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INCREASED HARASSMENT OF RIGHT WHALES (*EUBALAENA AUSTRALIS*) BY KELP GULLS (*LARUS DOMINICANUS*) AT PENÍNSULA VALDÉS, ARGENTINA

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Abstract

Kelp gulls at Península Valdés, Argentina, have recently developed the habit of feeding on pieces of skin and blubber that they gouge from the backs of southern right whales. In response, the whales flinch violently, submerge, and swim rapidly away underwater. The level of harassment in 1995 was almost five times higher than when first studied in 1984 by Thomas (1988). In 1995, 67% of attacks were aimed at large white lesions on the whales' backs. The proportion of whales with lesions increased from 0.01 in 1974 to 0.32 in 1990. Mother-calf pairs that were attacked traveled at medium and fast speeds for 3.1 h per day, compared to 0.8 h for undisturbed pairs. Mother-calf pairs are estimated to spend approximately 24% of their daylight hours in states of gull-induced disturbance. Little food is available at Península Valdés, so mothers must rely on blubber reserves to support their calves' growth, behavioral development, and migration to the feeding grounds. Even when undisturbed by gulls, mothers often curtail their calves' play and nursing bouts, suggesting that their energy reserves are limited. Increasingly intense harassment by gulls may therefore compromise calf development and might even induce right whales to abandon Península Valdés for other calving grounds.

Key words: southern right whale, *Eubalaena australis*, kelp gull, *Larus dominicanus*, harassment, Península Valdés.

Kelp gulls (*Larus dominicanus*) feed on pieces of skin and blubber that they gouge from the backs of right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina. This behavior may be a recently learned innovation, and it appears to be spreading in the gull population at the Península. Whales respond violently to attacks by suddenly arching their backs and swimming rapidly away underwater (Thomas 1988). Submergence may offer only temporary relief, however, because the gulls often fly above the submerged whales or wait on the water's surface, renewing their attacks when the whales surface again to breathe. The attack behavior may have developed from a behavior first reported by Cummings *et al.* (1972) in which kelp gulls and brown-hooded gulls (*Larus maculipenis*) were "occasionally" seen to ride on right whales at Península Valdés and peck at their backs. At that time we saw only brown-hooded gulls at the Península take strips of peeling skin, and we never saw them gouge out flesh.

In 1984 Thomas (1988) made a detailed study of kelp gull attack behavior at Península Valdés and of the right whales' immediate and longer-term responses to being attacked. Thomas saw attacks on 25 of the 81 d he observed mothers with calves. He recorded 151 gull-attack episodes in 628 whale-hours of observation (0.24 episodes/whale-hour). Ninety-six per cent of the attack episodes occurred in one bay (Fracaso in Golfo San José, Fig. 1), though only

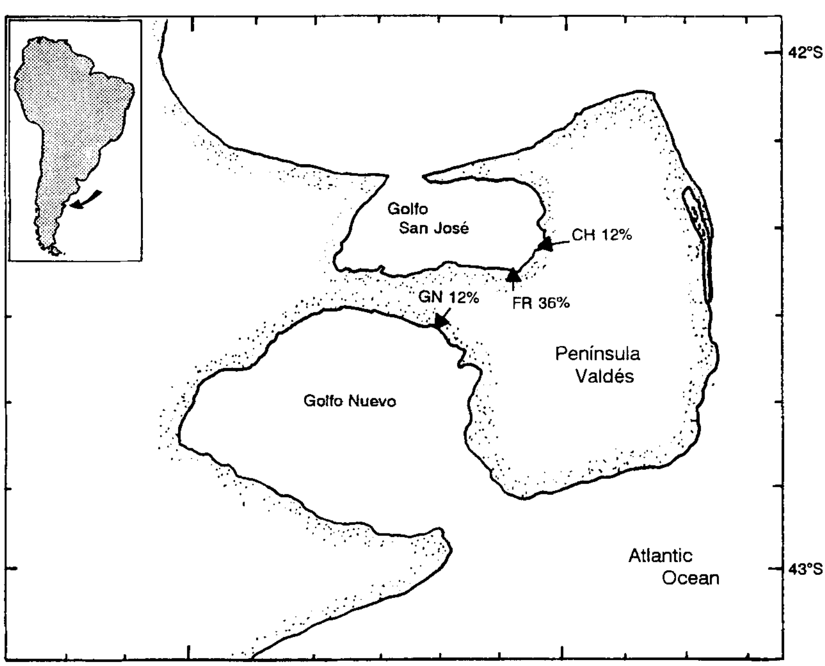

Figure 1. Map of Península Valdés, Argentina, showing the observation sites and the proportion of 5-min intervals with gull attacks at each site. CH: Cliff Hut; FR: Fracaso; GN: Golfo Nuevo.

