Rivera, J., and R. F. Thomson. 2026. From generalist to specialist? Diet shift in the Gray Gull (*Leucophaeus modestus*) outside its Atacama breeding range. Journal of Field Ornithology 97(3):6. https://doi.org/10.5751/JFO-00882-970306

Avian Behavior, Ecology, and Evolution

From generalist to specialist? Diet shift in the Gray Gull (*Leucophaeus modestus*) outside its Atacama breeding range

¿De generalista a especialista? Cambio de dieta en la Gaviota Gris (*Leucophaeus modestus*) fuera de su rango reproductivo en Atacama

Javier Rivera [1] and *Roberto F. Thomson* [2]

ABSTRACT. The Gray Gull (*Leucophaeus modestus*) is a unique seabird that breeds primarily in the Atacama Desert of northern Chile but forages in highly productive coastal ecosystems. Although its diet has been described for breeding populations, little is known about the trophic ecology of birds occurring outside the breeding range. We analyzed 75 regurgitated pellets collected from three sandy beaches in central Chile during the austral summer to evaluate whether Gray Gulls maintain the broad marine diet described for breeding populations or instead concentrate on the dominant prey available in sandy-beach ecosystems. *Emerita analoga* occurred in every analyzed pellet and was the only prey taxon recorded at all three study sites. More than half of the pellets from every locality, and all pellets from Mantagua, contained exclusively *E. analoga*, while fish remains were absent from all samples. Terrestrial arthropods occurred only occasionally and always together with *E. analoga*. These findings reveal a marked contrast with the diverse marine diet previously reported for breeding populations and indicate a strong reliance on a single intertidal prey among Gray Gulls occurring outside the breeding range during the austral summer. The remarkable consistency of this trophic pattern across geographically separated sites suggests that specialization on surf-zone mole crabs characterizes Gray Gulls using central Chilean sandy beaches during this period. Our results highlight the importance of sandy beaches as key foraging habitats for Gray Gulls outside the Atacama Desert breeding range and emphasize the role of local prey availability in shaping trophic specialization.

RESUMEN. La Gaviota Gris (*Leucophaeus modestus*) es un ave marina única que se reproduce primariamente en el Desierto de Atacama del norte de Chile, pero forrajea en ecosistemas costales altamente productivos. Aunque su dieta ha sido descrita para poblaciones reproductoras, poco se sabe sobre la ecología trófica de aves que ocurren fuera de su rango reproductivo. Analizamos 75 egagrópilas colectadas de tres playas arenosas en Chile central durante el verano austral, para evaluar si las Gaviotas Grises mantienen la amplia dieta marina descrita para poblaciones reproductoras o si en cambio, se concentran en las presas dominantes disponibles en ecosistemas de playas arenosas. *Emerita analoga* ocurrió en todas las egagrópilas analizadas y fue el único taxón presa registrado en los tres sitios de estudio. Más de la mitad de las egagrópilas de todas las localidades, y todas las egagrópilas de Mantagua, contenían exclusivamente *E. analoga*, mientras que los restos de peces se mantuvieron ausentes en todas las muestras. Los artrópodos terrestres ocurrieron solo ocasionalmente y siempre junto con *E. analoga*. Estos hallazgos revelan un contraste marcado con la diversa dieta marina reportada previamente para poblaciones reproductoras, e indican una dependencia fuerte en una sola presa intermareal entre las Gaviotas Grises que ocurren fuera del rango reproductivo durante el verano austral. La consistencia notable de este patrón trófico a lo largo de sitios separados geográficamente sugiere que la especialización en cangrejos topo de las zonas de rompiente caracteriza a las Gaviotas Grises que usan las playas arenosas de Chile central durante este periodo. Nuestros resultados resaltan la importancia de las playas arenosas como hábitats clave de forrajeo para las Gaviotas Grises fuera del rango reproductivo del Desierto de Atacama y enfatizan el rol de la disponibilidad local de presas en moldear la especialización trófica.

