Condor 83:289–301

A COMPARISON OF VOCALIZATIONS OF WESTERN GULLS (*LARUS OCCIDENTALIS OCCIDENTALIS* AND *L. O. LIVENS*)

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ABSTRACT.—Two of the three recognized subspecies of the Western Gull (*Larus occidentalis*) breed along the west coast of the United States and Baja California and closely resemble each other (*L. o. occidentalis* and *L. o. wymani*). The third subspecies (*L. o. livens*), endemic to the Gulf of California, differs in several characteristics, including voice. I compared eight vocalizations of *L. o. occidentalis* with *L. o. livens*, and compared Long Calls of all *L. occidentalis* subspecies to species breeding to the north (*L. glaucescens*) and south (*L. dominicanus*). Vocalizations of *livens* are distinctive and further support its classification as a separate species. Long Calls of *livens* are low pitched, presumably adapted for long distance propagation in a relatively quiet environment; *occidentalis/wymani* Long Calls have features that may facilitate their localization by receivers.

Three subspecies of Western Gulls are recognized: *Larus occidentalis occidentalis* breeds from northern Washington (Destruction Island) southward to Southeast Farallon Island in northern California; *L. o. wymani* breeds from central California (Monterey Bay) to western Baja California as far south as Asunción Island, and on Guadalupe Island; *L. o. livens* breeds entirely in the Gulf of California (A.O.U. Check-list 1957).

Aside from brief accounts (Bent 1921, Tinbergen 1959), little information was published on *L. occidentalis* until the late 1960's. Schreiber (1970) and Harper (1971) investigated basic breeding biology and their studies have been followed by others (see references in Hand 1979).

L. o. livens is a resident of the Gulf of California (Devillers et al. 1971), rarely moving elsewhere, and is isolated geographically from *wymani* and *occidentalis* (Devillers et al. 1971, Hand 1979). Because of differences between *L. o. livens* and the two other subspecies (reviewed in Hand 1979), a number of investigators have suggested that *livens* be recognized as a separate species.

The Glaucous-winged Gull (*Larus glaucescens*) is the nearest gull of similar size and appearance breeding to the north of *L. occidentalis* (along the Pacific coast of Washington north to Alaska). The Kelp Gull (*L. dominicanus*) is the nearest breeding to the south (widespread in the southern hemisphere and breeding as far north as 4°S off the coast of South America). Mayr and Short (1970) treated *L. occidentalis* and *L. glaucescens* as separate species, yet members of the same (Herring Gull; *Larus argentatus*) species group; they tentatively assigned *L. dominicanus* to a separate group with the Great Black-backed Gull (*L. marinus*). Devillers (unpubl. data) suggested that *livens* and *wymani* may have been derived (probably separately) from the southern hemisphere *dominicanus*, or a common ancestor, while *L. o. occidentalis* and *L. glaucescens* may represent stabilized hybrid swarms, produced by contact between southern forms, such as *dominicanus* and *wymani*, and the Glaucous Gull (*L. hyperboreus*), a still more northern species.

Other studies have examined morphological or behavioral traits of these populations (Devillers 1971, unpubl. data; LeValley 1975; Hand et al. 1981). In this study, I compared the vocal repertoires of *L. o. occidentalis* and *L. o. livens*. Additionally, since Long Calls of gull species are strikingly different (Tinbergen 1959:57), I compared Long Calls of the three *L. occidentalis* subspecies with Long Calls of *L. glaucescens* and *L. dominicanus*.

MATERIALS, METHODS, STUDY SITES

RECORDING SITES

Virtually all recordings were of breeding adults in breeding colonies. Those of *L. o. occidentalis* were made on Southeast Farallon Island, approximately 48 km west of San Francisco, between 6 May and 1 June 1975. Recordings of *L. o. wymani* were made on Bird Rock, Catalina Island, California between 6–11 April and 11–12 May 1974. *L. o. livens* was recorded at the north and south ends of Isla Angel de la Guarda and at Isla Cardinosa, all located in the northern half of the Gulf of California, between 15–19 June 1974, 19–23 April 1975, and 11–29 April 1976. Recordings of *L. dominicanus* were made on a beach, during the breeding season, in Antofogasta, Chile, and those of *L. glaucescens* are from breeding adults on Mandarte Island, British Columbia.

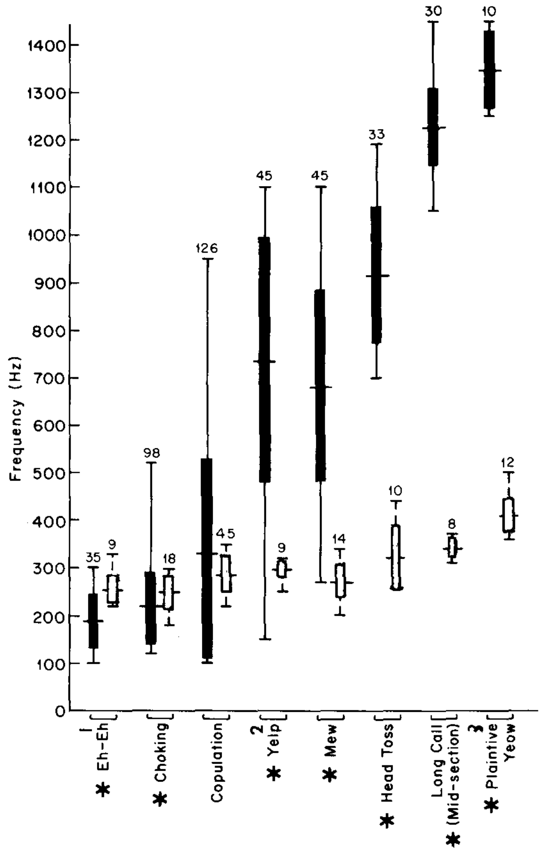

FIGURE 1. Mean harmonic band intervals (MHIs). Range, mean, and 1 SD. MHIs were estimated (±7.0 Hz) as described in the text. Numbers on top of bars indicate sample size. Solid bar is *L. o. occidentalis*; open bar is *L. o. livens*. A star indicates that the difference is significant (0.05 rejection level, Mann-Whitney U-test, 2-tailed). 1 = equivalent to Alarm Call, Tinbergen 1959. 2 = equivalent to Yelp of Stout 1975, Long Call Note of Moynihan 1962:54, and Call Note of Tinbergen 1959. 3 = equivalent to Plaintive Long Call Notes of Moynihan 1962:55.

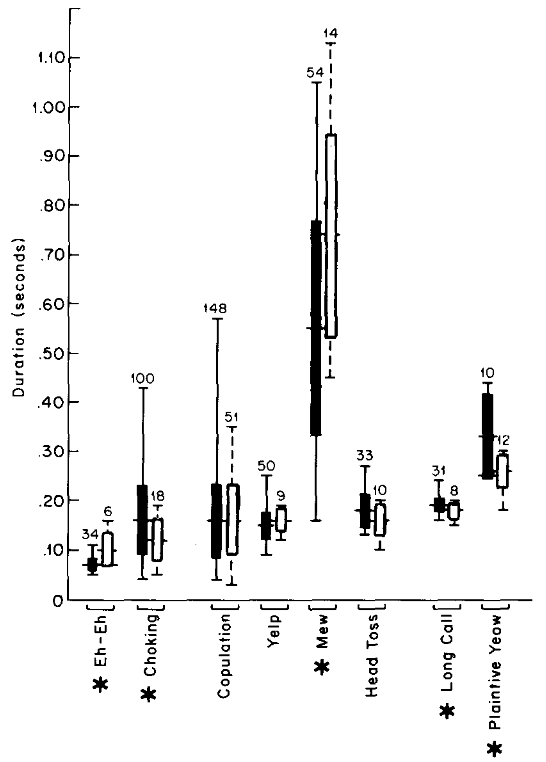

FIGURE 2. Figure durations. Range, mean, and 1 SD. All symbols are the same as in Figure 1.

