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REPRODUCTIVE ECOLOGY OF WESTERN GULLS AND XANTUS' MURRELETS WITH RESPECT TO FOOD RESOURCES IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Western Gull (*Larus occidentalis*) and Xantus' Murrelet (*Endomychura hypoleuca*) reproduction on Santa Barbara Island, California, showed considerable sensitivity to changes in pelagic fish populations in the Southern California Bight. Western Gulls responded to decreases in the availability of schooling fish by failing to breed or by switching to alternate foods. The use of alternate foods may result in lower growth rates and chick survival. Timing of breeding was not significantly changed. Xantus' Murrelets foraged on larval fish, particularly larval northern anchovies (*Engraulis mordax*). Murrelets responded to the unavailability of larval anchovies either by failing to breed or by delaying breeding until larval anchovies became available. Our results demonstrate not only the sensitivity of marine bird reproduction as an indicator of the availability of their food resources, but also how specific differences in reproductive biology influence the flexibility of response to environmental change.

RESUMEN

La reproducción de la gaviota del oeste (*Larus occidentalis*) y el arán de Xantus (*Endomuchura hypoleuca*) en la Isla de Santa Bárbara, California, presentaron gran sensibilidad a los cambios en las poblaciones de peces pelágicos en la Bahía del Sur de California. Las gaviotas no criaron o variaron su régimen alimenticio cuando se produjo un descenso en la abundancia de peces en los cardúmenes. Al utilizar otros alimentos se puede producir una disminución en el índice de crecimiento y en la supervivencia de los polluelos. El tiempo de crianza no cambió significativamente. El arán de Xantus se alimentaba de larvas de peces, particularmente de anchoveta del norte (*Engraulis mordax*). Cuando hubo una escasez de larvas de anchoveta, el arán no lograba criar o retrazaba la época de cría hasta que las larvas de anchoveta eran abundantes. Nuestros resultados muestran no sólo la sensibilidad de la reproducción de aves marinas como un indicador de la disponibilidad de sus recursos de comida, sino también muestran cómo las diferencias especificas en la biología de reproducción influyen en la flexibilidad de respuestas a cambios en el medio ambiente.

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INTRODUCTION

Ashmole (1963) hypothesized that "... short term and even slight fluctuations in the availability of food . . ." would have " . . . a profound effect on the breeding success in a particular season . . ." for tropical seabirds. He documented a number of cases in which reproductive success was diminished by chick mortality due to starvation. Harris (1978) also discussed the impact of food availability on temperate-breeding Common Puffins (*Fratercula arctica*). He found that supplemental feedings allowed chicks to grow faster and attain a heavier weight, and he suggested that these extra reserves of fat could be of survival value in brief episodes of food shortage.

Other workers have found that changes in food availability may affect not only reproductive success but also the number of birds attempting to breed. In both the guano industries of South Africa and of Peru, declines in fish abundance have been reflected by declines in the number of adult birds attempting to breed (Crawford and Shelton 1978; Jordan 1967; Murphy 1973). Ainley and Lewis (1974) also suggest that certain bird populations on the Farallon Islands, California, have been reduced due to the demise of the Pacific sardine (*Sardinops caerulea*), but their evidence is mostly circumstantial.

Evidence that fluctuations in the availability of a single food species might have a significant impact on the reproductive biology of a presumably generalized forager was presented by Hunt and Hunt (1976b). They found in Western Gulls (*Larus occidentalis*) nesting on Santa Barbara Island, California, a strong inverse correlation between the percent of chicks found empty and the percent of chicks containing anchovies in any one day's sampling. Gull chick survival is linked to food not only through starvation, but more importantly through behavioral differences in satiated and hungry chicks (Hunt and McLoon 1975; Hunt and Hunt 1976a).

