occurred at the surface in groups, rather than solitarily. Solitary avian feeders had greater diet diversity than flock-feeders, particularly pelecaniforms. Appreciable diet overlap existed among the solitary and flock-feeding groups. Diet partitioning was evident within each feeding group, primarily exercised by using different feeding strategies and through selection of prey by species and size: larger birds ate larger prey. We classified five of the predominant ETP species, Sooty Shearwater (*Puffinus griseus*), White-necked Petrel (*Pterodroma cervicalis*), Murphy's Petrel (*Pterodroma ultima*), Stejneger's Petrel (*Pterodroma longirostris*), and Parasitic Jaeger (*Stercorarius parasiticus*), as migrants; based on stomach fullness, these species fed less often than the residents and were more opportunistic, using each of the four feeding strategies.

Using generalized additive models and at-sea survey data, we estimated that the ETP avifauna consisted of about 32,000,000 birds (range 28.5–35 million) with a biomass of 8,405 mt (metric tonnes). They consumed about 1,700 mt of food per day. Flock-feeding species were most consistent in choice of foraging strategy. Considering the contribution of each of the four feeding strategies, 78% of prey were obtained when feeding in association with aquatic predators, 14% when feeding nocturnally, and 4% each when scavenging dead cephalopods or feeding diurnally on non-cephalopod invertebrates and fish eggs. Results underscored two important groups of fishes in the ETP upper food web—tunas and vertically migrating mesopelagic fishes. Compared to an analogous study of a polar (Antarctic) marine avifauna that found little prey partitioning, partitioning among the ETP avifauna was dramatic as a function of sex, body size, feeding behavior, habitat and species. In the polar system, partitioning was only by habitat and behavior (foraging depth). The more extensive partitioning, as well as more diverse diets, in the tropics likely was related to much lower prey availability than encountered by polar seabirds. The importance of the association between seabirds and a top-piscine predator in the tropical system was emphasized by its absence in the polar system, affecting the behavior, morphology and diet of ETP seabirds. Further investigation of this association is important for the successful management of the tropical Pacific Ocean ecosystem.

Key Words: cephalopod, diet partitioning, feeding behavior, foraging ecology, myctophid, seabirds, trophic partitioning, tropical ocean, tuna.

DINÁMICAS DE FORRAJE DE AVES MARINAS EN EL ESTE TROPICAL DEL OCÉANO PACÍFICO

Resumen. Durante un período de 9 años, 1983–1991, estudiamos la ecología de alimentación de la avifauna marina del este tropical del océano pacífico (ETP), definida en el presente como aguas pelágicas de la costa de las Américas, 70° W, dentro los 20° del Ecuador. El presente estudio es uno de los pocos sobre la dieta de una avifauna marina entera, incluyendo residentes reproductores y no reproductores, como también migrantes pasajeros; también es el primer estudio de este tipo para el océano tropical, el cual comprende el 40% de la superficie terrestre. Durante la primavera y el otoño, mientras participábamos en cruceros para definir las dinámicas climáticas marinas ecauatorianas y sus efectos en comunidades de aves marinas, colectamos 2,076 especimenes representando estos, basándonos en muestreos de mar, las 30 especies más abundantes del ETP (de aquí en delante; ETP avifauna). Estas muestras contenían 10,374 presas, las cuales, fueron identificadas utilizando otolitos de peces y picos de cefalópodos, e invertebrados completos no cefalópodos fueron identificados al taxa menor posible.