RECORDING AND ANALYSIS METHODS

While recording, I wrote descriptions of the sound recorded, the context of occurrence, the identity of the caller and other individuals if known (some individuals were individually recognizable: see Hand 1979 for details). Extensive analyses of call use and speculations on call functions and caller motivations were based on my work on Southeast Farallon Island (Hand 1979).

The *L. occidentalis* calls were recorded at 19 cm/s (except for three recorded at 9.5 cm/s) using a Uher Report L tape recorder and M 514 microphone. The microphone was usually placed beside a nest or in the center of a territory or feeding group of gulls, covered with a wind screen of camouflage material. Calls in Gulf colonies were sometimes recorded using the microphone mounted in a parabolic reflector since nests were widely spaced, making a stationary microphone placement unsatisfactory. *L. dominicanus* calls were recorded with a small cassette recorder; *L. glaucescens* calls were recorded with a portable Sony machine and copied before analysis using a Uher Report L recorder.

I made sound spectrograms using the Kay Sona-Graph 6061-B with a 40-Hz (narrow band) filter. Gull vocalizations vary considerably, both within and between some call types (Tinbergen 1953, Moynihan 1962) and I used only clearly recorded calls, categorizable by their structure or an accompanying visual display, to compare *L. o. occidentalis* and *L. o. livens* repertoires.

Names of calls and visual displays are capitalized and most follow Tinbergen (1959)—exceptions are explained in the legend to Figure 1. The terminology used to describe call structure is that of Davis (1964).

I compared eight homologous call types, examining mean harmonic band intervals (MHIs) within sound figures (Fig. 1), figure durations (Fig. 2), and general configurations (Figs. 4–7).

The mean harmonic band intervals were *estimated* by placing a grid calibrated in 50-Hz intervals over the sound figures at the highest point. Frequencies of visible harmonics at this point were estimated to the nearest 10 Hz and compared to values on a numbers table, these values being integral multiples of possible intervals. For example, a Choking sound had visible bands at the following Hz: 180, 320, 450, and 650. The value from the numbers table producing the best fit to the observed bands corresponds to a harmonic interval of 160 Hz. A calculated mean interband interval for this call would be 156.6 Hz, which closely fits the 160 Hz estimate determined by my method.

Harmonic intervals within a sound figure can correspond to the fundamental frequency of the sound, but since this is not necessarily the case (see Watkins 1967 for a description of the relationship of fundamental frequency, harmonic interval, and pulsed tones to sound spectra), I use the purely descriptive phrase "mean harmonic interval" (MHI) throughout, rather than the precisely defined term "fundamental frequency."

TABLE 1. Context of use and quality of eight *L. o. occidentalis* calls.[1]

Call[2]	Most common use[3]	Configuration and quality[4]
1. Eh-Eh (alarm)	Usually the first call given as a predator (usually on foot) enters a colony. Birds may subsequently begin Yelping or fly, uttering Plaintive Yeows.	A staccato, low-pitched call. Most commonly two, three, or four brief sounds uttered in rapid succession.
2. Choking	Uttered during agonistic encounters between territory owners and neighbors or intruders; during early courting, when males and females engage in Choking bouts with potential mates; during some nest exchanges.	A series of low-pitched sounds with tightly spaced harmonic bands, usually uttered rather irregularly in short bouts of four or more. The sounds are not necessarily produced in synchrony with neck movements of the visual Choking display.
3. Copulation	Uttered by copulating males.	Characteristic sounds are loud, regular in rhythm, guttural in quality, and repeated continuously while the bird is mounted. Considerable variability in form occurs (see text).
4. Mew[4]	Uttered during courting and other sexual behavior; during aggressive encounters between territory owners and intruders; during parent–young interactions; during some nest exchanges. Accompanies the visual Mew display.	Varies in duration, from short, rather rough calls to more prolonged, plaintive sounds. Uttered singly or in a series. Shorter sounds have one segment with closely spaced harmonics. More commonly, calls have two segments (see text).
5. Long Call[4]	Uttered during courting and territory establishment, when males direct them to rivals and potential mates; by residents when their mates return to the territory after an absence; by combatants that break contact during a prolonged fight; by territory owners as intruders converge on the caller's territory because food is present.	A series of loud sounds, always more than six, uttered in relatively quick succession. An initial downward arching sweep of the head, which can be omitted, is accompanied by one or two "introductory" calls and the remaining "mid-section" and "terminal" figures are uttered in an Oblique posture.
6. Yelp[4]	Uttered when a predator enters the colony; by gull observers, including an intruding male's mate, during prolonged fights; by a bird that has been struck, either during a fight or during courtship; by a female when a rapist has mounted her; as an extension of or following a Long Call.	Sounds like yapping or barking. Sound figures can be uttered separately, or in short bouts, or in a long series at more or less regular intervals. Intervals between calls appear to be inversely related to degree of arousal. Form is variable, some figures consisting of a single segment of tightly spaced harmonics (resembling some terminal Long Call notes), some with two segments resembling mid-section Long Call notes.
7. Head Toss[4] (begging)	Used by females during pair formation; by both sexes prior to copulation; by young of both sexes and by females prior to being fed; during some nest reliefs. Usually accompanies the visual Head Toss display.	Is usually uttered as a separate sound, but can occur at regular intervals during long interactions. Figures resemble some Yelps and Long Call sounds: all have a rough first segment, a second segment of higher pitch, and similar durations. Most have a "clear" sound, created by stress on odd-numbered harmonics of the second segment.
8. Plaintive Yeow	Most often uttered in flight, when a predator enters the colony and the birds circle overhead or when circling in a group over food. A sudden stimulus change, such as an investigator stepping from a blind, can elicit the call from non-flying birds.	A clear, high-pitched cry of prolonged duration, descending in pitch throughout. Can be uttered singly or in bouts of variable duration. Intervals between calls appear to be inversely related to degree of arousal.

[1] Other calls were heard that were not described in earlier works (e.g., Tinbergen 1959, Moynihan 1962; *L. modestus*)—all were difficult to record. Five are discussed and spectrograms of four of the five are presented elsewhere (Hand 1979).
[2] Where my name for a call differs from Tinbergen's (1959), the latter is given in parentheses. Plaintive Yeow has no 1959 Tinbergen equivalent.
[3] See Hand 1979 for more extensive descriptions. This table includes only contexts of use in breeding colonies.
[4] Indicates that the configuration of the homologous *L. o. livens* call differs markedly from *L. o. occidentalis*.