We here examine the foraging preferences of two species of seabirds, the Western Gull and the Xantus' Murrelet and the effect of changes in northern anchovy availability on their reproduction at Santa Barbara Island. In particular, we show that as the availability of anchovies fluctuates, Western Gulls on Santa Barbara Island have different responses to these changes than Xantus' Murrelets nesting on the same island.

METHODS

To measure the impact of changes in prey availability on seabird reproductive ecology, it is necessary to determine prey availability or abundance, the number of birds attempting to breed, and their reproductive performance. Three measures of reproductive are phenology, chick growth rates, and the number of chicks surviving to some age or weight criterion.

The number of Western Gulls attempting to nest on Santa Barbara Island was determined by direct counts of incubating and territorial gulls. Counts were made during the incubation period from a series of vantage points that allowed us to enumerate all nesting birds. Counts were repeated as often as once per week in some years to insure accuracy. Xantus' Murrelet numbers were not censused with sufficient accuracy to allow a quantitative assessment of their numbers. However, qualitative assessments of changes in abundance were made by individuals studying murrelet biology around the periphery of Santa Barbara Island.

The reproductive phenology of Western Gulls was measured on the major portion of Western Gull population in 1972 and 1974, and in 1975-77 in five 100 x 100-m grids on the west side of the Island. By concentrating our efforts consistently in these five grids, we avoided the potential problems of variability in the age or experience of the gulls biasing our year-to-year comparisons. Although formal study quadrants were not set up for Xantus' Murrelets, the same areas were used for study each year. Breeding phenology of Western Gulls and Xantus' Murrelets was determined by checking staked nests at least once every four days. In some years checks were made more frequently.

Growth rates of gull chicks were calculated using the slope of the linear portion of the growth curve (Spaans 1971; Hunt 1972; Hunt and Hunt 1975, 1976a) that occurs when Western Gull chicks weigh between 125 and 600 g. Weights were checked approximately once every four days. Xantus' Murrelet chicks are not fed in the short interval between hatching and their departure to sea, so growth rates could not be obtained for this species.

Gull chicks were recorded as surviving when they attained a weight of 500 g. Xantus' Murrelet chick survival is not relevant to the present study, as the major source of their mortality is predation by mice (Hunt et al. 1979).

Samples of food used by Western Gulls were obtained from chicks when they voluntarily regurgitated material during handling for banding or weighing. Occasionally samples were extracted by inserting an index finger down a chick's throat and withdrawing the contents of the proventriculus (Hunt 1972). Samples were obtained from chicks of all sizes and throughout the period when chicks were present on the Island. Most samples were obtained before 1000 or after 1600 in order to avoid subjecting chicks to heat stress during midday. Except for 1972, when samples were identified in the field (Hunt and Hunt 1976b), food samples were preserved and subsequently identified in the laboratory. Since anchovies appear to be a preferred food in the diet of Western Gulls at Santa Barbara Island, the percent weight or percent occurrence of anchovies in the diet of chicks is assumed to be a measure of their availability to foraging Western Gulls.

A second method for estimating changes in the abundance, and presumably the availability of anchovies, was to compare the year-to-year changes in the tonnage of anchovies reported by commercial fish spotters (Squire 1972). An index of northern anchovy abundance was calculated on the estimated total tons of anchovies reported by commercial spotters for daytime flights during the first and second quarters of each year, divided by the number of times pilots flew through the foraging areas used by Western Gulls nesting on Santa Barbara Island. The foraging area was determined from studies of radio-tagged and color-banded gulls reported in Hunt et al. (1979).

RESULTS

Adult Western Gulls feed their chicks by regurgitating food to them at the nesting territory. Western Gulls in the Southern California Bight use a wide variety of foods (Table 1). Foods used varied from colony to colony, presumably depending upon what was consistently most readily available near the colony. Likewise for a given colony, the types of foods used varied from year to year, again presumably reflecting changes in availability (Tables 2-4).

