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TERRITORY DEFENSE AND ASSOCIATED VOCALIZATIONS OF WESTERN GULLS

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Ewald et al. (1980), Pierotti (1981), and Hunt et al. (1984) have described aspects of territorial behavior of Western Gulls (*Larus occidentalis*), although only Hunt et al. include some analysis of the use of vocalizations (to the extent that certain calls are regularly associated with displays included in their study). I have described (Hand 1981a) the structure of the vocalizations of this species and the general extent and use of the vocal repertoire. Here I present data on territorial behavior, comparing male and female participation, and use of vocalizations by owners and the intruders on their territories.

METHODS

Displays.—Excluding slight differences in the form of Long Call movements, the display repertoire of Western Gulls appears identical to that of Glaucous-winged (*L. glaucescens*) and Herring (*L. argentatus*) gulls (Tinbergen 1959). My terminology for displays and calls follows that of Tinbergen (1959, 1960). I have capitalized display names which, unless stated otherwise, refer to the vocalizations, although several calls (Head Toss, Mew, Choking, and Long Call) are almost always paired with a visual display (see Stout 1975; Stout and Brass 1969; Tinbergen 1959, 1960 for details of the relationship between sounds and movements).

Study site and observation conditions.—Observations were made from a blind for 3–6 h daily from 6 May through 1 June 1975 (26 d, ca 108 h) in a large, dense colony of Western Gulls on S. E. Farallon Island, California. I watched 15 heterosexual pairs that had bred and been observed on the same territories for at least 3 years (Pierotti, pers. comm.) and what appeared to be 2 pairs, of unknown origin (see "Invaders" below) that attempted to establish territories within the study plot. Territory sizes in this area of the Southeast Farallon colony averaged 9–11 m in 1973 and 1974 (Pierotti 1981). The 15 resident pairs were not banded but were individually recognizable on their territories (where all observations were made) as each had permanent, unique markings (tears in foot-webbing, marks on bills, etc.) used for identification for 3 prior years (Pierotti 1981). Most observations were made between 0800 and

1400, although some lasted until 1600 and one ended at 1800. Descriptions of interactions and use of vocalizations were dictated into a recorder and transcribed subsequently.

Most of the data reported here were collected in 43 h of observation that included a period in which courting, nest building, and territorial interactions were frequent (7–12 May, 27 h 45 min), a relatively quiet period during the height of incubation (17–18 May, 8 h 45 min), and a period of increased activity due to the presence of newly-hatched chicks on 3 territories (28 May, 6 h 40 min). During these periods, I recorded only 16 territorial disputes involving neighbors (pairs whose territories were adjacent or which were among the 22 identifiable resident pairs at the study site) and I have not included these neighbor/neighbor interactions in this analysis. Since fights are relatively uncommon, I included any fight observed during the entire 26-day period if I observed the interaction from its inception and knew the identity of at least 1 participant.

Intruder types.—Excluding neighbors, whose intrusions are not treated here, I called any gull that entered a resident's territory an intruder. At 2 sites, 2 pairs appeared repeatedly that would remain, together or singly, for long intervals, often several hours. I could not distinguish them by appearance, but their behavior and owners' responses to them contrasted sharply with behavior of and owner responses to other intruders at these sites and to most intruders at other sites. When challenged by an owner, most intruders left a territory (see below), but these pairs commonly engaged owners in Grass-pulling, Bill-jabbing, and Choking "contests." They also fought owners and engaged in nest construction and copulation on the disputed areas. Consequently, I established two classes of intruders: *invaders*—birds observed on the 2 disputed sites that, at any point in an observation period, responded to owner challenges by Grass-pulling, Bill-jabbing, or fighting, or that engaged in nest construction; and *trespassers*—all other intruders (except neighbors). The pair invading at 1 site was successful and produced 2 eggs. The pair at the second site disappeared after at least 22 consecutive days of observation.

Data recorded.—The following were recorded for each territorial interaction:

(1) behavior of defenders, defined and categorized as follows:

Approaches—(Probably corresponds to Moving Aggressive Upright [Stout 1975]). Defender walks toward intruder.

Charges—(Probably corresponds to Attack [Stout 1975]). Defender immediately or utlimately rushes toward intruder, wings elevated to varying degrees. The bird's feet may leave the ground and its wings may be spread, especially on windy days (Aerial Charge). At the end of the rush, the bill may be thrust forward in a jabbing motion but does not make contact. Other action patterns and signals (e.g., Choking, Mewing, Grass-pulling) may precede the Charge; however, the Charge forces intruder withdrawal at least momentarily, ending the encounter.