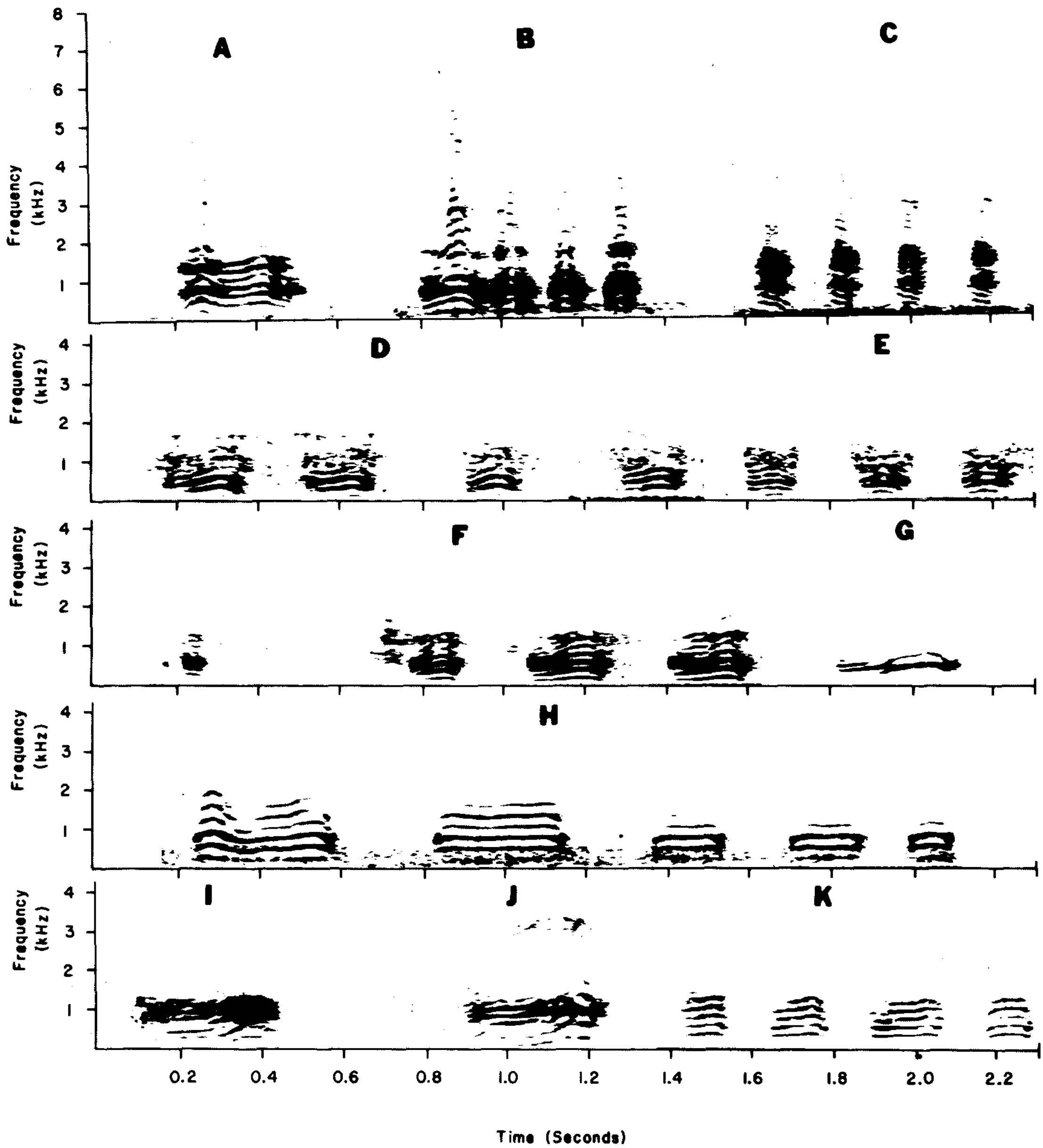

FIGURE 3. Eh-Eh, Choking, and Copulation calls. A. Eh-Eh (*livens*). B. Eh-Eh (*livens*). C. Eh-Eh (*occidentalis*). D. Choking (*livens*). E. Choking (*livens*). F. Choking (*occidentalis*). G. Choking (*occidentalis*). H. Copulation (*livens*). I. Copulation (*occidentalis*). J. Copulation (*occidentalis*). K. Copulation (*occidentalis*).

RESULTS

The contexts in which the calls described below are commonly used are summarized in Table 1. I detected no obvious differences between *L. o. occidentalis* and *L. o. livens* in ways calls were used or their effects on other individuals.

COMPARISON OF HARMONIC INTERVALS AND DURATIONS OF CALLS

All types of *livens* and *occidentalis* calls, except Copulation calls, were significantly different with respect to mean harmonic interval (Fig. 1). Only *occidentalis* Choking and Eh-Eh calls had MHIs smaller than *livens'*; in all others, the *livens* MHI was smaller (particularly in Yelp, Mew, Head Toss, Long Call, and Plaintive Yeow calls; Fig. 1).

Several calls of the two subspecies (Eh-Eh, Mew, Choking, Long Call, and Plaintive Yeows) differed significantly in duration (Fig. 2), but not in any consistent pattern.