Key Words: *diet specialization; foraging ecology; pellet analysis; sandy beach ecosystems; surf zone*

INTRODUCTION

Seasonal dietary shifts are widespread in seabirds because energetic demands, prey availability, and the constraints imposed by central-place foraging change markedly across the annual cycle (Phillips et al. 2017). During reproduction, adults must satisfy the energetic demands of egg production and chick provisioning while remaining tied to breeding colonies, often resulting in diets that track breeding stage, prey availability, and short-term environmental variation (Howells et al. 2017). As these constraints change over the annual cycle, individuals may exploit a broader range of habitats and resources, frequently expanding or shifting their trophic niche (Cherel et al. 2007). Such dietary shifts may reflect both changes in predator requirements and seasonal turnover in prey communities. For example, seabird assemblages in the North Water Polynya shift their diets as energy flows from herbivorous zooplankton to higher trophic levels during the annual production cycle (Karnovsky et al. 2008). Consequently, seasonal changes in prey use are increasingly recognized as an important mechanism linking seabird ecology to ecosystem dynamics.

These patterns are particularly evident within the family Laridae, whose species span almost the entire continuum from trophic specialization to broad opportunism. Kelp Gulls (*Larus dominicanus*), for example, modify their diet throughout the breeding cycle, shifting from marine invertebrates during

[1]Pontificia Universidad Catolica de Valparaiso, [2]LEVS - Wildlife Ecology Lab, Universidad de Chile

incubation to a higher proportion of fish while provisioning chicks (Bertellotti and Yorio 1999). Outside the breeding period they often broaden their trophic niche by exploiting fisheries discards, refuse, and other anthropogenic food sources (Burgues et al. 2020). In contrast, the threatened Olrog's Gull (*Larus atlanticus*) remains highly specialized, feeding almost exclusively on crabs throughout the breeding season despite occurring sympatrically with the much more generalist Kelp Gull (Yorio et al. 2013). Together, these examples illustrate how annual-cycle stage, local prey availability, and environmental context interact to determine where populations lie along the generalist-specialist continuum.

The Gray Gull (*Leucophaeus modestus*) provides a particularly interesting case. Unlike any other gull, it breeds primarily in the hyper-arid Atacama Desert of northern Chile, often tens of kilometers inland (Howell et al. 1974, Aguilar et al. 2012), from where adults undertake nocturnal commuting flights to forage in the productive waters of the Humboldt Current (Howell et al. 1974, Catoni et al. 2021). This remarkable breeding strategy has selected for extreme physiological adaptations associated with desert nesting, including reduced eggshell water-vapor conductance and strict thermal constraints during embryonic development (Guerra et al. 1988, Aguilar et al. 1998). During the austral summer, however, large numbers of Gray Gulls also occur along the Pacific coast from Ecuador to southern Chile, outside the Atacama Desert breeding range. These birds are generally assumed to represent individuals that are not breeding, although their reproductive status is rarely known. Recent observations demonstrate that breeding outside the Atacama Desert, while exceptional, can occur in south-central Chile (Thomson et al., in press), indicating that reproductive status cannot be inferred solely from geographic location.

Despite this unusual life history, the trophic ecology of the Gray Gull has been studied almost exclusively at its northern breeding grounds, where the diet includes fish, crustaceans, and other marine invertebrates associated with the Humboldt Current system (Howell et al. 1974, Luna-Jorquera et al. 2003). Much less is known about the diet of Gray Gulls occurring outside the breeding range, particularly in central Chile, where large flocks regularly use sandy beaches during the austral summer. These beaches are physically dynamic ecosystems characterized by strong hydrodynamic forcing, relatively simple food webs, and macrofaunal communities dominated by a few abundant invertebrates, especially the mole crab (also called sand flea) *Emerita analoga* (Hippidae), which can reach exceptionally high densities in the swash zone (Defeo and McLachlan 2005, 2011, Jaramillo et al. 2001, 2017, Brante et al. 2019). Although such environments provide abundant and predictable intertidal prey, Gray Gulls are highly mobile foragers capable of exploiting a wide variety of adjacent coastal habitats. Whether birds occurring outside the breeding range concentrate on these dominant beach resources or instead maintain the broader marine diet described for breeding populations remains unknown.

Based on information from breeding populations, we hypothesized that Gray Gulls occurring in central Chile during the austral summer would continue to exploit a diverse assemblage of marine prey, including fish and crustaceans. Alternatively, if local prey availability overrides seasonal carry-over in trophic behavior, individuals should concentrate on the dominant resources available within sandy-beach ecosystems. To evaluate these alternative expectations, we analyzed regurgitated pellets collected from three coastal sites differing in the degree of anthropogenic influence.