22% of his observations were made there. Calves were rarely attacked (0.8% of attacks). In 1994 we regularly saw gull attacks in Fracaso, as well as in other regions of the Península. Between 1984 and 1990 our aerial photographic surveys of the whales (Payne 1986) show a steady increase in the number of whales with large (5–20 cm) round white lesions on their backs. Thomas (1988) reported gulls repeatedly attacking an area of gouged-out skin on a whale and enlarging it through the nursery season. The research reported here was undertaken to determine the current extent of gull harassment, the relationship between gull attacks and the white lesions on the whales' backs, and the effect that gull harassment is having on the activity patterns of right whales on the Península Valdés nursery ground.

The whales at Península Valdés have migrated over 2,000 km from their feeding grounds (Best *et al.* 1993) to calve and rear their young in the protected shallow bays of the area (Payne 1986). During the two to three months that right whale calves are on the nursery grounds they grow two to three meters in length (Whitehead and Payne 1981, Best and Rüther 1992) and develop strength and coordination (Thomas and Taber 1984). This growth occurs at a time when a female consumes little food (Thomas and Taber 1984, Payne 1986), and thus the energy for the calf's growth and migration must come primarily from fat reserves in the mother's blubber. The fact that right-whale mothers curtail their calves' nursing and play bouts (Payne 1972, 1976; Thomas and Taber 1984) implies that a mother's energy reserves are limited and may not be sufficient to support growth, extensive vigorous activity of the calf, and the migration that both mother and calf must make before any significant feeding can begin. Gull attacks disrupt the quiescent behavior that is typical of lactating right whales (Thomas and Taber 1984, Thomas 1988).

Materials and Methods

Behavioral observations—In 1995 one to three observers used spotting scopes (20× wide-angle) to track individual adult or subadult whales continuously for periods ranging from 15 min to 6.9 h (mean = 1.3 h, SD = 1.0 h). We refer to the process of making such observations as "following" a whale and to the resulting record as "a follow." As many as three whales were followed at any one time, with each observer following a single focal animal. The task of note-taking rotated among the observers. The notetaker also followed a focal animal. Whales were identified by callosity patterns and back markings (Payne *et al.* 1983) and were followed to distances of two kilometers from three cliff-top observation sites (Cliff Hut, Fracaso, and Golfo Nuevo, Fig. 1). Whales were identified in enough detail to distinguish them from their immediate neighbors on a given day. Except for a few individuals discussed below, too little information about a whale's individual characteristics was recorded to permit its re-identification on a subsequent day. The length of our field season was limited, such that time devoted to making secure, individual identifications would have compromised the behavioral observations. Whales were selected by their proximity to the observation site and their direction of travel and were abandoned when they were too far away to be followed easily.

The temporal sequences of all 183 "follows" of lone mother-calf pairs are shown in Appendices A and B. Seven mother-calf pairs that were easily recognized by white pigmentation on their backs were followed on two or more days of the study (whales 200–206, Appendix A). The other less distinctive individuals (Appendix B) were undoubtedly the subjects of multiple follows without being recognized as previously followed individuals. However, the mean sighting rate (2.2 sightings/individual) and the maximum number of resightings (5) of distinctively marked mother-calf pairs would seem to suggest that around 83 (183/2.2) different individuals are represented in the 183 "follows." The short mean observation period for each whale (1.3 h) is a consequence of the whales' tendency to pass through an observation area. These patterns imply that the subject pool was not dominated by a few individuals.