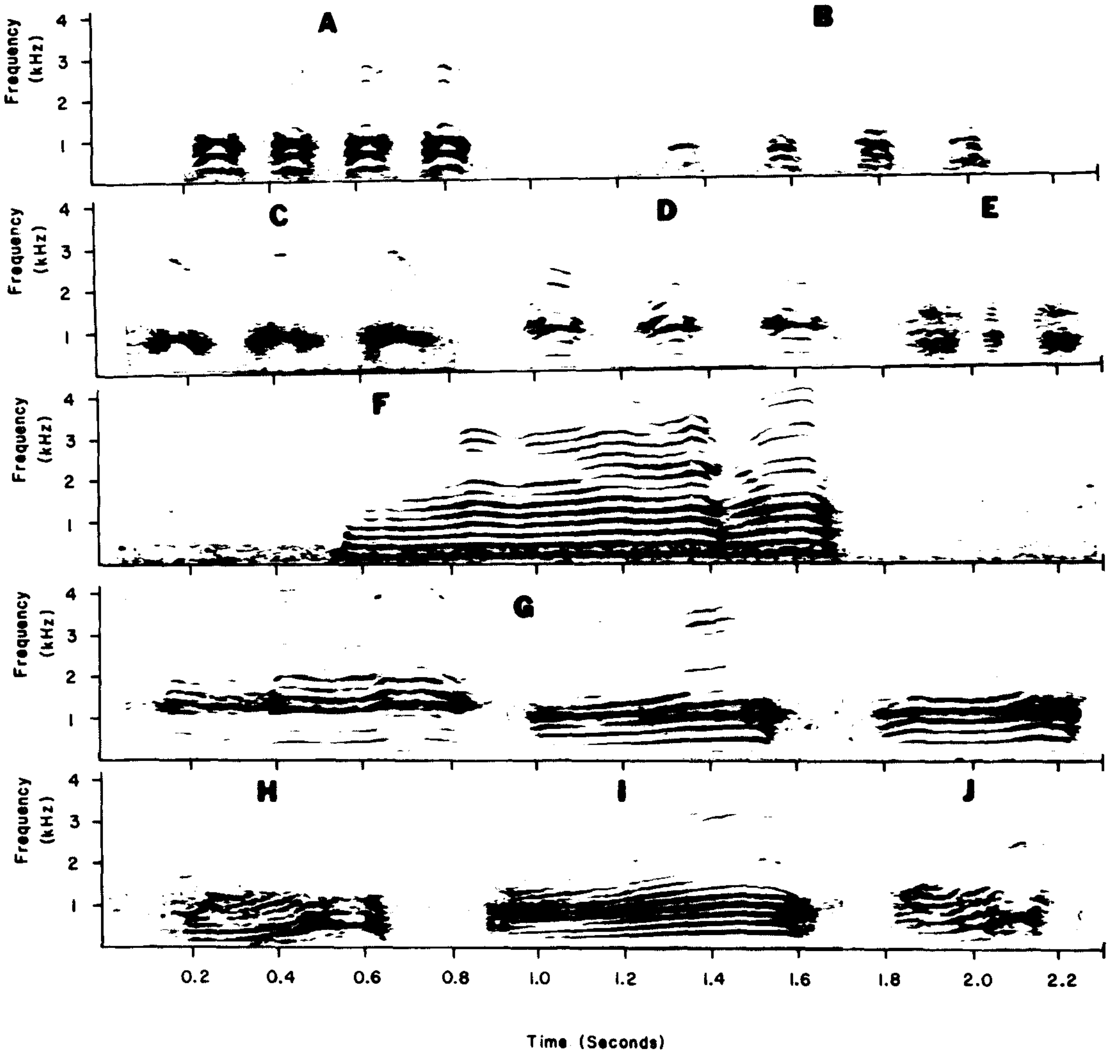

FIGURE 4. Copulation and Mew Calls. A. Copulation (*livens*). B. Copulation (*livens*). C. Copulation (*occidentalis*). D. Copulation (*occidentalis*). E. Copulation (*occidentalis*). F. Mew (*livens*). G. Mew (*livens*). H. Mew (*occidentalis*). I. Mew (*occidentalis*). J. Mew (*occidentalis*).

The narrow range of variation in harmonic intervals of *livens* calls constitutes a striking difference in the two repertoires. The smallest interval recorded for *livens* was 180 Hz (a Choking call) and the largest was 500 Hz (a Plaintive Yeow), a range of only 320 Hz in the entire *livens* repertoire, while the *occidentalis* repertoire included intervals from 100 Hz (Eh-Eh and Copulation) to 1,450 Hz (Long Call and Plaintive Yeow), a total range of 1,350 Hz (Fig. 1).

COMPARISON OF CONFIGURATIONS OF CALLS

Substantial differences in the form of several homologous *occidentalis* and *livens* calls occur primarily because some *occidentalis* calls have a two-segment configuration while *livens* calls have only one segment, and the MHIs of the *occidentalis* second segments are greater than MHIs of single-segment *livens* calls (i.e., the pitch of the *occidentalis* second segments is higher). Calls that differ most are Mew (whenever *occidentalis* Mews have two segments—H, Fig. 4 vs. A–D, Fig. 5), Long Call (E–G, Fig. 5), Yelp (A–G, Fig. 6), and Head Toss (H–N, Fig. 6). Thus, excepting Plaintive Yeows, calls differing substantially in form also differ markedly in pitch (Plaintive Yeows do have similar form, but also differ in pitch; O–T, Fig. 6). Although Eh-Eh, Choking, and Copulation calls differ slightly in MHIs and durations (Figs. 1 and 2), they are more similar in both configuration and pitch (Fig. 3; A–E, Fig. 4) than any other calls.

Since there are no two-segment figures, configurations of *L. o. livens* calls suggest

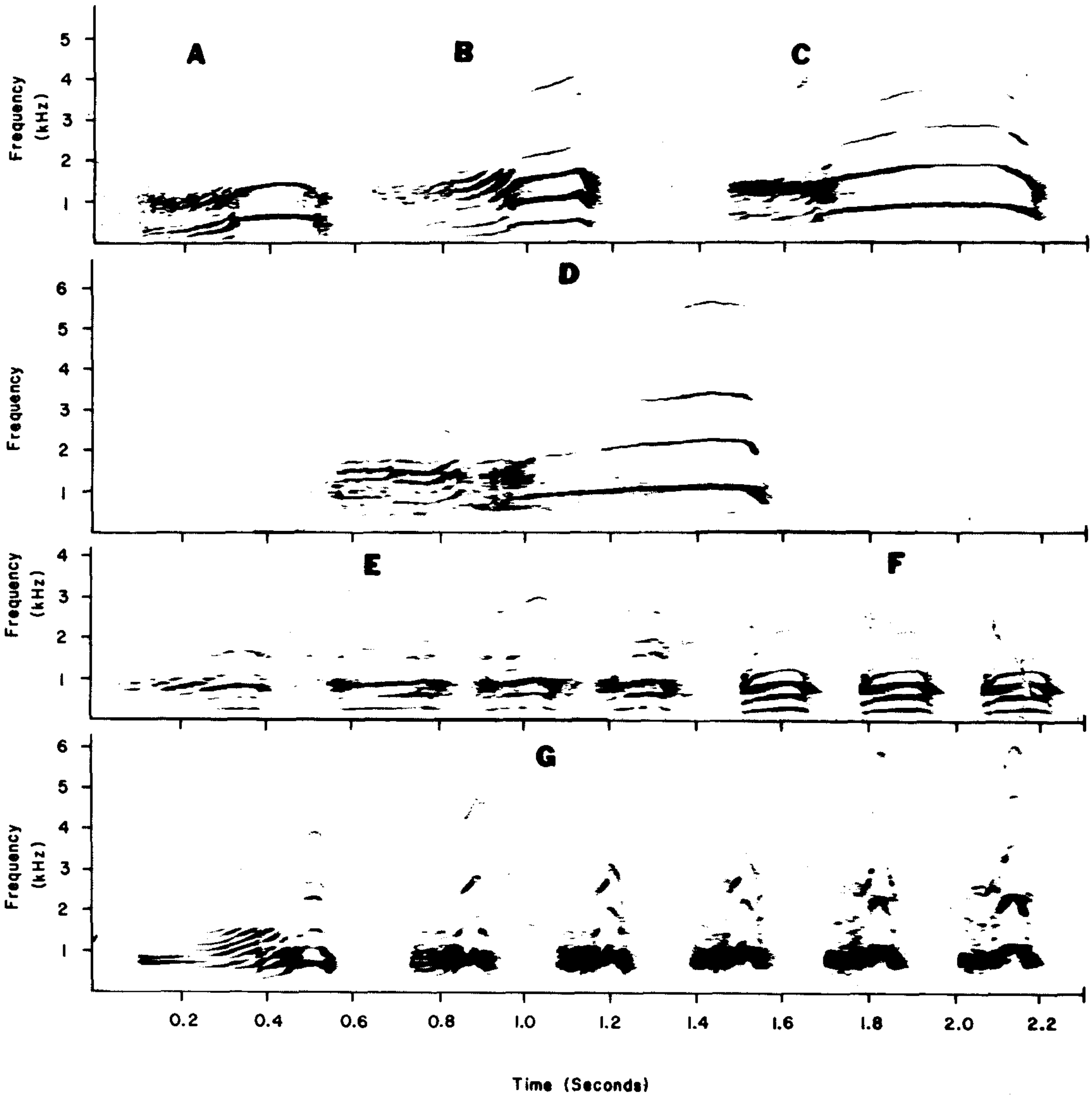

FIGURE 5. Mew and Long Calls. A. Mew (*occidentalis*). B. Mew (*occidentalis*). C. Mew (*occidentalis*). D. Mew (*occidentalis*). E. Long Call (*livens*—introductory and next three calls). F. Long Call (*livens*—mid-section calls). G. Long Call (*occidentalis*—first six figures in call).

a relatively simpler process of sound production. During a given *livens* utterance, MHIs do not vary greatly. The two-segment, and sometimes three-segment, *occidentalis* calls stand in sharp contrast: a first segment with tightly spaced harmonic bands is followed by the second segment in which the MHI is greater, and occasionally calls terminate by returning to tightly spaced harmonics in a brief third segment.