Attacks—Defender strikes, pulls on, bites, or otherwise contacts intruder. Fights (repeated or sustained contacts lasting from several seconds up to 15 min) are treated separately.

Long Calls (Aerial Intruder)—Defender Long Calls in response to a bird in the air above its territory. Aerial intruders do not land and no further interaction transpires.

Chokes—Defender goes to the nest and Chokes, or if already present there, Chokes at the nest. If both pair members present, both may Choke. If an owner does not proceed with other behavior, the event is placed in this category whether the intruder leaves or not.

Bill-jabs, Silent-squats, Grass-pulls—When an intruder does not leave, typically at locations that will become (or are) territorial boundaries, prolonged disputes may occur in which these three actions frequently alternate with each other and with vocalizations such as Mewing and Choking. These acts can also be used singly or in combination in less intense encounters. Also included in this category are cases where incubating birds jabbed at intruders without leaving their nests. In Bill-jabbing a seated or standing gull thrusts its bill toward, but does not contact, a nearby individual. When Grass-pulling, the gull holds onto a clump of grass and either pulls backwards or shakes its head from side-to-side. When Silent-squatting, a gull assumes a squatting posture resembling Choking, except it is crouched, breast on the ground. The bird's rear end is elevated, its head is usually in an Aggressive Upright position, and it is silent as it watches the other individual. Silent-squatting typically occurs at the end of or during lulls in intense bouts of Grass-pulling and Bill-jabbing, but also at other times.

No Effective Defense (may Long Call)—Owner assumes an alert Upright Posture, but does not move toward intruders or engage in any behavior described above other than Long Calling. Although Long Calls may occasionally be used, this category differs from the Long Calls category above in that the intruder is on the site. The owners' acts are judged non-effective since, as seems true for *L. glaucescens* (Stout 1975), intruders seldom withdraw upon hearing the call, and postural components of the Aggressive Upright, unaccompanied by movement, are seldom correlated with intruder withdrawal.

(2) sex and status of interactants (owner, invader, or trespasser): There is a notable sexual size dimorphism in Western Gulls, females being smaller than males (Pierotti 1981). Therefore, an intruder's sex was judged to be male or female whenever reasonably possible to do so (in 62.6% of 252 events) by comparing its size to that of a nearby bird of known sex (an owner or invader): a size difference was obvious in male/female interactions; sizes were similar in male/male and female/female interactions. In 15 events (16.3%) involving male owners, it was difficult to classify intruder sex since the owners did not provide clues to indicate which member of an invader pair had their attention. The cases involved No Effective Defense, simple Approach toward an invading pair, or Jabbing towards invaders from some distance. An additional 4 Charges by owner males seemed directed to the male and female simultaneously. Since the invader male was present and in the vast majority of cases was clearly the object of the owners' attention, these 19 cases were tallied under male owner responses to male invaders. Events

involving male owners and female invaders either took place when the male invader was absent or directional clues indicated unequivocally that the female was the object of the owners' attention.
(3) conditions on site: was the owner free to defend the territory because its mate was incubating or was it constrained to cover the eggs or chicks because its mate was absent.
(4) stage of reproductive cycle (pre-nest, pre-egg, eggs, post-hatch).
(5) calls given by owners and intruders.

The following were recorded for each attack or fight:

(1) sexes of participants (see above).
(2) whether a vocal signal and/or visual display was given immediately preceding attack. Behavior tallied was any vocalizations, Oblique, Hunched, or Choking postures, or an Approach or Charge. Non-moving Aggressive Upright (Stout 1975) was not included: it is a finely graded signal and I could not reliably judge when it was used unless it was pronounced.
(3) calls of onlookers (by sex when possible).
(4) calls of participants upon separating after long physical contact during a fight or after an attack.
(5) calls of participants at some point before (but not immediately preceding) or immediately after attack.

Statistical analysis.—For 252 territorial interactions, I compared absolute frequency of use by male and female owners of the 7 response patterns above using χ^2 tests ($\alpha = 0.05$). The relative frequency of use by male and female owners of all 7 response patterns was compared using a 2-way contingency table (Texas Instruments 1977; $\alpha = 0.05$). For Choking and Long Calling, I compared percentage of encounters and numbers of encounters in which owners directed the call to invaders ($n = 92$) vs. trespassers ($n = 160$), using a χ^2 test ($\alpha = 0.05$).