METHODS

Study sites

Fieldwork was conducted during the austral summer (December 2024–February 2025) at three sandy beaches in central Chile that supported large non-breeding flocks of Gray Gulls. The sites are visited monthly as part of ongoing monitoring programs of their associated estuarine ecosystems. From north to south these were: (i) Mantagua Beach (32°53′S, 71°31′W; Valparaíso Region), an extensive sandy beach with moderate recreational use related to tourism and residential development; (ii) the Maipo River mouth (33°37′S, 71°38′W; Santo Domingo, Valparaíso Region), adjacent to a highly urbanized watershed influenced by the metropolitan area of Santiago and nearby industrial activities; and (iii) Reloca estuary (35°44′S, 72°35′W; Maule Region), a low-disturbance site associated with a coastal wetland and small artisanal fishing village (Fig. 1).

Pellet collection

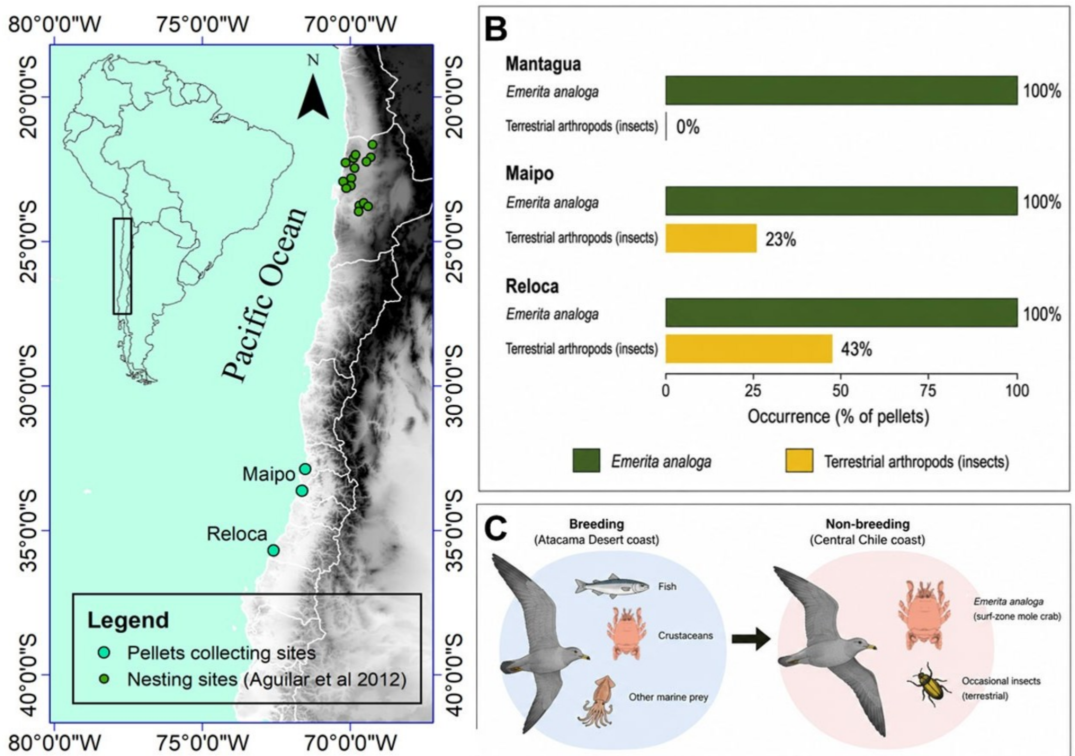
Pellets were collected opportunistically during a single visit to each study site when monospecific resting flocks of Gray Gulls were encountered. Before and during each collection event, flocks were observed with 10 × 42 binoculars to confirm species identity and ensure that no other gull species, particularly Kelp Gulls or Franklin's Gulls (*Leucophaeus pipixcan*), were present in the aggregation. Pellets were collected directly beneath the resting birds immediately after the flock departed. Only fresh, intact pellets, identified by their moist appearance, compact structure, dark coloration, and absence of weathering or fungal growth, were retained (cf. Bertellotti and Yorio 1999, Ludynia et al. 2005). A total of 25 pellets were collected at Mantagua, 22 at the Maipo River mouth, and 28 at Reloca (75 pellets in total). Pellets were individually stored in labeled plastic bags and transported to the laboratory for analysis.