VARIATION OF SOUND FIGURES WITHIN CALL TYPES

Some call types are more stereotyped than others. For example, in both *livens* and *occidentalis,* Eh-Eh sound figures from the same or different individuals vary relatively little in duration, frequency, or configuration (A–C, Fig. 3). In other calls, conspicuous consistent variations are shared by both subspecies. Although the nature of the variations is similar for both subspecies, the degree of variability is generally more pronounced in *L. o. occidentalis.*

Copulation (H–K, Fig. 3; A–E, Fig. 4). When copulating, males of both populations utter loud, distinctive sounds, somewhat guttural in quality and regular in rhythm, that typically have energy concentrated in one or two bands between 0.7 and 1.2 kHz (A, C, D, Fig. 4).

The first few sounds produced immediately after mounting (H–J, Fig. 3), however, are usually of longer duration than the more

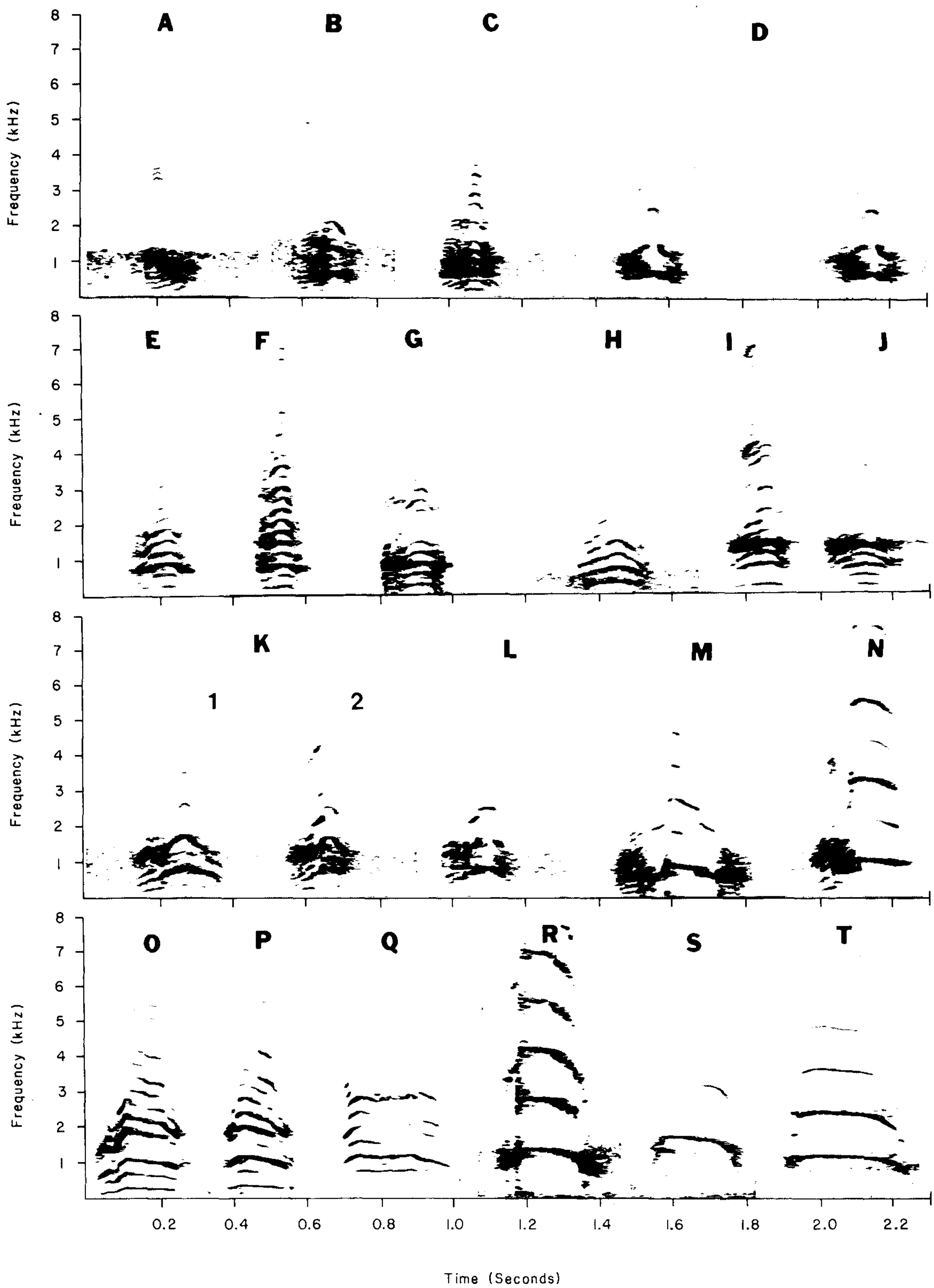

FIGURE 6. Yelps, Head Toss, and Plaintive Yeow calls. A–D. Yelps (*occidentalis*). E–G. Yelps (*livens*). H–J. Head Toss (*livens*). K–N. Head Toss (*occidentalis*). O–Q. Plaintive Yeow (*livens*). R–T. Plaintive Yeow (*occidentalis*).

intense, staccato calls that follow, and sound energy in the introductory calls is more evenly distributed in several harmonics (compare H, Fig. 3 with E, Fig. 4). If a male's footing becomes unsure, or if for any reason copulation does not proceed "successfully," calls may again become less staccato and may be uttered in a less regular temporal pattern than the characteristic sounds (K, Fig. 3 and B and E, Fig. 4). As a sequence ends, intense sounds may again be replaced by less staccato calls. Sounds uttered during a single copulation attempt (I–K, Fig. 3 and E, Fig. 4) illustrate the broad range of variation that can occur, especially in *occidentalis*.

Mew (F–J, Fig. 4; A–D, Fig. 5). Mew calls of both subspecies vary considerably in duration (Fig. 2). Mews of *L. o. occidentalis* also vary in the relative durations of first and second segments (J, Fig. 4 and A–D, Fig. 5), and some *occidentalis* Mews have no second segment (H, I, Fig. 4).

Mews of *L. glaucescens* resemble those of *L. o. occidentalis* in having a two-segment configuration, and Stout (1975) concluded that there are three types of *glaucescens* Mews, distinguishable by the lengths of (or absence of) the two segments: Courtship Mews, Parent-young Mews, and Aggressive Mews. My sample of Mew calls from each of these contexts is too small to make a similar comparison between call structure and behavioral context.

Long Call (E–G, Fig. 5). Long Call sounds are a tightly integrated accompaniment to the visual display of the same name. I did not detect any marked differences in any of the visual displays of *L. o. occidentalis* and *L. o. livens*. In both populations, the initial movements of this display include a downward arching sweep of the head so that the bill, head, and neck are directed between the legs, then the head and neck are subsequently elevated into an Oblique posture from which the call is completed. The head is not thrown back as in some gulls, and displays may be incomplete, lacking the initial downsweep.