There were 252 interactions involving the responses of individually identified owners to intruders, hence the total n of 252 above. I also wished to compare the calls used by invaders and trespassers. In addition to the above 252 interactions, there were 49 interactions in which invaders ($n = 36$) or trespassers ($n = 13$) entered territories adjacent to those in the study plot and interacted with the territory owners. Thus, for 301 interactions (252 + 49), I compared, using a χ^2 test, the relative frequencies and numbers of encounters in which invaders and trespassers used Long Call, Mew, or Choking when interacting with owners ($\alpha = 0.05$).

RESULTS

Owner defense behavior.—Owners most commonly charged an intruder to terminate intrusions (41%, Fig. 1). The second most common reaction, No Effective Defense (20%), typically occurred when an owner's mate was absent and seemed due to an unwillingness of incubating birds to

TABLE 1. Summary of attacks.

Behavorial interaction	*n*
Male attackers	
1. Male Owner attacks intruder on his own or on a neighbor's site.	5
2. Male Owner attacks a neighbor male.	1
3. Male Owner attacks a neighbor female.	1
4. Male Invader attacks a male Owner.	1
5. Male attempting rape attacks an interfering male neighbor of the female.	1
6. Male Invader attacks a female courting him.	6
Female attackers	
7. Female Owner attacks Trespassing female.	1
8. Female Trespasser courting a male attacks a rival female.	2
9. Female Owner attacks a philanderer.[1]	1
Attackers of either sex	
10. Owner attacks a third year (immature) bird (1 male, 1 female attacker).	2
11. Context preceding attack not recorded (7 male, 1 female attacks).	8
	29

[1] A male that approached a female, not his mate, using behavior identical to that he would direct towards his mate to solicit copulation, but which never mounted the female. Philanderers used Hunched posture and Mewing vocalizations or Head Tossed. Sexual intent of such behavior was suggested by observations where males acting in this way subsequently attempted unsuccessfully to fly onto a female's back (4 cases) or stood on a slightly elevated rock next to a female, giving copulation calls and making tail-wagging movements (1 case). A male that mounted a female that was not his mate and that had not Head Tossed to him was identified as a rapist.

leave the nest: apart from assuming an Upright posture, incubating owners frequently made no further response.

Male owners engaged in significantly more defense interactions than females (male $n = 167$, female $n = 89$; $P < 0.001$), although differences were statistically significant ($P < 0.05$) only for Charges and No Effective Defense (Fig. 1). There were no significant differences (2-way contingency table, $n = 252$, $P = 0.94$) in the relative frequency of the 7 defense patterns used by male and female owners, however, several behavioral patterns that might show sexual differences are lumped together in the next-to-last category and fights, which show a marked sexual difference, are treated separately. Although females defended absolutely less than males, when they defended they used these 7 patterns with the same relative frequency as males.

Although both male and female invaders were commonly present during encounters with owners (72 of 92 invader events), owners' orientations indicated clearly that the male invader was the object of the owners' directed responses in most interactions (79.3% of 92 events). When both owners were present, established pairs did not act in tandem (i.e., by running side-by-side and either Mewing or Choking simultaneously) as they may do before eggs are laid (Pierotti 1981) since one always re-