Pellet processing and prey identification

Pellets were soaked in water and gently disaggregated in Petri dishes under a Leica S6E stereomicroscope (6.3–55× magnification). Prey remains were separated and identified to the lowest possible taxonomic level using preserved diagnostic structures. Marine prey was identified from exoskeletal fragments, chelipeds, pereiopods, antennal structures, otoliths, vertebrae, jaw elements, and other skeletal remains following Bertellotti and Yorio (1999) and Ludynia et al. (2005). Terrestrial arthropods were identified from mandibles, elytra, wings, antennae, legs, and other sclerotized structures using Artigas (1994) and comparison with reference specimens from the entomological collection of the Museum Room, Institute of Sciences, Curauma Campus, Pontificia Universidad Católica de Valparaíso.

Because most prey consisted of fragmented remains, the minimum number of individuals in each prey category was estimated using paired diagnostic structures following standard pellet-analysis procedures for Laridae (Bertellotti and Yorio 1999). For each pellet, both the occurrence (presence/absence) and the minimum number of individuals were recorded for every

Fig. 1. Seasonal trophic shift in Gray Gulls (*Leucophaeus modestus*) outside the breeding range. (A) Location of the three non-breeding sampling sites in central Chile relative to the Atacama Desert breeding range. (B) Frequency of occurrence of the principal prey categories in regurgitated pellets. (C) Conceptual summary illustrating the transition from a relatively broad marine diet during breeding to a highly specialized reliance on the surf-zone mole crab *Emerita analoga* during the non-breeding season.



prey category. Diet composition was summarized using two complementary metrics: (i) frequency of occurrence, expressed as the percentage of pellets containing each prey category, and (ii) relative abundance, calculated as the proportional contribution of each prey category to the total minimum number of prey individuals identified across all pellets. Anthropogenic items (e.g., plastic fragments, fishing line, and food packaging) were recorded separately but excluded from dietary analyses.

RESULTS

A total of 75 regurgitated pellets were analyzed across the three study sites. Remains of the mole crab *Emerita analoga* were detected in every pellet, making it the only prey taxon recorded at all localities (Table 1).

Diet composition was remarkably consistent among the three study sites. At Mantagua, all 25 analyzed pellets consisted exclusively of *E. analoga*. Similarly, most pellets from the Maipo River mouth (77%) and Reloca (57%) also contained only *E. analoga*. Whenever insects were detected, they always co-occurred with *E. analoga*; no pellet contained terrestrial arthropods in the absence of the mole crab.

Based on the minimum number of prey individuals identified, individual pellets generally contained between one and three *E. analoga*. Mean minimum numbers per pellet were highest at the Maipo River mouth (1.95 individuals/pellet), intermediate at Mantagua (1.36), and lowest at Reloca (1.18).

Terrestrial arthropods were recorded only at the Maipo River mouth and Reloca, occurring in 23% and 43% of pellets, respectively. Coleoptera was the dominant insect order and included representatives of the families Ptinidae, Carabidae, Staphylinidae, and Coccinellidae. Diptera (Ephydridae and Tipulidae) and Hymenoptera (Ichneumonidae and Apidae) were detected only occasionally. No fish remains were detected in any analyzed pellet.

Overall, Gray Gulls occurring along the coast of central Chile exhibited a remarkably consistent diet overwhelmingly dominated by a single intertidal crustacean, with terrestrial arthropods representing only a minor supplementary dietary component.

DISCUSSION

Our results reveal an exceptionally consistent trophic pattern in Gray Gulls occurring outside the Atacama Desert breeding range during the austral summer. *Emerita analoga* occurred in every analyzed pellet and was the only prey taxon recorded at all three study sites. Moreover, more than half of the pellets from every locality, and all pellets collected at Mantagua, contained exclusively *E. analoga*. This remarkable consistency among individuals and across geographically separated sites indicates that reliance on this surf-zone crustacean is not simply a local response to prey availability but appears to characterize Gray Gulls occupying central Chilean sandy beaches during this period of the annual cycle.

Table 1. Characteristics of regurgitated pellets collected from Gray Gulls (*Leucophaeus modestus*) at three sandy beaches in central Chile. Values indicate the number (percentage) of pellets containing each prey category and the mean minimum number of *Emerita analoga* individuals (MNI) per pellet (range).