On Santa Barbara Island, not only do we have a longer time period over which sampling has been done, but also we have obtained considerable independent data on anchovy availability and reproductive success. From Table 4 it is clear that Santa Barbara Island Western Gulls depend primarily on fish, and to a lesser extent on the market squid, *Loligo opalescens*. These gulls did not make extensive use of intertidal organisms, and in only one year, 1976, did sea lion (*Zalophus californicus*) placentae or garbage and offal constitute a significant portion of their diet.

The species of fish taken by the Western Gulls on Santa Barbara Island have varied from one year to another. Most striking is the marked decline in the use of northern anchovies from a high of 42% of the diet in 1972 to a low of 18% in 1977. Alternative species taken have included Pacific saury, *Cololabis saira*, and the market squid. Only in 1976, when apparently there were no alternative marine species available, did gulls resort to using sea lion placentae and garbage, the availability of which is unlikely to change from one year to the next.

Over the course of the study, not only has the percentage of anchovies fed to gull chicks declined, but also the number of pairs laying eggs at Santa Barbara Island has decreased (Figure 1). This drop in the number of nesting birds has paralleled a decline in the amount of anchovies seen during daytime surveys in the first quarter of the year by commercial spotter pilots (Anchovy Stock Index; Figure 1). The correlation between numbers of breeding gulls and the Anchovy Stock Index is statistically significant ($r = 0.97$, $N = 4$). Given the relative importance of anchovies to the reproductive biology of this population of Western Gulls, it is reasonable to assume that changes in the yearly availability of anchovies influence the number of gulls attempting to breed.

The amount of anchovies fed to chicks also correlates with the abundance of anchovies (Figure 2), although in an unanticipated way. There is a very strong correlation ($r = 1.00, N = 4$) between the percentage of anchovies in the chick diets and the log of the Anchovy Stock Index for the first quarter of the year, during which gulls are preparing to nest. There is no statistically significant correlation between the Anchovy Stock Index during the second quarter when nesting and chick growth is occuring and the percentage of anchovies in the diets of chicks ($r = 0.33$, $N = 4$).

Gull chick survival has been correlated with growth rates in this study (Figure 3; $r = 0.99$, $N = 4$) and other

TABLE 1

Foods Commonly Fed to Western Gull Chicks, 1975-77

	Percent by occurrence			
Island	Prince	San Nicolas	Santa Barbara	Anacapa
N	87	76	250	36
Food type				
Euphausiacea	0	7	4	0
Loligo opalescens	21	15	4	3
other Cephalopods	7	1	2	8
other mollusks	0	9	1	0
Engraulis mordax	5	14	24	11
Porichthys notatus	2	4	1	3
Merluccius productus	5	1	3	3
Cololabis saira	1	1	30	8
Atherinops affinis				
Sebastes sp.	14	9	6	17
Perciformes	1	5	2	25
unidentified and other fish	45	29	15	31
all fish	68	63	81	98
sea lion placenta	3	18	4	0
garbage and offal	7	3	6	14

TABLE 2

Food Commonly Fed to Western Gull Chicks, Prince Island

	Percent by weight		
Year	1975	1976	1977
N	26	27	34
Food type			
Euphausiacea	1	0	0
Loligo opalescens	58	7	28
other Cephalopods	0	1	4
other mollusks	0	0	0
Engraulis mordax	0	21	0
Porichthys notatus	0	16	0
Merluccius productus	0	3	19
Cololabis saira	0	2	0
Atherinops affinis	0	0	0
Sebastes sp.	0	13	8
Perciformes	0	5	2
unidentified and other fish	30	22	17
all fish	30	82	46
sea lion placenta	3	3	0
garbage and offal	8	7	25
other	0	1	0