The first and sometimes second sounds are "introductory calls," accompanying the downward sweep of the head (first figures in E and G, Fig. 5). The next sounds, "mid-section calls," are emitted from the Oblique posture (Fig. 5 E, last two figures, and F; Fig. 5 G, last five figures). First and second figures are commonly longer than mid-section figures, a pattern also true for *L. glaucescens* (Stout 1975). Some sequences begin immediately with a mid-section figure, apparently cases where birds omit the downsweep.

L. o. livens Long Call figures (E–F, Fig. 5) are simple structures with several harmonic bands. Spectrograms show energy concentrated in the second, third, or fourth bands which regularly lie between 0.8 and 1.0 kHz. Introductory and mid-section figures of *L. o. occidentalis* and *L. o. wymani* have a first segment with harmonics so closely spaced they form a band of noise lying between 0.7 and 1.8 kHz (G, Fig. 5); the most prominent band of energy in the second segment is the lowest, lying between 1.0 and 1.5 kHz. Thus mid-section figures of all three subspecies emphasize frequencies between 0.8 and 1.5 kHz. In *occidentalis/wymani*, however, the second segment has virtually no energy below 1.0 kHz and typically has a number of widely spaced harmonic bands ranging up to 6.0–6.5 kHz. Energy in *livens* calls is mostly below 1.8 kHz, with the result that the voice is noticeably lower pitched than in *occidentalis* and *wymani*.

A Long Call can terminate abruptly, with a figure of mid-section form, or with several Yelps (see below). Like *L. glaucescens* (Stout 1975), *L. o. occidentalis* most commonly ends the Long Call by letting the upper harmonics drop out of the last few figures, or it may utter only the rough first segment of the last two or three figures. When either happens, the Long Call sounds as if it is dropping in pitch, although the main band of energy in terminal sounds is in the same range as in mid-section figures. These terminal figures are similar, if not identical, to Yelps, which can be used entirely separately from Long Calls. Long Calls of *L. o. livens* typically change into a long series of Yelps (E–G, Fig. 6), the transition being so gradual it is difficult to say when Long Calling stops and Yelping begins.

In all three *L. occidentalis* subspecies, mid-section calls of a given individual vary remarkably little in MHI, figure duration, or relative distribution of energy between the harmonics. Although I made no quantitative analysis, qualitative examinations of sonograms suggest that the sounds are probably sufficiently distinctive to facilitate individual identification by voice. I did not examine variability of individual birds' introductory and terminal Long Call figures.

Yelp (A–G, Fig. 6). Yelps of *L. o. livens* vary little in configuration or duration—all resemble the samples in Figure 6 (E–G). *L. o. occidentalis* Yelps also vary relatively lit-

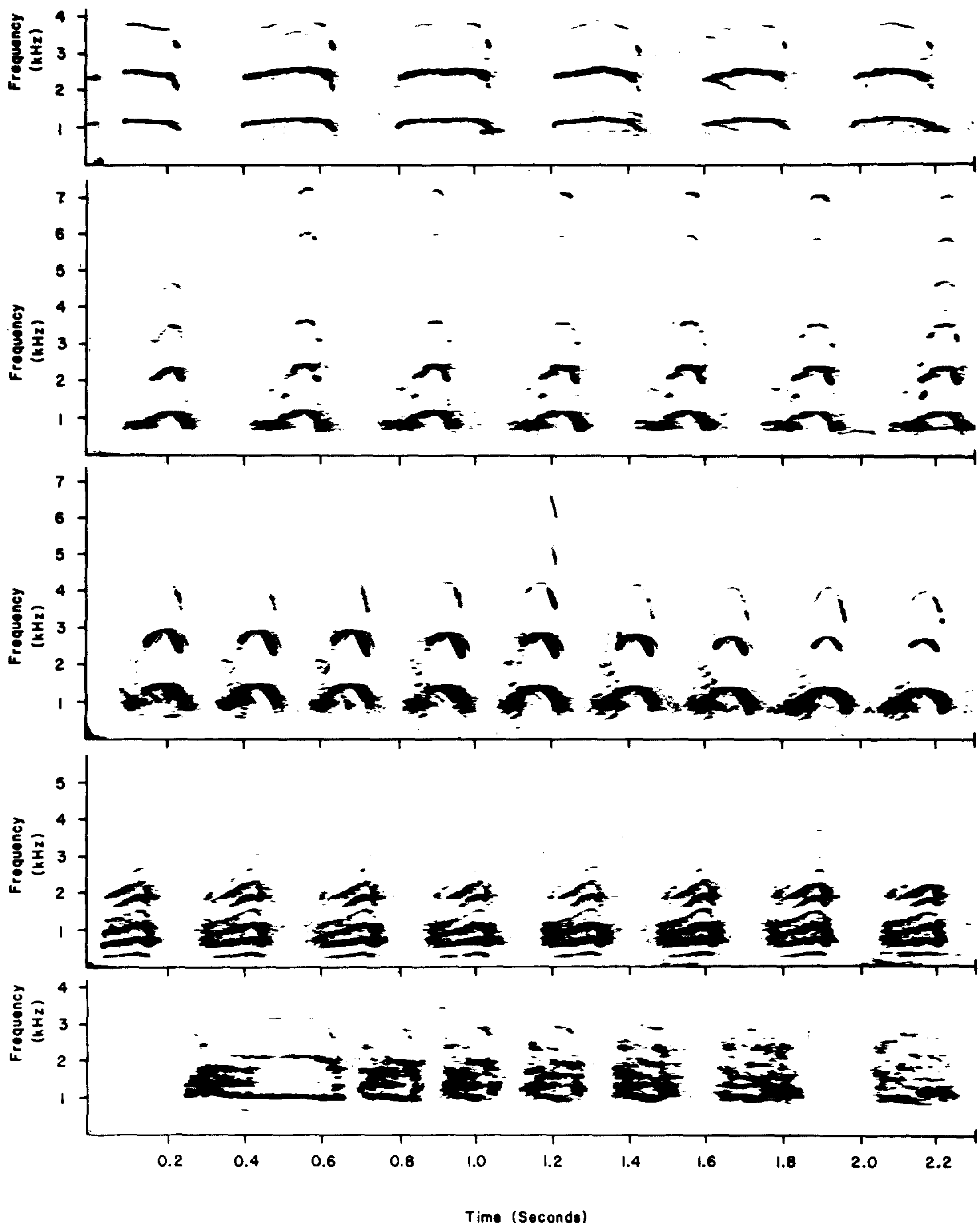

FIGURE 7. Mid-section Long Call figures of five gulls. Line 1. *L. glaucescens*. Line 2. *L. o. occidentalis*. Line 3. *L. o. wymani*. Line 4. *L. o. livens*. Line 5. *L. dominicanus*.

tle in duration (Fig. 2), but show a wide range of configurations. Some (A and B, Fig. 6) resemble terminal Long Call figures in which only the band of noise comprising the first segment is present; others (C and D, Fig. 6) resemble mid-section Long Call figures, and many forms intermediate to these were recorded. Yelps of both *livens* and *occidentalis* also resemble the Head Toss calls of each subspecies.