A variety of techniques was used in data collection and analyses. Instantaneous sampling (Altmann 1974) was used to record the proportion of time whales spent in different behavioral activities. One-zero sampling (Martin and Bateson 1986, Thomas 1986) was used to provide a large-scale description of the attack behavior of gulls. During some follows detailed information was collected about individual attacks: in 96 instances we recorded the exact time between individual attacks; in 1,184 attacks we recorded whether a mother or a calf was the target; in 159 attacks we recorded whether the attacking gull was an adult or a juvenile; and in 326 attacks we recorded where the gull's bill contacted the whale.

The behavioral activity of a focal whale was recorded at the beginning of each 5-min interval (instantaneous sampling, Altmann 1974). Activities were assigned to one of five mutually exclusive categories: (1) surface activity (whale active at the surface of the water, causing white water); (2) fast travel (speed subjectively estimated); (3) medium travel; (4) slow travel; (5) rest (whale motionless).

A gull attack was defined as occurring when a gull landed on a whale's back and pecked one or more times at its skin. Gulls often made repeated attacks in rapid succession on the same whale, and sometimes more than one focal whale was under attack at the same time. We did not have an event recorder, and when attacks occurred simultaneously on two focal whales, the notetaker could not make a continuous record of the time of both attacks. Also, a record of attacks could not be collected at the instant a whale's behavioral activity was noted, because attacks were brief and rarely coincided with the instantaneous sampling of activity. We therefore employed a coarser level of resolution that could be scored consistently and accurately under all observation conditions. Each focal animal was followed continuously when it was at the surface, so that the observer was aware of every gull attack, and each 5-min interval was scored for whether attacks had (1) or had not (0) occurred (one-zero sampling; Martin and Bateson 1986, Thomas 1986). One-zero sampling cannot be used to make unbiased estimates of frequencies and durations of events (Martin and Bateson 1986), but under the conditions of our study it provided the only feasible way to collect data on whale behavior and gull attacks simultaneously. Procedures used to compensate for problems that arise in the statistical analysis of one-zero and instantaneously sampled data will be discussed below.

An "attack episode" was said to occur when a single focal animal was attacked once or repeatedly. Attacks separated by more than five minutes with no intervening attacks were considered to belong to different attack episodes (Thomas 1988). Behavioral data were collected only on subadult or adult whales. However, when the calf in a focal mother-calf pair was attacked we scored the mother's interval as having an attack, because when either member of a mother-calf pair was attacked the behavior of both individuals changed in similar ways, as noted also by Thomas (1988).

Analysis of behavioral observations—To study the long-term effects of gull attacks on the behavior of whales, we compared the behavior of lone mother-calf pairs on days when we never saw them attacked by gulls (days in which they were presumably in "undisturbed" states) to the behavior of lone mother-calf pairs during and after attack episodes. For these analyses we examined the behavior of lone mother-calf pairs during 183 focal follows (Appendices A and B) comprising a total of 2,783 5-min intervals. Sixty-one follows of mother-calf pairs contained no gull attacks. These form the "undisturbed" sample. Since the whales in the undisturbed sample could have been attacked before our observations began, we removed the first 60 min (first twelve 5-min intervals) of each follow. The resulting "baseline" data were then compared to the whales' behavioral states during an attack (behaviors in intervals marked with an X in Appendices A and B) and in the 5-min intervals following an attack episode. Data from the first 5-min interval in an attack episode were excluded from the analysis, since behavioral activity was recorded at the beginning of each interval and attacks usually began later in the interval. Only intervals without gull attacks were included in the post-attack period. For example, in Appendix A, whale 205 experienced three different attack episodes on September 28 and contributed three examples of behavioral states in the first 5-minute interval after an attack had ceased.