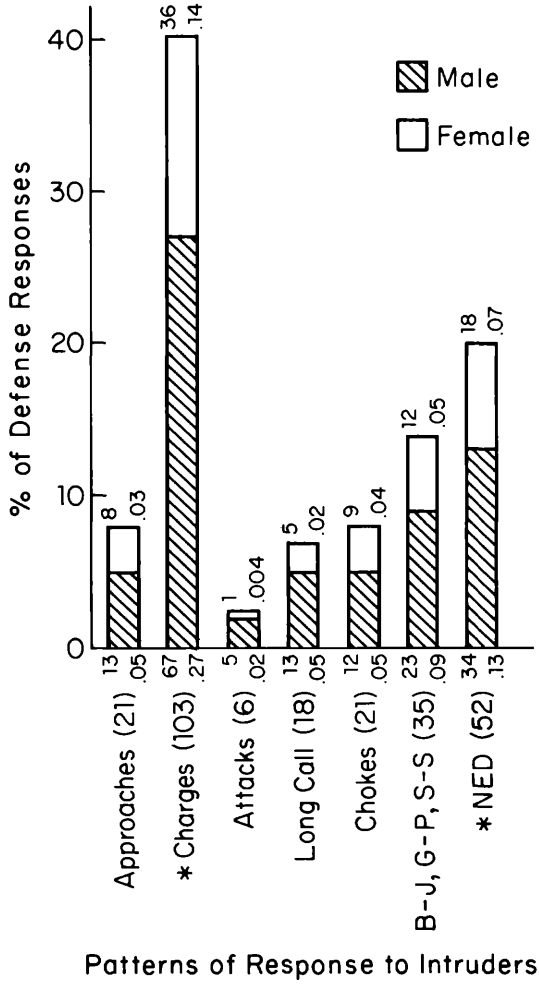

FIGURE 1. Owner responses to intruders. The seven patterns are defined in Table 1. In 4 events, both mates responded and I tallied their actions independently: this gives 256 interactions but only 252 defense responses to intruders. Whole numbers in parentheses are total responses. Numbers by hatched parts of bars refer to male owners, those by open parts to female owners: the whole numbers indicate numbers of events and decimal numbers indicate proportion of 252 events. The numbers of male vs. female responses were compared in each defense category using the χ^2 test: * = significant difference ($P \leq 0.05$).

mained on the nest, but invader mates often acted together, displaying simultaneously or alternately with Long Calling or Choking.

Owners' responses to intruders: male owners compared to females when incubating and not incubating.—When free to defend the territory (left half of Fig. 2), a male's most frequent interaction with a male invader

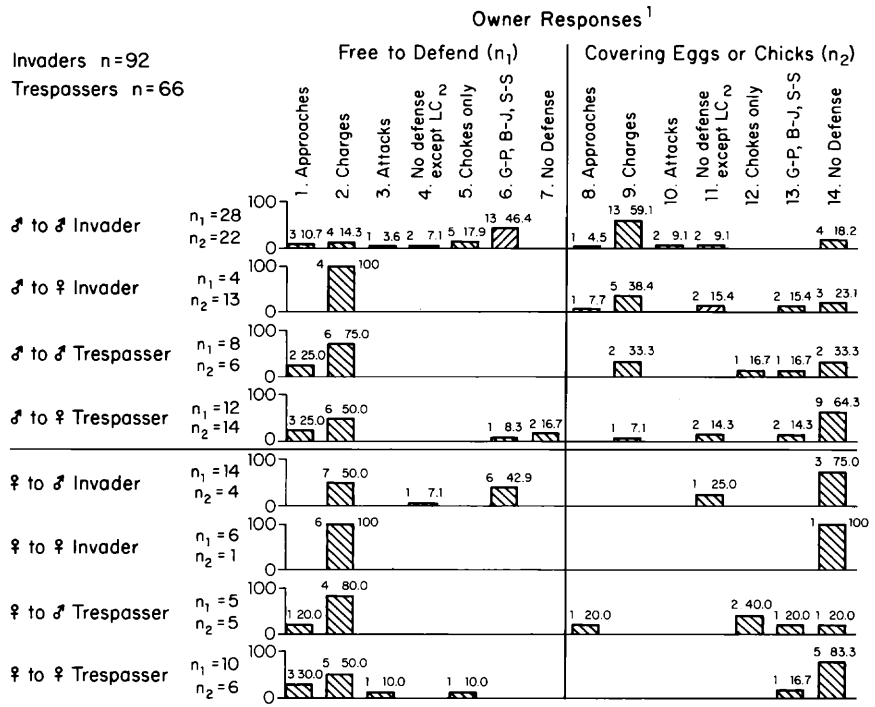

FIGURE 2. Owners' responses to intruders of different sex and class. (n_1—values indicate the number of interactions in which owners were "free" (see text) to defend the territory (left half of figure). n_2—values indicate the number of interactions in which owners were "not free" (brooding eggs or chicks) to defend (right half of figure). Whole numbers on tops of bars indicate number of events; decimal numbers indicate proportion of interactions between the owner and a particular class of intruder (either by "free" or brooding owners, not both, e.g., the proportion of interactions in row 1, columns 1–7).

[1] Categories are as described in Table 1, with the exception of category 4.