Head Toss (H–N, Fig. 6). L. o. livens Head Toss calls resemble *livens* Yelps in configuration (compare E–G, Fig. 6 with H–J), in MHIs (Fig. 1), and in figure durations (Fig. 2). Similarity to mid-section Long Call figures (compare H–J, Fig. 6 to Fig. 5 mid-

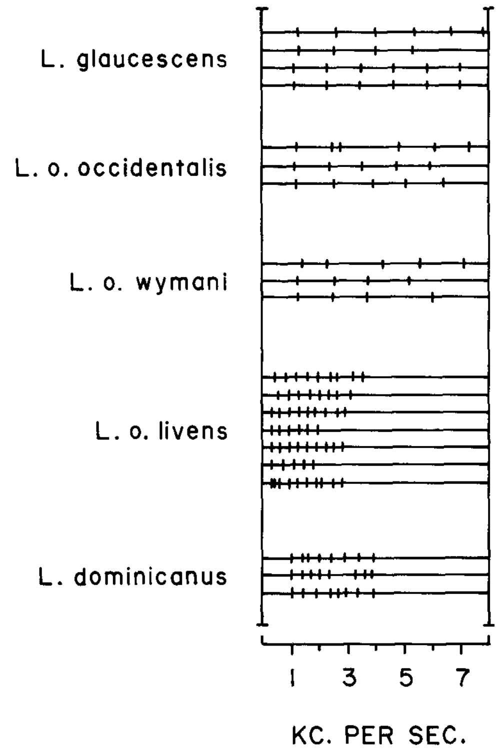

FIGURE 8. Locations of major sound energy bands in mid-section Long Call figures of five types of gull. Samples are from the same populations as those in Figure 7. Each horizontal line represents one sound figure from the Long Call of one bird; altogether, 20 birds are represented. Each vertical bar represents the location of major bands of sound energy. Measurements were taken at the highest point in a given figure.

section Long Call figures E and F) is also evident, although, on average, Head Toss calls have slightly lower pitch (smaller MHIs) and shorter durations (Figs. 1 and 2).

L. o. occidentalis Head Toss calls also resemble some *occidentalis* Yelps; they share a rough first segment, a second segment with larger MHIs, and similar note lengths. It would be difficult to distinguish Head Tosses K2 and L (Fig. 6) (which were accompanied by a visual Head Toss display) from Yelp D (Fig. 6). Other *occidentalis* Head Toss calls have a clear or hollow sound that distinguishes them from Yelps (for the human hearer). The Head Tosses M and N (Fig. 6) have this "clear" sound. They also show distinctive spectra: odd-numbered harmonic bands are stressed—one, three, and when present, five. This physical characteristic presumably gives these notes their distinctive tone (Marler 1969). Head Tosses can also resemble mid-section Long Call figures (compare K and L, Fig. 6 with the second and sixth figures of Fig. 5 G). Close similarities between Head Toss and Long Call notes can apparently occur in other larids as well (Moynihan 1962:126).

LONG CALLS OF *L. OCCIDENTALIS*, *L. GLAUCESCENS*, AND *L. DOMINICANUS*

Long Calls of *L. o. occidentalis* and *L. o. wymani* have similar shapes and figure durations and are readily distinguishable from spectrograms of *L. glaucescens* (Lines 1–3, Fig. 7). *L. glaucescens* calls differ most obviously by having longer durations, and although MHIs of all three are similar, *glaucescens'* energy lies primarily between 2 and 3 kHz, whereas it lies primarily between 1 and 2 kHz in *occidentalis/wymani*. Consequently, *L. glaucescens* Long Call notes are longer and higher pitched, to the human ear, than *occidentalis/wymani* notes. The similarities in *occidentalis* and *wymani* Long Calls suggest that they are properly regarded as the same species, and are more closely related to each other than to any other gulls sampled in this study.

As already described, the *L. o. livens* Long Call differs radically from that of *occidentalis* and *wymani*, having smaller MHIs, lower energy distribution, and no "rough" first segment (Line 4, Fig. 7). The voice is *at least* as different from the two Pacific subspecies of *L. occidentalis* as is the voice of *L. glaucescens*.

At first glance, *dominicanus* calls (bottom line, Fig. 7) bear little resemblance to *livens*. To the human ear, they are noisier and higher pitched. The spectrogram shows a broken internal structure within each figure, accounting for the noisiness, and all sound energy lies above 1 kHz, accounting for the higher pitch. On the other hand, there appears to be more similarity between *livens* and *dominicanus* than between *livens* and *occidentalis/wymani* in that both have only one segment, and bands of energy within sound figures are closely spaced. Figure 8 indicates locations of major bands of sound energy of several calls from each of these same five populations.

To the human observer, visual Long Call display components of *L. glaucescens*, of Pacific *L. occidentalis*, and of *L. o. livens* show no notable differences (Tinbergen 1959, pers. observ.), although the sounds are distinctive. This also seems to be true for Mew calls. This situation illustrates the tendency, noted by other gull investigators (e.g., Goethe 1963), for changes, detected by humans, to occur in vocal components of displays of the large gulls more readily than in the visual components.

DISCUSSION

SELECTION PRESSURES AND VOCAL CHARACTERISTICS

When compared with *L. o. occidentalis*, the narrow range of low-pitched sounds in the *livens* repertoire is striking, particularly in view of *livens'* otherwise close similarities to Pacific populations in behavior, body size, and use of calls. Some calls of Gulf and Pacific populations do show energy maxima at similar frequencies (e.g., most recorded energy in *livens* and *occidentalis* mid-section Long Call figures lies between 0.8 and 1.5 kHz, and recorded Mews from both populations emphasize bands between 1.0 and 2.0 kHz). Nevertheless, *livens* generally restricts energy output in most calls to below 2.5 kHz, while *occidentalis* regularly produces calls with considerable energy in bands ranging up to 5.0–7.0 kHz.

The differences between the populations is not equal with respect to all calls, however. Three of four calls used by individuals already in close contact (Eh-Eh, Choking, Copulation) are not very different in mean frequencies between the two subspecies. It is the four threat, alarm, or advertisement calls—which probably function to communicate over greater distances (Yelp, Long Call, Mew, Plaintive Yeow)—that show the greatest differences, having emphasis on lower frequencies in *livens*.

A comparison of physical features of the breeding environments and colony structures of Gulf of California and Pacific populations suggests why selection might favor lower frequency transmission in advertisement or alarm calls of *livens* and higher frequencies in homologous calls of *occidentalis*. *L. o. livens* nests almost entirely on beaches, preferably within 30 m of the high tide line; consequently the colonies are more or less linear and differ from the clustered colonies of most white-headed gulls, including Pacific *L. occidentalis* (Hand et al. 1981). Visual access to potential mates and approaching aerial predators is restricted in a *livens* colony compared to that available in Pacific colonies. Many Gulf islands are small and beachlines are irregular, so a *livens* gull flying along a beach commonly may see (or be seen by) only a fraction of the pairs that ring the island. Many *livens* pairs may occupy a small cove and be visually isolated from any neighbors. Since low frequency sounds propagate better around obstacles and over greater distances than higher frequencies (Morton 1975, Marten and Marler 1977, Wiley and Richards 1978), selection may favor the use of low frequencies in calls that facilitate long distance advertisement of or contact with other individuals in *livens* because population density in breeding colonies is low and visual contact with conspecifics is relatively restricted.