To estimate the rate at which individuals returned to pre-attack behavioral states following the end of an attack, we fit exponential decay models (by the method of least squares) to the data for rest and slow travel (Fig. 2a) and medium and fast travel (Fig. 2e). In each case the baseline (undisturbed) frequency of the behavior was rescaled to a "disturbance value" of zero, and the level seen during attacks was rescaled to a value of one, indicating complete disturbance. The equation $y = e^{-kt}$ was then fit to the rescaled data, yielding an estimate of k and thus of the apparent "half-life" of the disturbance induced by attacks. By this criterion the data for rest and slow travel (Fig. 2a) imply a half-life of 5.1 min, and the data for medium and fast travel (Fig. 2e) imply a half-life of 9.9 min. In other words, the amounts of time spent in rest and slow travel appeared to return to undisturbed or normal levels faster than the amounts of time spent in medium and fast travel. It seems likely that the overall level of disturbance decayed with a half-life somewhere between these

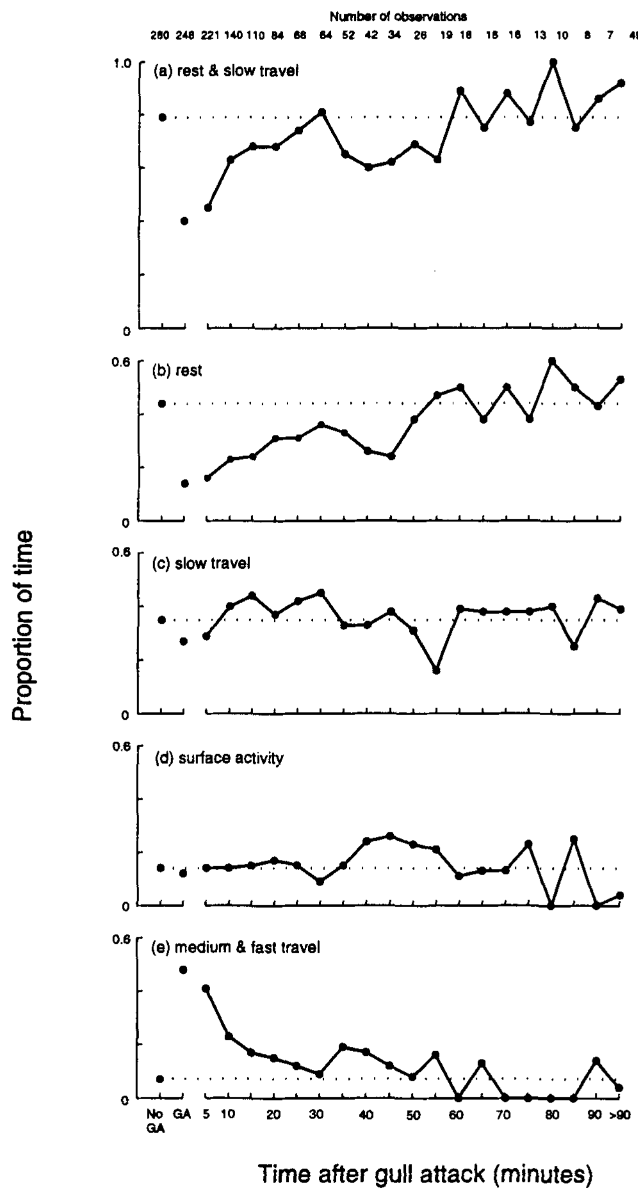

Figure 2. Behavioral responses of lone mother-calf pairs to gull attacks. "No GA" and the dotted lines indicate the behavioral states of mother-calf pairs on days when we did not see the pair attacked by gulls and when they were presumably "undisturbed." "GA" indicates the behavioral states of mother-calf pairs in the second and subsequent 5-min intervals with gull attacks. The points connected by solid lines are behavioral states of mother-calf pairs in the 5-min intervals following the last interval with a gull attack.

two estimates, so we use their average, 7.5 min, in some subsequent calculations.

To generate a quantitative estimate of the amount of time that mother-calf pairs spent under attack and recovering from attacks, we created a model in which the behavioral after-effects of being attacked are assumed to "decay" exponentially with a half-life of 7.5 min. We calculated an average "disturbance score" using the actual pattern of attacks in the follows shown in Appendices A and B. If a 5-min interval was scored as containing an attack, we assumed that the attack took place briefly in the middle of the interval, at which point the whale's disturbance score was set to its maximum value of 1.0 and allowed to begin decaying at a rate determined by the half-life (7.5 min). If the next interval also contained an attack, then the disturbance score (which had decayed for 5 min) would be reset to 1.0, but if there were no attack in the next interval then the score would continue to decay toward zero. The average disturbance score is the integrated area under the curve described by this procedure, over all follows in the data set. It can be interpreted as the proportion of time that a whale was in a state of gull-induced disturbance (*i.e.*, clock time weighted by the relative severity of the disturbed state). A whale that suffered attacks in every interval of a follow would have an average disturbance score near 1.0, while a whale that was never attacked during a follow would have a disturbance score of zero.