Site	Pellets analyzed	Pellets containing *E. analoga*	Pellets containing insects	Pellets containing only *E. analoga*	*E. analoga* MNI per pellet (mean, range)
Mantagua	25	25 (100%)	0 (0%)	25 (100%)	1.36 (1–3)
Maipo	22	22 (100%)	5 (22.7%)	17 (77.3%)	1.95 (1–3)
Reloca	28	28 (100%)	12 (42.9%)	16 (57.1%)	1.18 (1–3)

The predominance of *E. analoga* is consistent with the ecological characteristics of exposed sandy beaches. Mole crabs are among the most abundant and predictable macroinvertebrates inhabiting the swash zone of the Humboldt Current coastline, where they can reach extremely high densities and constitute a major trophic resource for numerous predators (Jaramillo et al. 2000, Defeo and McLachlan 2005). Their high abundance, accessibility and spatial predictability likely make them an energetically profitable resource for Gray Gulls, favoring repeated exploitation of a single prey despite the species' capacity to forage across a broad range of coastal habitats. In contrast to the broader marine diet described for breeding populations in northern Chile, Gray Gulls occurring in central Chile during the austral summer appear to concentrate on the dominant prey available within sandy-beach ecosystems.

Terrestrial arthropods formed only a minor component of the diet and were recorded exclusively in Reloca and the Maipo River mouth. Importantly, insect remains always co-occurred with *E. analoga* and never replaced it as the dominant prey. This pattern suggests opportunistic exploitation of complementary food resources rather than a shift in feeding strategy. Sandy beaches receive substantial allochthonous inputs in the form of wrack and other organic material that support diverse assemblages of terrestrial and supralittoral arthropods (Dugan et al. 2003). The predominance of Coleoptera among the insects identified is consistent with these wrack-associated communities and suggests that Gray Gulls occasionally consume terrestrial prey while foraging along the upper beach or swash zone.

Interestingly, pellets from the Maipo River mouth contained the highest minimum number of *E. analoga* individuals per pellet. One possible explanation is that gulls at this site were feeding on smaller mole crabs, requiring more prey individuals to obtain similar energetic returns. Under such conditions, terrestrial arthropods stranded within the swash or deposited among beach wrack may be consumed incidentally during rapid foraging events. Although prey size was not measured in the present study, this hypothesis remains speculative and deserves further investigation.

Previous studies have identified *E. analoga* as an important prey of Gray Gulls in Peru and northern Chile (Howell et al. 1974). However, these studies were geographically restricted or largely descriptive. By quantifying pellet composition across multiple localities separated by several hundred kilometers, our study demonstrates that this trophic pattern is remarkably consistent among Gray Gulls occurring along much of the central Chilean coast during the austral summer. This finding places the Gray Gull toward the specialist end of the trophic continuum described for Laridae. Whereas Kelp Gulls typically exploit a wide variety of marine prey and readily incorporate fisheries discards and anthropogenic food subsidies (Bertellotti and Yorio 1999, Burgues et al. 2020), the Gray Gull closely resembles the specialized crab-based feeding strategy described for the threatened Olrog's Gull (Yorio et al. 2013). Although these species exploit different crustaceans and occupy distinct coastal environments, both illustrate how predictable and locally abundant prey can promote a high degree of trophic specialization within an otherwise predominantly generalist family.

The complete absence of fish remains also contrasts sharply with the diverse marine diet reported for breeding Gray Gulls in northern Chile (Howell et al. 1974, Luna-Jorquera et al. 2003), indicating marked differences in prey use between breeding populations and birds occurring outside the breeding range in central Chile. Several non-mutually exclusive mechanisms may contribute to this contrast. Breeding adults must obtain food not only for self-maintenance but also for chick provisioning, and prey may differ in energetic density, nutrient composition, digestibility, and ease of transport. In other gull species, the use of particular foraging habitats and prey types has been associated with breeding performance, and adults may deliver prey to chicks that differs from that used for self-feeding (O'Hanlon et al. 2017, Pais de Faria et al. 2021). These considerations may be especially relevant for Gray Gulls because inland breeding colonies require adults to transport food over long distances, whereas birds nesting at coastal colonies provision chicks more frequently (Simeone et al. 2022). Nevertheless, our data do not allow us to determine whether the observed dietary differences primarily reflect reproductive requirements, local prey availability, or differences in the composition of birds occurring outside the breeding range.