TABLE 3

Foods Commonly Fed to Western Gull Chicks, San Nicolas Island

	Percent by weight		
Year	1975	1976	1977
N	21	39	15
Food type			
Euphausiacea	0	6	0
Loligo opalescens	9	18	26
other Cephalopods	0	6	3
other mollusks	0	6	0
Engraulis mordax	16	22	0
Porichthys notatus	0	6	4
Merluccius productus	0	0	14
Cololabis saira	0	0	0
Atherinops affinis	0	13	6
Sebastes sp.	0	3	3
Perciformes	0	3	0
unidentified and other fish	59	2	13
all fish	75	49	40
sea lion placenta	14	16	10
garbage and offal	0	0	13
other	0	1	8

TABLE 4

Foods Commonly Fed to Western Gull Chicks, Santa Barbara Island

	Percent by weight			
	1972	1975	1976	1977
N	157	18	79	153
Food type				
Euphausiacea	0	0	0	0
Loligo opalescens	12	8	4	3
other Cephalopods	0	0	2	1
other mollusks	0	2	0	0
Engraulis mordax	45	32	28	18
Porichthys notatus	2		0	4
Merluccius productus			2	2
Cololabis saira	3	4	7	53
Atherinops affinis			6	0
Sebastes sp.			13	3
Perciformes			2	2
unidentified and other fish	30	46	9	7
all fish	80	82	65	89
sea lion placenta	0	4	15	1
garbage and offal	7		13	3
other	0	5	0	2

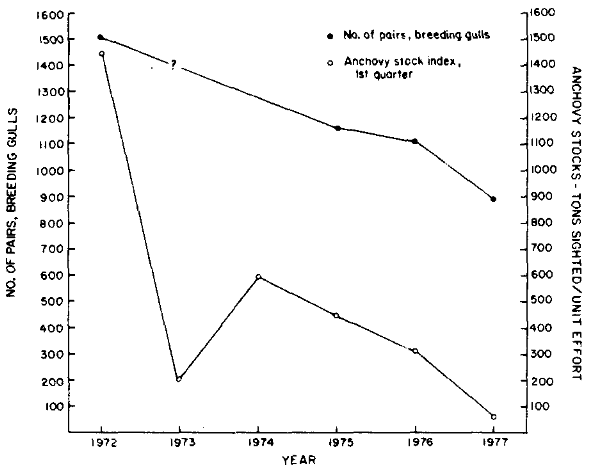

Figure 1. Recent changes in the number of Western Gulls breeding on Santa Barbara Island showing similar changes in the abundance of northern anchovies (see text for an explanation of the Anchovy Stock Index).

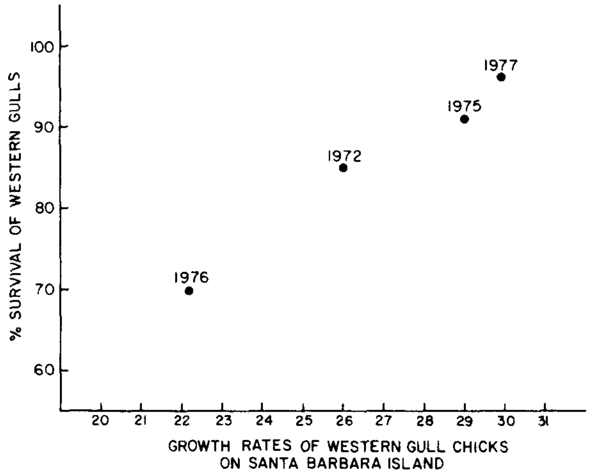

Figure 3. Relationship of Western Gull chick survival to their growth rates on Santa Barbara Island.

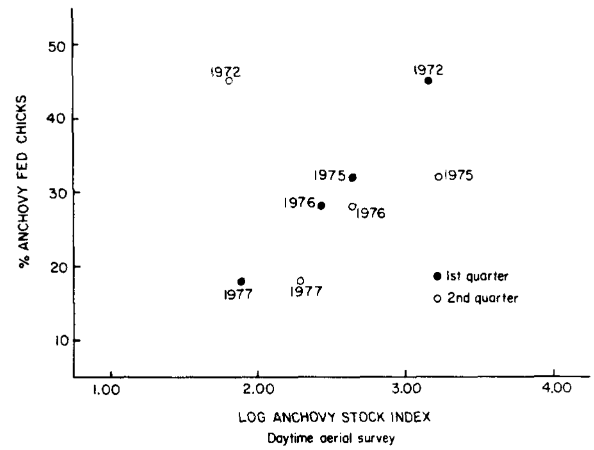

Figure 2. Relationship between the Anchovy Stock Index in the first quarter (January-March) and the second quarter (April-June) and the percent anchovies in the diets of Western Gull chicks.