Statistical analyses of gull attacks and behavioral states recorded at 5-min intervals are complicated by the fact that attacks and behavioral states of whales will inevitably be correlated between successive intervals, giving rise to artificially inflated degrees of freedom (a form of "pseudoreplication"). An attack episode may continue for tens of minutes, and a gull may return to initiate a second episode on a given whale after searching for other potential targets in the area. Thus, adjacent intervals may be highly non-independent, and smaller degrees of non-independence may contaminate observations made many minutes (even hours) apart. Autocorrelations of this kind clearly occur in our data, as can be seen by inspection of Appendices A and B. Because the behavioral observations associated with 5-min intervals cannot be treated as independently sampled points in any formal statistical test of a hypothesis that assumes independence, we calculated an average attack rate for each follow (number of 5-min intervals with attacks/total number of intervals in a follow) and weighted each rate by the square root of the length of the follow. This approach is conservative, since events at opposite ends of a long follow are likely to be effectively independent. All formal analyses were carried out with JMP version 3.1 (SAS Institute Inc. 1995).

Lesion analyses—Every year since 1971 we have made aerial surveys of the population of right whales at Península Valdés by photographing the callosity pattern of each whale encountered while flying along the perimeter of the Península (Payne 1986). To determine the proportion of whales with lesions we reanalyzed the survey photographs from 1974 through 1990. (1980 and 1981 were excluded from analyses because of poor survey coverage.) We examined all individually identified whales and recorded whether their backs were clearly visible in the photographs, and if so, the number of lesions that were seen. Between-year comparisons of 18 whales allowed us to examine the temporal history of lesions.

Results

Between 8 September and 17 October 1995 we made 242 focal-animal follows of whales during 139 hours of observation on 29 days. We recorded behavioral activity at the beginning of 3,499 5-min intervals that were distributed among the observation sites as follows: Cliff Hut 1,824; Fracaso 759; Golfo Nuevo 916. Mothers in lone mother-calf pairs were the most frequent focal animals (79% of all 5-min intervals) followed by individuals in multi-whale groups (including mother-calf pairs accompanied by adults or subadults) (14%), followed by lone adults or subadults (7%).

Frequency of attack—Whales were attacked by gulls on all days of the study. Lone mother-calf pairs experienced 264 gull-attack episodes in 232 whale-hours of observation (1.14 episodes/whale-hour). Gull attacks occurred in 17% of the 3,499 5-min intervals, but the frequency was much higher at Fracaso (36%) than at the nearby Cliff Hut (12%) or at Golfo Nuevo (12%) (Fig. 1). The threefold difference in rate between sites is highly significant (one-way ANOVA of the average attack rate of entire focal-animal follows: $F = 31.6$, df = 2, $P < 0.0001$, r^2adj. = 0.25). Attack episodes ranged in length from single attacks lasting just a few seconds to an episode that lasted 1.4 h. Most attack episodes (55%) began and ended in the same 5-min interval; 76% lasted less than 15 min; only 3% lasted more than 30 min. Within an episode, attacks occurred at an average rate of one every 78 sec (SD *t* 67.1, 135 attacks, 96 interattack intervals on 13 whales over a six-day period).

Lone mother-calf pairs were attacked significantly more often (mean attack rate of 0.19 for follows of lone mother-calf pairs) than other groupings of whales (mean attack rate of 0.09 for follows of individuals in groups containing lone adults, mothers and calves with other whales, and mating groups) (one-way ANOVA: $F = 9.7$, df = 1, $P = 0.002$). This effect, and that of site, remained nearly identical in magnitude and significance in a two-way ANOVA incorporating effects of group type and site (group type: $F = 9.3$, df = 1, $P = 0.0025$; site: $F = 33.5$, df = 2, $P < 0.0001$). Attacks on mother-calf pairs were directed at the calves almost as often as at the mothers (44% of 1,184 attacks). Juvenile gulls (determined by plumage) were the attackers in 31% of the attacks when the age of the attacking gull was noted (159 attacks in five days at Cliff Hut, seven days at Fracaso and two days at Golfo Nuevo).