La masa consumida de presa por avifauna ETP consistió de 82.5% peces (57% por número), 17.0% cefalópodos (27% por número), y 0.3% invertebrados no cefalópodos (16% por número). Peces fueron la presa predominante de los Procelariformes y láridos, pero los Pelicaniformes consumieron casi las mismas proporciones de peces y cefalópodos. Con base en el comportamiento observado durante los muestreos de mar, la avifauna ETP se clasificó en dos grupos—15 especies que generalmente se alimentaron solitariamente y 15 especies que generalmente se alimentaban en multitudes de multiespecies. De no ser así, la avifauna utilizó una combinación de cuatro estrategias alimenticias: (1) asociación con depredadores de piscina de alimentación de superficie (primordialmente atún [*Thunnus* and *Euthynnus* spp.]), (2) alimentación nocturna en ciclo regular diario, presa mesopelágica migratoria verticalmente, (3) barrer cefalópodos muertos, y (4) alimentación diurna de invertebrados no cefalópodos (ej., scyphozoanos, moluscos, crustáceos, e insectos) y huevos de peces. Debido a los diferentes usos de las cuatro estrategias, las dietas de dos grupos de aves marinas difirieron; el grupo solitario obtuvo la mayoría de sus presas mientras se alimentaba nocturnamente, principalmente de peces mesopelágicos (mictófidos, bregmacerotidos, diretmidos, y melamfaidos), mientras especies de multitud se alimentaron primordialmente de peces voladores (exocoetidos y hemirhamfidos) y calamar ommastrefido (*Sthenoteuthis oualaniensis*) atrapado durante la alimentación diurna asociada al atún. Muchas de las especies pequeñas solitarias de alimento, particularmente paiños y gaviotas, suplementaron notablemente sus dietas por la alimentación diurna de invertebrados no cefalópodos epipelágicos y por barrer cefalópodos muertos. Procelariformes de alimentación en multitud también suplieron su dieta por alimentación nocturna de los mismos peces mesopelágicos tomados por las especies solitarias, como también por barrer cefalópodos muertos. Algunas diferencias espaciales y temporales en la dieta fueron evidentes en las diferentes especies.

Un análisis de condiciones otolitícas que relacionó la hora del día en que las aves fueron colectadas demostró que las especies procelariformes capturaron peces mesopelágicos principalmente entre 2000 y 2400 H. La selección por tamaño de estos peces indica que ellos aparecen en la superficie en grupos, en vez de solitariamente. Aves que se alimentan solitariamente, tienen una mayor diversidad de dieta que las que se alimentan en multitud, particularmente Pelecaniformes. Existe un evidente traslape en la dieta entre los grupos solitarios y de multitud. La repartición de dieta fue evidente dentro de cada grupo alimenticio, sobre todo al utilizar diferentes estrategias de alimentación y a través de la selección de presa por especie y tamaño: aves más grandes comieron presas más grandes. Clasificamos cinco de las especies ETP predominantes, Pardela gris (*Puffinus griseus*), Petrel, cuello blanco(*Pterodroma cervicalis*), Petrel (*Pterodroma ultima*), Petrel de stejneger (*Pterodroma longirostris*) y Salteador parásito (*Stercorarius parasiticus*), como migratorias; basado en lo lleno del estómago, estas especies se alimentan menos a menudo que las residentes y fueron más oportunísticas, utilizando cada una de las cuatro estrategias alimenticias.

Utilizando modelos aditivos generalizados y datos de muestreos de mar, estimamos que la avifauna ETP consistió de cerca de 32,000,000 aves (rango 28.5–35 millón) con una biomasa de 8,405 tm (toneladas métricas). Consumieron cerca de 1,700 tm de alimento por día. Especies que se alimentan en multitud fueron más consistentes al elegir la estrategia de forraje. Considerando la contribución de cada una de las cuatro estrategias, el 78% de las presas fueron obtenidas al alimentarse con asociación de depredadores acuáticos, 14% al alimentarse nocturnamente, y 4% cuando barrían cefalópodos muertos o se alimentaban durante el día de invertebrados no cefalópodos y huevos de peces. Los resultados resaltaron a dos grupos importantes de peces en la cadena alimenticia más alta de ETP—atunes y peces mesopelágicos verticalmente migratorios. Comparado a un estudio análogo de avifauna marina polar (Antártica) que encontró poca repartición de presa, la repartición entre la avifauna ETP fue dramática como función de sexo, tamaño del cuerpo, comportamiento alimenticio, hábitat, y especies. En el sistema polar, la repartición fue solamente por hábitat y comportamiento (profundidad de forraje). La repartición más extensiva, como dietas más diversas, estaba probablemente relacionado a la disponibilidad mucho más baja de presa, de la encontrada en aves marinas polares. La importancia de la asociación entre aves marinas y depredadores de tope de piscina en el sistema tropical se enfatizó por su ausencia en el sistema polar, afectando el comportamiento, morfología y dieta de aves marinas ETP. Mayor información de dicha asociación es importante para el manejo exitoso de ecosistemas tropicales del Océano Pacífico.