[2] Long Calls to intruders: all intruders were on the ground in territories.

was some form of Grass-pulling, Bill-jabbing, or Silent-squatting encounter (Fig. 2, row 1, column 6, 46.4% of 28 male owner/male invader events). Approach (Fig. 2, column 1) or Charge (Fig. 2, column 2) caused male invader withdrawal only 25% of the time. Choking (frequently while facing the opponent across an invisible "boundary" on the outskirts of the disputed territory) with no other follow-through was fairly common (Fig. 2, column 5, 17.9%), although Choking also occurred frequently in conjunction with or after Charges, Bill-jabbing, Silent-squatting, or other hostile acts. In contrast, all encounters with trespassing males (Fig. 2, row 3, $n = 8$) were terminated by Approaches (25%) or Charges (75%). Unlike trespassers, invader males rarely left when Approached or Charged which led to Grass-pulling, Choking, or other owner behavior. Most trespassing females (Fig. 2, row 4) left the study

plot if the male owner merely began to Approach (50%, $n = 12$). In contrast, encounters between male owners and female invaders ($n = 4$) were most often ended by Charges (Fig. 2, row 2, 75%). Invading females typically did not leave immediately when an owner began to Approach. Moreover, female invaders either returned immediately after being supplanted or moved to an adjacent territory where owners were alone and incubating and unlikely to challenge them. Twice ($n = 12$) males free to do so did not eject loafing female trespassers (Fig. 2, row 4, column 7).

When free, female Western Gulls generally responded as their mates did. If females (or males) are compared individually, some variation is apparent, as reported by Hunt et al. (1984) for *L. o. wymani*. For example, Bill-jabbing and Choking bouts at the territorial periphery occurred between one owner female and the male invader while the female owner at the second disputed site never similarly challenged the invading male. Female owners did not allow trespassers to remain ($n = 15$) (Fig. 2, rows 7 and 8). In the one apparent exception (Fig. 2, row 8, column 5) the returning female Choked and probably would have displaced the intruder, but was jabbed by a neighbor, diverting her attention, at which point the intruder left. Sub-adult males were most readily supplanted (Fig. 2, row 7, columns 1 and 2) and my impression is that some, but probably not all, females were reluctant to Charge adult males, which are larger, although they eventually would do so.

When not free (right half of Fig. 2), male owners showed an increase in No Effective Defense (Fig. 2, column 14) or passive defense (Fig. 2, columns 11, 12, and 13), particularly with trespassers ($n = 20$, Fig. 2, rows 3 and 4, column 14). Bill-jabs occurred while owners remained on the nest (column 13). The number of times males left eggs uncovered to challenge invaders of both sexes ($n = 35$, Fig. 2, rows 1 and 2, columns 8 and 9) contrasts sharply with the passive patterns used with trespassers. Indeed, in three cases I assumed, perhaps incorrectly, that the intruder was a trespasser (Fig. 2, rows 3 and 4, column 9). These incidents occurred at sites several territories from the hotly contested areas, and although I could not identify these intruders, the male owners may at once have correctly recognized them as the invaders at the two disputed sites and responded accordingly. An incubating owner Attacked an invader twice (row 1, column 10): in one case, the owner returned immediately to his nest, but in the other the ensuing fight exposed his eggs for at least 10 min.

Incubating Western Gull females (Fig. 2, rows 5–8, columns 8–14) responded differently: they seldom challenged trespassers ($n = 11$) and never challenged invaders ($n = 5$) (also true of the Laughing Gull [*L. atricilla*], Burger and Beer 1975). The large number of male owner/invader interactions results from male owners leaving the nest to challenge invaders while female owners remained on the nest. Invaders did not come onto the owner's territory more when the male was incubating. Behavior directed by owner females on the nest to trespassing males

appeared to be responses to copulation attempts (Fig. 2, row 7, columns 12 and 13).

Use of calls by owners and intruders.—Of 252 interactions, owners used Long Calls in only 45 cases (18%). They used Long Call in 14% of 92 interactions with invaders and 20% of 160 interactions with trespassers, a difference that is not significant. Owners used Choking in 16% of the 252 interactions. In any given interaction, owners tended to use either a Long Call or Choking or, less commonly (4%) Mew, rather than any combination of calls (in only 3% of events were 2 or 3 calls used). Choking was used in 22% of interactions with invaders and 13% of those with trespassers, a suggestive but not statistically significant difference. While expected values were too small to justify statistical comparison of owners' use of Mews or multiple calls when interacting with invaders (Mew n = 8; Multiple Call $n = 7$) versus trespassers (Mew $n = 3$; Multiple Call $n = 2$), the trends were in the same direction: more use with invaders than with trespassers.