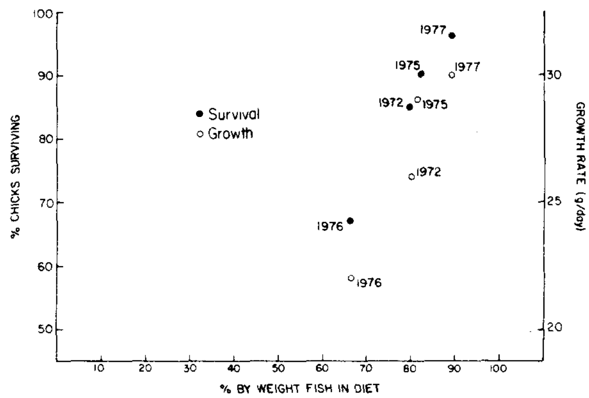

Figure 4. Relationship between the amount of fish in the diet fed young Western Gulls by adults and the growth and survival of gull chicks on Santa Barbara Island.

studies (Hunt and Hunt 1975, 1976a). Growth rates in turn were influenced by the amount of fish in the diets of chicks (Figure 4; $r = 0.98, N = 4$), but they were not significantly correlated with the percent of anchovies in the diet ($r = 0.30, N = 4$). In 1977 growth rates were high, despite the reduced use of anchovies. The use of sauries clearly made up for the lack of anchovies in 1977.

The timing of egg laying by Western Gulls might have also been expected to be sensitive to food availability (Hunt and Hunt 1976a). However, on Santa Barbara Island there was virtually no difference in the mean date of egg laying for any of the four years studied (Figure 5).

In contrast, Xantus' Murrelet clutch initiation varied in 1976, 1977, and 1978 (Figure 6). In 1978, murrelet egg laying was delayed by five to six weeks. When laying did begin, the number of birds nesting appeared reduced. Additionally, the interval between laying of eggs and the period of time between exchange of incubating adults was increased (Hunt et al. 1979).

Murrelets eat larval fish, particularly larval anchovies (Hunt et al. 1979). According to Lasker (1979), in 1978 larval anchovies failed to survive the stage of first feeding until after March. Thus, the late-larvae of the anchovies, upon which these birds appear to be specialized foragers, would not have been available until late April or early May, instead of in late February or early March as is more usual.

DISCUSSION

This study shows that Western Gulls feed their chicks a wide variety of foods, most of which are pelagic in origin

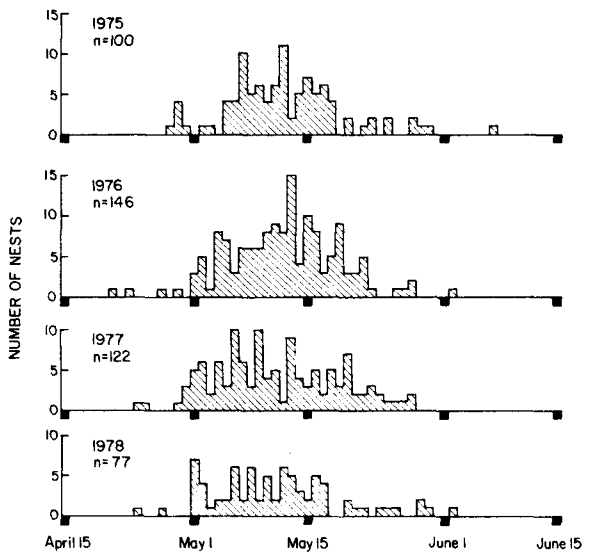

Figure 5. Clutch initiation in Western Gulls, Santa Barbara Island.