Understanding the factors that affect community organization among seabirds requires detailed information on inter- and intraspecific differences in diet and foraging behavior to define trophic niches and their overlap (Ashmole 1971, Duffy and Jackson 1986). Several studies have examined the diets of entire marine avifaunas during the breeding season at colonies located on a specific group of islands: three tropical (Ashmole and Ashmole 1967, Diamond 1983, Harrison et al. 1983), two temperate (Pearson 1968, Ainley and Boekelheide 1990), and three polar (Belopol'skii 1957, Croxall and Prince 1980, Schneider and Hunt 1984). These studies have provided considerable information on choice of prey fed to nestlings. However, they provided little information on: (1) diet during the remainder of the annual cycle, (2) diet of the non-breeding component of the community, (3) factors that affect prey availability and how these affect diet, or (4) the methods and diel patterns by which seabirds catch prey. Given the logistical difficulties involved in at-sea studies in order to obtain such information, it is not surprising that few of these broader studies have been conducted (Baltz and Morejohn 1977, Ainley et al. 1984, Ainley et al. 1992); those that have have been completed in temperate or polar waters.

Only three studies, as noted above, have been concerned with diet partitioning among seabird communities in the tropics (between 20° N and 20° S), despite the fact that tropical waters cover about 40% of the Earth's surface. Furthermore, none of these studies have considered the highly pelagic component of seabird communities that is not constrained to remain within foraging range of breeding colonies. The results presented herein are the first to examine diets in a tropical, open-ocean avifauna, in this case occupying the 25,000,000 km^2 expanse of the eastern tropical Pacific (ETP) and defined here as pelagic waters within 20° of the Equator and from the Americas to 170° W.

Two factors that characterize pelagic waters, as opposed to coastal, neritic waters, have a major effect on the structure of seabird avifaunas and the strategies used by component species to exploit them (Ballance et al. 1997). The first is the relatively greater patchiness of potential prey over the immense expanses of these oceans (Ainley and Boekelheide 1983, Hunt 1990). These conditions require that tropical seabirds, especially, possess energy-efficient flight to allow them to search for and find food (Ainley 1977, Flint and Nagy 1984, Ballance 1993, Ballance et al. 1997, Spear and Ainley 1997a, Weimirskirch et al. 2004). Another important factor is the minimal structural complexity of the open ocean compared to coastal, neritic areas (McGowan and Walker 1993) and polar waters (Ainley et al. 1992). In regard to the tropics, the intense vertical and horizontal gradients, e.g., water-mass and water-type boundaries and other frontal features that serve to concentrate prey in somewhat predictable locations (Hunt 1988, 1990, Spear et al. 2001) are widely dispersed. For one thing, no tidal fronts or currents occur in the open ocean, which often provide a micro- to meso-scale complexity to coastal waters. The primary frontal feature in the ETP is the Equatorial Front, a boundary on the order of 200 km wide between the South Equatorial Current and the North Equatorial Countercurrent (Murphy and Shomura 1972, Spear et al. 2001; Fig. 1). A second important physical gradient, the thermocline, exists on a vertical scale. This feature has an important effect on the distribution of tuna (*Thunnus*, *Euthynnus* spp.; Murphy and Shomura 1972, Brill et al. 1999), which in turn are important in chasing seabird prey to near the surface (Au and Pitman 1986, Ballance and Pitman 1999).

In fact, the tropical ocean, especially that of the ETP, has the most intense gradients of any ocean area due to the fact that surface waters are very warm but waters as cold as those of subpolar areas lie beneath at less distance than the height of the tallest of trees on continents (Longhurst and Pauly 1987). This water upwells along the equatorial front, bringing a high degree of spatial complexity to mid-ocean surface waters. This complexity and the increased productivity affect the occurrence of seabirds and the prey available to them at multiple spatial scales (Ballance et al. 1997, Spear and Ainley 2007).

Because morphology of tropical seabirds is adapted for efficient flight in order to search large areas for food, nearly all tropical seabirds are able to obtain prey only within a few meters of the ocean surface. This is a result of their large wings, which are not well suited for diving more than a few meters subsurface. In fact, tropical seabirds use four foraging strategies, in part affected by their flight capabilities (Ainley 1977, Imber et al. 1992, Ballance et al.