Because the birds sampled in central Chile were not individually marked, we cannot determine whether they represented failed breeders, adults that did not attempt reproduction during that year, or other segments of the population occurring outside the breeding range. Consequently, the dietary pattern described here should be interpreted as characterizing Gray Gulls occurring outside the Atacama Desert breeding range during the austral summer, rather than the trophic ecology of the species as a whole. Future studies integrating pellet analyses with stable-isotope approaches, prey availability assessments, individual marking, and direct observations of foraging behavior and chick provisioning would help distinguish among these alternative explanations and determine how trophic specialization varies among individuals throughout the annual cycle.

Author Contributions:

J.R. and R.F.T. conceived and designed the study. J.R. conducted the sample analyses and processed the data. J.R. and R.F.T. jointly wrote and revised the manuscript.

Acknowledgments:

We thank J. Ríos for assistance with laboratory sample analyses and M. A. Vukasovic for support during fieldwork. We are also grateful to the Wildlife Ecology Laboratory (LEVS) for providing equipment and materials for sample processing. We sincerely thank the Subject Editor and the anonymous reviewers for their constructive comments and thoughtful suggestions, which substantially improved the quality and clarity of this manuscript.

Data Availability:

The data supporting the findings of this study are available from the corresponding author upon reasonable request. No custom code was used in the analyses.

LITERATURE CITED

Aguilar, R., C. Guerra, L. C. Fitzpatrick, and G. Luna. 1998. Thermobiology of Gray Gull (*Larus modestus*) embryos and hatchlings: correlates of nesting in the Atacama Desert. Estudios Oceanológicos 17:7-12.

Aguilar, R., M. Perucci, T. Cisternas, M. Torres, M. Silva, A. Marín, A. Silva, and P. Bolados. 2012. La nidificación de la gaviota garuma y su vulnerabilidad a las actividades antrópicas en el Desierto de Atacama. Fondo de Protección Ambiental, Chile.

Artigas, J. N. 1994. Entomología económica. Insectos de interés agrícola, forestal, médico y veterinario (nativos, introducidos y susceptibles de ser introducidos). Ediciones Universidad de Concepción, Concepción, Chile.

Bertellotti, M., and P. Yorio. 1999. Spatial and temporal patterns in the diet of the Kelp Gull in Patagonia. Condor 101:790-798. https://doi.org/10.2307/1370066

Brante, A., G. Guzmán-Rendón, E. M. Barría, M. L. Guillemin, I. Vera-Escalona, and C. E. Hernández. 2019. Post-disturbance genetic changes: the impact of the 2010 mega-earthquake and tsunami on Chilean Sandy Beach fauna. Scientific Reports 9 (1):14239. https://doi.org/10.1038/s41598-019-50525-1

Burgues, M. F., J. Lenzi, E. Machín, L. Genta, and F. T. de Mello. 2020. Temporal variation of Kelp Gull's (*Larus dominicanus*) diet on a coastal island of the Río de la Plata estuary, Uruguay: refuse as an alternative food source. Waterbirds 43:65-74. https://doi.org/10.1675/063.043.0107

Catoni, C., R. Aguilar-Pulido, C. B. Zavalaga, and G. Dell'Omo. 2021. Radar reveals the nocturnal flights of breeding Grey Gulls *Leucophaeus modestus* in the Atacama Desert, Chile. Bird Study 68:351-358. https://doi.org/10.1080/00063657.2022.2092067

Cherel, Y., K. A. Hobson, C. Guinet, and C. Vanpé. 2007. Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. Journal of Animal Ecology 76:826-836. https://doi.org/10.1111/j.1365-2656.2007.01238.x

Defeo, O., and A. McLachlan. 2005. Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. Marine Ecology Progress Series 295:1-20. https://doi.org/10.3354/meps295001

Defeo, O., and A. McLachlan. 2011. Coupling between macrofauna community structure and beach type: a deconstructive meta-analysis. Marine Ecology Progress Series 433:29-41. https://doi.org/10.3354/meps09206

Dugan, J. E., D. M. Hubbard, M. D. McCrary, and M. O. Pierson. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuarine, Coastal and Shelf Science 58:25-40. https://doi.org/10.1016/S0272-7714(03)00045-3

Guerra, C., R. Aguilar, and L. C. Fitzpatrick. 1988. Water vapor conductance in Gray Gull (*Larus modestus*) eggs: adaptation to desert nesting. Colonial Waterbirds 11:107-109. https://doi.org/10.2307/1521176

Howell, T. R., B. Araya, and W. R. Millie. 1974. Breeding biology of the Gray Gull, *Larus modestus*. University of California Publications in Zoology 104:1-57.