Attack frequencies appeared to vary with the tide cycle and time of day. Attacks occurred throughout the tide cycle but were relatively less frequent at low and rising tides (Fig. 3). Gull attacks were more frequent toward the end of the day (attacks in 16% of 1,742 intervals between 0800 and 1500 compared to 32% of 970 intervals between 1500 and 2000). This pattern occurred at each of the three observation sites (CH: 12% *vs.* 17%; FR: 36% *vs.* 42%; GN 8% *vs.* 21%). The effects of tide and time approach or reach

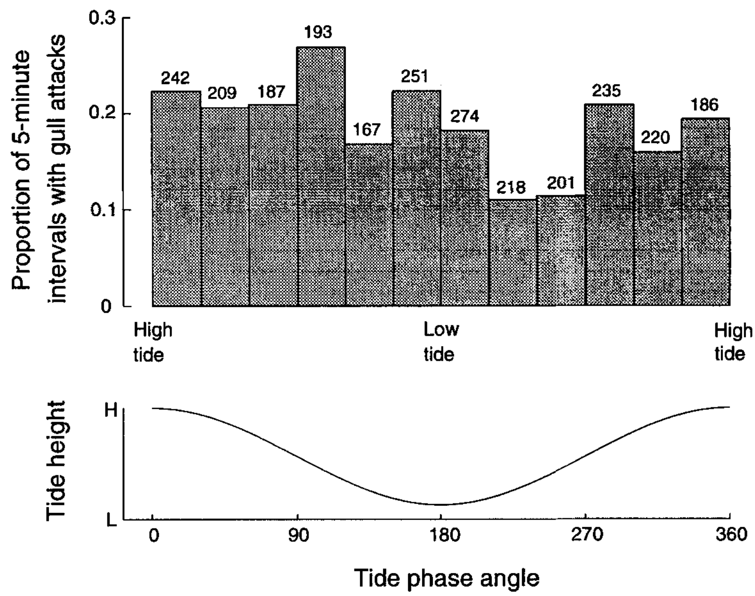

Figure 3. Frequency of gull attacks during different phases of the tide cycle in 2,583 5-min intervals recorded at Cliff Hut and Fracaso. The number of 5-min intervals of observation at each tide height is shown at the top of each column.

nominal significance in logistic multiple-regression analyses of the 5-min-interval data, but such significance must be viewed skeptically for reasons explained above.

Other possible causes of heterogeneity in the frequency of attack seem unlikely to explain as much of the variation as those mentioned above. For example, the average attack rate did not vary significantly among days within sites (CH: $F = 1.23$, df = 16, $P = 0.26$; FR: $F = 0.82$, df = 6, $P = 0.56$; GN: $F = 0.46$, df = 0.46, $P = 0.71$). Individual whales did not vary significantly in their inherent attractiveness to gulls, as judged by a two-way ANOVA of the attack rates of the seven individuals that were seen on two or more days (whales 200–206, Appendix A) with individual and site as the main effects (individual: $F = 0.76$, df = 5, $P = 0.59$; site: $F = 2.01$, df = 1, $P = 0.18$). The effect of individual is only slightly stronger in a one-way ANOVA that ignores the effect of site ($F = 0.95$, df = 6, $P = 0.50$).