An important environmental factor that may permit *livens* to profitably transmit at these lower frequencies (between 25 and 1,000 Hz) may be the relative absence of low frequency noise. Western Gulls of Pacific island colonies nest in clusters on suitable terrain all over an island. Colony noise and wind characteristics are very different from those in the Gulf of California: the Gulf is relatively quiet, commonly having no pounding surf or strong winds, and the background noise level from animal sources (e.g., the gulls or other seabirds or pinnipeds in nearby rookeries) is also much lower; a crowded *occidentalis* colony is a cacophony of animal sounds and a wind screen is usually needed while recording.

What factors might favor emphasis on higher frequencies in *L. o. occidentalis* advertisement and alarm calls? One possibility, suggested by the preceding comments, is that background noise in Pacific coast colonies may provide too much competition to make lower frequency vocalizations useful over more than short distances. Also, features that are correlated with the expected spacing of individuals in relation to the degradation of sound in a particular habitat may sometimes be more relevant (Schleidt 1973, Wiley and Richards 1978) than the simple ability for the sound to propagate as far as possible. Signals that degrade in ways that allow receivers to judge the signal's distance from them—i.e., signals that emphasize locatability—might be more important than those that merely maximize distance of transmission. Maximum distance of transmission, per se, might not be as important, or any more so, in *wymani* and *occidentalis* colonies than the ability to be localizable within the milieu of a crowded, noisy, and windy colony where visual contact with other birds is readily possible. Some *occidentalis*/*wymani* calls have features that could improve locatability in two ways (Yelps, B–D, Fig. 6; Long Call, G, Fig. 5; Mews, A–D, Fig. 5). First, wide band sound (i.e., noise) found in the first segment is thought to enhance locatability (Konishi 1973, Wiley and Richards 1978), and second, spectral characteristics of second segments could facilitate ranging. If the spectral structure of a signal is known (as it is emitted), ranging can be accomplished by comparing separate features of the received signal; for example, because high frequencies attenuate faster, a receiver knowing the spectral structure of a signal at its source can, in theory, judge its own distance from the source by comparing the relative attenuation of the frequency bands (Wiley and Richards 1978).

In calls presumed to transmit information at a distance (Long Calls, Yelps, Mews, Descending Yeows), the presence of four to six widely spaced harmonic bands in *occidentalis/wymani* would seem to make them suited for ranging. Ranging can only be used, however, when the emitted spectrum and the amplitude envelopes are stable with each utterance. Redundant transmission also facilitates ranging. The likelihood that these three criteria are consistently met seems particularly plausible in the case of Long Calls. Mid-section figures have stereotyped form, they show redundancy (each utterance repeating the mid-section figures a number of times), and although recorded amplitudes vary with distance from the source, as would be expected, I have the impression that the amplitudes at which they are uttered are remarkably consistent.

The Long Call functions importantly in all gull species (that have been investigated) in proclaiming territory ownership and attracting females; in some species, parts of the call are individually distinctive and used for recognition by a caller's mate or chicks (Beer 1970a, b, Wooller 1978). The stereotyped nature of the sound figures has been noted by many investigators, although rarely quantified (but see Wooller 1978). The call may have become a *long* one (with repeated similar elements) not only because these features get attention and indicate that a specific gull is present, but also because they may facilitate a receiver's ability to spot a particular calling individual. This might be important under particularly crowded conditions, or when making visual contact speedily (e.g., by mates out of visual contact) is advantageous.

TAXONOMIC SIGNIFICANCE OF VOCAL DIFFERENCES

L. o. livens differs notably from the two other *L. occidentalis* subspecies in adult leg and foot color (yellow in *livens* versus flesh in *occidentalis/wymani*), characteristics of juvenile plumages and plumage sequences (Devillers, unpubl. data), iris and eye-ring colors (irides: *livens*—clear, golden-yellow; *occidentalis/wymani*—yellow with varying degrees of brown flecking, ranging from almost clear yellow to almost brown; eye-rings: *livens*—yellow-orange; *occidentalis/wymani*—varying from "washed-out" yellow to yellow-orange), and nest site preference (*livens*—only on beaches, just above high tide line; *occidentalis/wymani*—suitable terrain anywhere on an island). My study has revealed both similarities and differences in vocalizations. All calls are homologous, used with virtually identical visual components in similar social contexts. The calls of all subspecies also share similar variability within call types (e.g., first figures in Long Calls and in Copulation calls are of longer duration than subsequent sounds, and within all subspecies, Head Toss, mid-section Long Call figures, and Yelps show close similarities).

Many calls differ significantly in pitch and general configuration, but these differences would not necessarily contribute to reproductive isolation. Other members of the Herring Gull complex with demonstrably different voices may hybridize when sympatric (Swarth 1934, Williamson and Peyton 1963, Ingolfsson 1970, Patton and Weisbrod 1974, Hoffman et al. 1978). There is no compelling reason to believe that Gulf and Pacific Western Gulls would not interbreed if the populations were to meet.

How successful such interbreeding might be is another question, particularly in view of potentially critical differences in nest site preferences (Hand et al. 1981). Although Mayr (1969) recommended that isolated populations classified as subspecies should probably be left as such, his suggested criterion for making these moot decisions was that classification should be in line with that used for related members of the same genus. Therefore, it is relevant that even though *L. occidentalis* and *L. glaucescens* hybridize successfully, Hoffman et al. (1978) argued that *L. occidentalis* and *L. glaucescens* are semispecies, and they favored continued recognition of species status for both.

L. o. livens is as much or probably more divergent from Pacific *L. occidentalis* in calls, nest site preferences, immature plumages and perhaps in other characteristics, as the latter are from *L. glaucescens*. Furthermore, unlike *L. glaucescens*, *L. o. livens* is geographically (i.e., reproductively) isolated from Pacific *L. occidentalis*. Additionally, since the physical environment in the Gulf of California differs radically in many respects from the Pacific coast, it seems likely that *livens* experiences a notably different selective regime than that affecting Pacific coast populations. For all these reasons, I conclude that, like *L. glaucescens*, *L. o. livens* is, *at the very least*, a semispecies that merits classification distinct from *L. occidentalis.*

L. o. livens' closest affinities remain unresolved. Comparisons of immature plumages (Devillers, unpubl. data) suggest closer affinities to *dominicanus* than to *L. o. occidentalis. L. o. livens* Long Calls also show similarities to *dominicanus* Long Calls in some respects, but the significance of the differences and similarities cannot be evaluated until we know more about how selective agents affect the structure of gull vocalizations during speciation.

ACKNOWLEDGMENTS

This study was conducted for a doctoral dissertation at the University of California at Los Angeles. Partial financial aid was provided by U.C.L.A. and by the Frank M. Chapman Memorial Fund, American Museum of Natural History. I thank the Point Reyes Bird Observatory for logistic support for work on Southeast Farallon Island and the U.S. Fish and Wildlife Service for permission to work there. The staff of the University of Southern California Marine Station provided logistic support for work on Bird Rock, Catalina Island. I am grateful to the Departamento de la Fauna Silvestre of Mexico for the opportunity to study *L. o. livens,* and F. Armas and A. Diaz for aid during expeditions to Baja California. Tape recordings of *L. glaucescens* and *L. dominicanus* were donated by G. L. Hunt, Jr. and Sr. B. Araya, respectively. I also thank: D. W. Anderson, L. Auzins, L. F. Baptista, N. E. Collias, W. Hoffman, C. Jacobs, R. LeValley, J. Miller, E. S. Morton, B. Nelson, R. J. Pierotti, P. L. Bernstein, S. L. Gish, J. R. Jehl, Jr., and especially my professor, T. R. Howell.

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