Attacks and fights.—Most aggressors in attacks and fights were males (79.3% of events, Table 1). Most attacks involved a sudden lunge or dash by the attacker which pecked the victim, pulled on the victim's wing or tail, or grabbed the victim by the neck. If grabbed, most victims were released after a short struggle. Attacks were commonly associated with territorial disputes (Table 1, behavioral interactions 1, 2, 3, 4, 7, 10), courting (generally males attacking females; Table 1, 6 and 8), and philandering (Table 1, 9). Protracted fights (several min duration) occurred only between male owners and male invaders (Table 1, 1), and commonly involved grasping and pulling each others' bills and attempts to twist the opponent off balance; if a bird succeeded in grasping the other by the neck, he would strike blows with his wings, attempt to down his opponent, and might attempt to peck the victim's head after releasing the neck.

Use of vocalizations or other signals in attack contexts.—I examined attacks and fights in two ways: (1) to see what signal, if any, immediately preceded an attack, and (2) to see what vocal signals were associated with a willingness to attack. The majority of attacks (69.6%, $n = 29$) were not immediately preceded by any signal I could detect. Attackers Choked immediately prior to 5 attacks (17.2%) and Mewed immediately prior to 4 attacks (13.7%). Moreover, absence of vocal signals characterized 50% of the interactions ($n = 29$). Choking was the most common call attackers used at some point before, but not immediately preceding or immediately after attack (11 cases, 37.9%, $n = 29$). Other calls used similarly were Long Call (6 cases, 20.6%), Mew (6 cases, 20.6%) and Copulation Call (1 case, 3.4%).

DISCUSSION

Use of calls: owners.—None of the calls was used frequently. Long Call and Choking occurred in nearly the same number of encounters, but each

was used in less than 20% of all interactions. The Long Call was used slightly more frequently in owner encounters with trespassers than in encounters with invaders although the difference was not significant. The Long Call does not appear to offer sufficient threat to cause intruders to leave. Both classes of intruders seldom withdrew following Long Calls: subsequently they were Approached or Charged when owners were free, were Approached or Charged by a neighbor (the owner had Long Called from the nest), or eventually left at some point well after the call. Stout (1975) also found low correlation between Long Calling and intruder withdrawal.

Choking was used proportionately more often in owner/invader encounters (22%) than owner/trespasser encounters (13%) and was used significantly more often with invaders than was the Long Call (in 22% and 14% of interactions respectively). If we assume that a greater threat evokes a stronger signal, the proportionately greater use of Choking to invaders suggests that Choking is a stronger or more threatening signal than Long Calling, an hypothesis bolstered by the fact that trespassers withdrew when the owner Choked (all 3 cases, Fig. 2, column 12) whereas invaders seldom did so. This supports Tinbergen's (1959) view that the value of Choking as a deterrent may be greater to casual intruders than to determined ones. When free, a male's most frequent interaction with a male invader was some form of Bill-jabbing, Grass-pulling, or Silent-squatting (Fig. 2, row 1, column 6). Approach and Charge caused invader withdrawal only 25% of the time (Fig. 2). In contrast, Approaches or Charges terminated all encounters with trespassers. These observations indicate that Choking is used when the opponent is unwilling to leave and is a higher level agonistic display than Charge, a distinction that can be unclear leading to misinterpretation of the degree of threat posed by various intruders. For example, in their study of the Greater Black-backed Gull (*L. marinus*), Butler and Janes-Butler (1982) consider Charge a "high level agonistic act" and they draw conclusions about the significance of Charge and Choking that are opposite to mine.

Mews were seldom used by owners but when used were most strongly associated with intrusion by invaders. Indeed 3 Mewing events involving an owner and trespasser may actually have involved invaders because the two invader pairs were not individually marked, but were identified by distinctive behavior performed when at the disputed locations (see methods). It is probable that members of these pairs would occasionally land on or fly over territories of owners in the area of, but not adjacent to, the disputed sites, and that such owners recognized them and treated them as invaders, not trespassers. If so, I would have mistakenly classified these events as owner/trespasser encounters when the owners had reacted to true invaders. Thus, the correlation of Mew by an owner with invader intrusions may be 100%. Encounters eliciting more than one call type from an owner were infrequent and also involved invaders more often than trespassers.