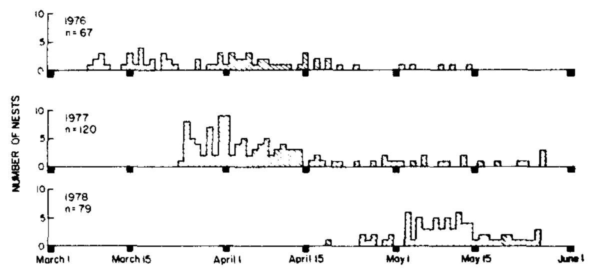

Figure 6. Clutch initiation in Xantus' Murrelets, Santa Barbara Island.

and few of which can be considered offal. Each colony tends to differ from other colonies in the kinds of foods taken, and these variations are believed to reflect relative availability of foods.

Hunt and Hunt (1975) concluded that the reproductive success of this population of Western Gulls was clearly related to the availability of anchovies. Daily fluctuations in the delivery of food to the chicks in 1972 were correlated with the percent of anchovies brought to Western Gull chicks. The present study also suggests the importance of anchovies to the Western Gulls of Santa Barbara Island. However, we now find that Western Gulls can make use of alternative foods and have nearly as good reproductive success. Early in the breeding season, anchovy availability may determine the number of gulls attempting to breed. Later, during the chick phase, the presence of abundant, nutritious pelagic forage fish, regardless of species, appears critical. When gulls turned to distant, less nutritious (Hunt 1972) garbage (Table 4, 1976), growth rates and reproductive success declined.

As additional data on anchovy abundance become available, it will be interesting to see if the number of gulls attempting to breed at Santa Barbara continues to track changes in anchovy populations. There appears to be uncertainty about the true size and health of the central stock of northern anchovies in the California Current. The numbers of breeding gulls at Santa Barbara Island may provide an index of their prey populations, much as have the guanay birds in Peru and southern Africa (Crawford and Shelton 1978; Murphy 1973; Jordan 1967).

The contrast between the reaction of the gull population and the murrelet population to food shortage is remarkable. In particular, the murrelets apparently delay reproduction while food is scarce. The Xantus' Murrelet has one of the largest eggs and clutches in relation to adult body weight of any seabird (Sealy 1975). This species may have a very precarious energy balance when it comes to egg production and may have no option but to delay egg-laying if its preferred foods are scarce. The delay in breeding in 1978, coupled with the greater interval between laying of eggs and incubation exchange, supports this hypothesis.

In contrast, the Western Gull showed no striking changes in the date of egg laying. For this species the ratio of egg weight or clutch weight to female body size is relatively small, and with the addition of courtship feeding by the male (Hunt in press), the female may not be under particularly strong energetic constraints. However, because Western Gulls nest in the open, unlike murrelets which nest in caves or under bushes, and because chicks are sensitive to thermal stress (Hunt et al. 1979; Bennett, unpublished field notes; Sayce, unpublished field notes) delay of gull reproduction may increase exposure of chicks to lethal thermal stress. Thus, Western Gulls that are unable to procure sufficient energy for egg production at the appropriate season may forego reproductive effort entirely for that season. The low chance for survival of chicks hatched late in the season would not compensate for the effort and risk expended in attempting to reproduce. Rather, these birds stay in the vicinity of the colony, but do not attempt to hold territory or lay eggs.

These differences in the reaction of two species of seabirds to apparent shortage of food provide a means of determining more precisely changes taking place in forage fish populations. Since the birds depend upon different life-history stages of the fish, changes in bird reproduction can be related to specific aspects of the fish populations and can be separated from effects due to weather, disturbance, etc. Thus, these seabirds provide a powerful, alternative tool for monitoring marine populations.

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