Howells, R., S. J. Burthe, J. A. Green, M. P. Harris, M. Newell, A. Butler, D. Johns, E. Carnell, S. Wanless, and F. Daunt. 2017. From days to decades: short- and long-term variation in environmental conditions affect offspring diet composition of a marine top predator. Marine Ecology Progress Series 583:227-242. https://doi.org/10.3354/meps12343

Jaramillo, E., H. Contreras, C. Duarte, and P. Quijón. 2001. Relationships between community structure of the intertidal macroinfauna and sandy beach characteristics along the Chilean coast. Marine Ecology 22:323-342. https://doi.org/10.1046/j.1439-0485.2001.01752.x

Jaramillo, E., J. Dugan, and H. Contreras. 2000. Abundance, tidal movement, population structure and burrowing rate of *Emerita analoga* (Anomura, Hippidae) at a dissipative and a reflective sandy beach in south-central Chile. Marine Ecology 21:113-127. https://doi.org/10.1046/j.1439-0485.2000.00701.x

Jaramillo, E., J. E. Dugan, D. M. Hubbard, H. Contreras, C. Duarte, E. Acuña, and D. S. Schoeman. 2017. Macroscale patterns in body size of intertidal crustaceans provide insights on climate change effects. PLoS ONE 12:e0177116. https://doi.org/10.1371/journal.pone.0177116

Karnovsky, N., K. Hobson, S. J. Iverson, and G. L. Hunt. 2008. Seasonal changes in diets of seabirds in the North Water Polynya: a multiple-indicator approach. Marine Ecology Progress Series 357:291-299. https://doi.org/10.3354/meps07295

Ludynia, K., S. Garthe, and G. Luna-Jorquera. 2005. Seasonal and regional variation in the diet of the Kelp Gull in northern Chile. Waterbirds 28:359-365. https://doi.org/10.1675/1524-4695(2005)028[0359:SARVIT]2.0.CO;2

Luna-Jorquera, G., A. Simeone, and R. Aguilar. 2003. Ecofisiología de animales endotermos en un desierto cálido y un mar frío. Pages 297-316 in F. Bozinovic, editor. Fisiología ecológica y evolutiva. Ediciones Universidad Católica de Chile, Santiago, Chile.

O'Hanlon, N. J., R. A. McGill, and R. G. Nager. 2017. Increased use of intertidal resources benefits breeding success in a generalist gull species. Marine Ecology Progress Series 574:193-210. https://doi.org/10.3354/meps12189

Pais de Faria, J., P. T. Vaz, C. S. Lopes, J. G. Calado, J. M. Pereira, S. N. Veríssimo, V. H. Paiva, A. M. M. Gonçalves, J. A. Ramos. 2021. The importance of marine resources in the diet of urban gulls. Marine Ecology Progress Series 660:189-201. https://doi.org/10.3354/meps13599

Phillips, R., S. Lewis, J. González-Solís, and F. Daunt. 2017. Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. Marine Ecology Progress Series 578:117-150. https://doi.org/10.3354/meps12217

Simeone, A., C. B. Zavalaga, R. Aguilar-Pulido, and P. Arce. 2022. Comparative nest attendance and chick provisioning strategies in coastal and desert nesting Grey Gulls (*Leucophaeus modestus*) in northern Chile. Emu-Austral Ornithology 122:203-207. https://doi.org/10.1080/01584197.2022.2112400

Thomson, R. F., M. A. Vukasovic, J. Rodríguez, and C. F. Estades. In press. Breaking the desert rule: breeding of Grey Gulls (*Leucophaeus modestus*) in coastal south-central Chile. Marine Ornithology.

Yorio, P., C. Marinao, M. V. Retana, and N. M. Suárez. 2013. Differential use of food resources between the Kelp Gull *Larus dominicanus* and the threatened Olrog's Gull *Larus atlanticus*. Ardeola 60:29-44. https://doi.org/10.13157/arla.60.1.2012.29