Use of calls: intruders.—Vocal differences between invaders and tres-

passers were marked. Invaders used some call in 38.3% of encounters with owners or other birds landing on the disputed sites whereas trespassers vocalized in only 9.8% of cases. The most striking distinction, however, between invaders and trespassers, was the high frequency of Choking by invaders (29% of events, $n = 128$) and lack of its use by trespassers (0%, $n = 173$). In many larids, Choking has been associated with presence of owners on their territories (e.g., Howell et al. 1974, Tinbergen 1960) and its use by invaders appears to reflect strong invader attachment to the disputed sites. Invaders used Choking in even more encounters than they used Long Calls. Mewing by invaders occurred most frequently in conjunction with Bill-jabbing/Choking bouts and in encounters leading to fights.

Trespassers that Mewed while on an owner's territory appeared to have non-territorial objectives. Two of the 4 cases of trespasser Mewing involved a female that seemed to have no territory or mate: she was seen as a frequent intruder for several days on many sites. Once she Head Tossed repeatedly to a subadult (3-yr) male and when he finally attempted to mount, she attacked him. During two Mewing events, she circled an incubating male owner, Mewing. Two other Mewing trespassers were males that appeared to direct calls to resident females, and one of these males also partially regurgitated food (a bolus moved from the crop approximately half-way up the neck). Thus, all 4 Mewing events involving trespassers appeared to have sexual, not territorial objectives. If so, Mewing in the context of territorial defense would be characteristic of invaders, and not trespassers, as appears also to be the case with Choking.

Grass-pulling, Bill-jabbing, and Silent-squatting.—The Glaucous-winged Gull is similar in appearance to the Western Gull, is the species breeding immediately to the north of the Western Gull, and interbreeds with the Western Gull (Hoffman et al. 1978). General features of territory defense of the two species are similar (e.g., Stout 1975), but some apparent differences warrant comment.

Silent-squatting is not mentioned in other Western Gull studies or by Stout (1975). It is a subtle pattern, infrequently discussed in gull literature, and may have been overlooked (but see "Face-off," Butler and Janes-Butler 1982). Since in my study it was most frequently associated with tense encounters between owners and invaders, it may not have occurred during Stout's study if invader pairs were not present.

Stout also reports that Bill-jabbing and Grass-pulling were infrequently directed to intruders. Because of this and because they were not associated with withdrawal, as were moving Aggressive Upright (my Approach) and Choking, Stout concluded that they did not appear to be an important threat display during intrusions (although they were used during border clashes between neighbors). Possibly conditions that elicit these behavioral patterns, viz., the presence of determined invaders, may have been absent in Stout's study or that of Butler and Janes-Butler, who place Grass-pulling as a "low-level agonistic act." Because my meth-

od of tabulating data does not allow me to separate Bill-jabbing, Silent-squatting, and Grass-pulling, I cannot determine the relative threat value of each, but I am inclined to agree with Tinbergen (1959) that Grass-pulling is an important threat display used in response to determined intruders: it was clearly associated with intrusions by determined intruders in this study. Stout points out that grass-pulling in his study occurred in neighbor/neighbor interactions, where attack is rare, and that its use may thus indicate reticence to attack. He also points out, however, that association of a display with subsequent attack is not necessarily a reliable indicator of its deterrent effect. This is because the most threatening displays would, presumably, elicit withdrawal by a weakly motivated opponent or deter attack by a highly motivated one; in both cases, the signaler avoids an attack or fight. I suspect the latter is the function of Grass-pulling in *L. occidentalis* and that its frequent use with neighbors indicates that neighbors, not assorted trespassers, are perceived by owners as the more serious threat to their breeding effort.

Attacks and fights.—Protracted fights occurred only on disputed sites and between male owners and invaders (Table 1, behavioral interactions 1 and 4), although a female fought briefly on 1 occasion. A female invader drove a rival, trespassing female from a disputed site, pursuing her in flight for some distance; both returned almost at once, and without landing the invader grasped her rival by the bill and dragged her from the ground several feet into the air. (High levels of female-female aggression may be linked to a shortage of breeding males in this colony [Hand 1981a, Pierotti 1981].) Females also struck adult males (Table 1, behavioral interaction 9) e.g., a mated male spent over 1 h soliciting (Mewing and/or Head Tossing) females on surrounding territories and one eventually attacked him. Female Laughing Gulls (Hand 1981b), Western Gulls (Pierotti 1981), and Herring Gulls (Tinbergen 1960) have commonly been reported to attack males that attempt to mount them.

There was a notable sexual difference in territorial behavior when an owner was incubating and its mate was absent. Male owners, especially those surrounding disputed sites, occasionally would leave the nest to expel or fight with invaders. Female owners virtually never left the nest under these conditions. The data support the general impression that female thresholds for aggression are higher, but could indicate that female incubation tendencies are stronger or more difficult to interrupt, 2 hypotheses that are not mutually incompatible.

The majority of attacks (69.6%) were not immediately preceded by a signal. Even in protracted conflicts, my field notes imply that victims could not easily predict an attack. The attacker would rise suddenly and strike, or if Charged would turn and retaliate with an attack rather than withdraw or signal, as was more commonly the case. Tinbergen also mentioned the "all at once" nature of genuine attack (1960:57). The frequent absence of any signal immediately preceding attack seems functionally appropriate, since an element of surprise is presumably favorable to attackers.

To determine which vocalizations were associated with demonstrated willingness to attack, I tallied all calls given at some point before or immediately after attacking. Absence of vocalizations characterized many events (50%). The data also show that, while Choking may not immediately precede attack in a predictable manner, it is used more frequently by birds that will subsequently or have already attacked (37.5% of 29 events) than are either Long Call or Mew (21.0% each).

Combatants were silent during fights, but immediately upon disengagement, one, or commonly both, might Long Call, although they did not invariably do so. Less commonly they might Choke or Mew. Since the outcome of a given "round" of a fight between owner and invader males was often difficult for me to judge, I could not determine which calls, if any, might be associated with winning and losing. Long Calls uttered by male invaders between bouts of fighting were sometimes terminated with a series of Yelps, and Yelps were also uttered (3 occasions) by a male invader being dragged by wing or tail.

Calls of non-combatants during fights or attacks.—All fights had observers, the neighbors of combatants plus birds that flew in from undetermined areas. Some observers occasionally uttered Long Calls, Yelps, or more rarely Mews; others watched silently.

Females of fighting owner males did not become involved in battles, probably because battles I observed occurred when residents had eggs and owner females simply remained on the nest. They appeared peculiarly uninvolved as they did not Long Call, Yelp, or Mew, as many observers did.

Females of fighting invader males remained on the disputed area during fights, often uttering Yelps, and occasionally Long Calling. On several occasions, one female came to her mate's side and uttered Yelps as he struggled with the owner. Yelping was frequently used by invader females, and relatively infrequently by their mates. When fighters separated, both might Mew or Choke, and invader females commonly joined their mates and vocalized similarly. With the exception of Yelps, female invaders generally vocalized less frequently than males, although they did use the same types of calls (Long Call, Choking, Mew).

An immature bird struck while courting on another's territory uttered the Shrill Waver (Hand 1979) and fled. When loafing immature birds (2nd and 3rd yr) were caught by wing or tail they commonly uttered Shrill Waver, Plaintive Yeow (Hand 1979, 1981a), or both before fleeing. After a male dismounted from a forced copulation attempt, the female bit him on the bill and he uttered the Shrill Waver call.

Defense of territory: male and female roles.—All of the relatively uncommon but strategically important fights were between males and nearly two-thirds of the more common responses by owners to intruders were by males. Pierotti (1981) has pointed out the efficiency that presumably can be achieved when the male provides the bulk of defense at the time the female must invest heavily in producing eggs. On the other hand, females during my study performed slightly over one third of the defense

acts (excluding fights). If the female contribution were eliminated, increased pressure might fall on the male to the detriment of the breeding effort. For example, female inattention to defense during male incubation or absence might allow intruders to develop attachment to the site, making their later eviction by the male more difficult. This might increase his energy expenditure for defense or his risk of injury. Either of these might, in turn, reduce his ability to forage for the chicks which could be disadvantageous to the breeding effort since males bring chicks as much or more food than do females (Pierotti 1981). Thus while Western Gulls exhibit a broad sex-role difference with respect to territory defense, the contribution by females is not negligible and may be an important component of a pair's territorial defense investment.

SUMMARY

This study describes territorial defensive behavior of Western Gulls, comparing male and female participation and vocalizations used by owners to two classes of intruder. The results contradict some conclusions from studies on other gull species about the significance of Charge, Choking, and Grass-pulling displays: Charge is the display (or behavior) most commonly used to expel casual intruders and is thus thought to be a relatively low-intensity display while the latter 2 are used most often with determined invaders that demonstrate an unwillingness to be supplanted and are thus considered relatively high-intensity displays. Males performed all fights and the bulk of more common, but less hazardous defensive behavior. Females executed slightly over one-third of the less risky defensive behavior and the female contribution, while less than that of the male, may be an important component of a pair's defense investment.

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