Behavioral response—Gull attacks caused abrupt and prolonged changes in whale behavior. Undisturbed mother-calf pairs spent 79% of their time in rest and slow travel which are the predominant behavioral states of mothers when not disturbed by gulls (Fig. 2a, "No GA"). But when attacked by gulls ("GA"), their rest and slow travel plummeted to 40%. The whales returned briefly to undisturbed levels of rest and slow travel (dotted line in Fig. 2a) after 30 min following an attack episode but did not maintain these levels until about 60 min following an attack. This pattern suggests that the length of time to recovery could be as little as 30 minutes but is probably closer to 60 min. In

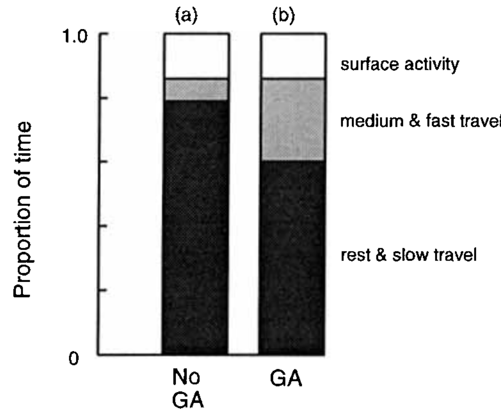

Figure 4. The proportion of time lone mother-calf pairs spent in different behavioral states when they were (a) undisturbed (280 5-min intervals), and (b) disturbed (1,246 5-min intervals) by gull attacks.

the interval 35–60 min after gull attacks, levels of rest were reduced, and surface activity and medium and fast travel were elevated (Fig. 2b, d, e). This period was followed by the highest observed levels of rest and slow travel (87% for intervals $\geq$ 60 min compared to 79% for undisturbed whales, Fig. 2a). (The variation in proportion of time spent in rest and slow travel after 60 min. is the result of small sample sizes.) Rest and medium and fast travel (Fig. 2b, e) appear to be the activities most affected by gull attacks, while surface activity and slow travel (Fig. 2c, d) appear least affected.

Mother-calf pairs that were attacked by gulls (Fig. 4, column b) spent 26% of their time in medium and fast travel—a large increase over the baseline rate of 7% for undisturbed mothers with calves (Fig. 4, column a). Averaged over a 12-h daylight period, this amounts to 2.3 h of additional high-energy swimming each day beyond what would have occurred in the absence of gull attacks (50 min).

Assuming a disturbance half-life of 7.5 min, the exponential decay model estimates an average disturbance score of 0.24 over all follows of lone mother-calf pairs. This figure implies that a mother-calf pair typically spent the equivalent of 24% of its daylight hours (or 2.9 h of a 12-h day) in a state of gull-induced disturbance. Lower (5.1 min) and higher (9.9 min) estimates of the half-life of disturbance give average disturbance scores of 0.19 and 0.27, respectively.

Relationship between gull attacks and white lesions—The white lesions occur on the whales' backs in areas exposed to air when the whales are resting or surfacing to breathe. Of the eighteen whales that allowed a between-year comparison of lesions, six had lesions that persisted over a two-to-four-year period, nine had lesions that disappeared in that time and three developed new lesions in a two-to-three-year period. Gulls directed their attacks at lesions on the whales' backs in 67% of the 326 instances in which we could clearly see where a gull's bill contacted the whale. Other attacks were directed at the head region

Figure 5. Lesions on the back of a right whale at Península Valdés, Argentina. (Photograph by R. Benegas)

(17%), the belly (10%), and smooth skin on the back (6%). Photographs of lesions on living whales (Fig. 5) show that the marks are concave and that the edges are ragged in a way consistent with their having been created by repeated stabs and gouges with an implement the size and shape of a gull's bill.

Our aerial survey data show that the proportion of identified right whales with lesions rose from 0.01 (of 88 identified whales with clearly visible backs) in 1974 to 0.32 (of 157 whales) in 1990. Between 1974 and 1985, whales with lesions were seen primarily in Golfo San José, rarely along the Outer Coast, and never in Golfo Nuevo (Fig. 6a). In 1986 they began to appear in Golfo Nuevo, and during the late 1980s the proportion of whales with lesions increased rapidly in both gulfs (Fig. 6b).

Discussion

Harassment by kelp gulls may now constitute a serious problem for the right whales at Península Valdés. The level of harassment in 1995 was almost five times higher than when it was first studied in 1984 (1.14 episodes/whale-hour compared to 0.24 episodes/whale-hour). The harassment has spread from a single bay to other regions of the nursery ground. Calves were rarely attacked in 1984 but now are attacked almost as often as their mothers (44% of attacks). Twenty-four percent of a nursing mother's day may now be spent under

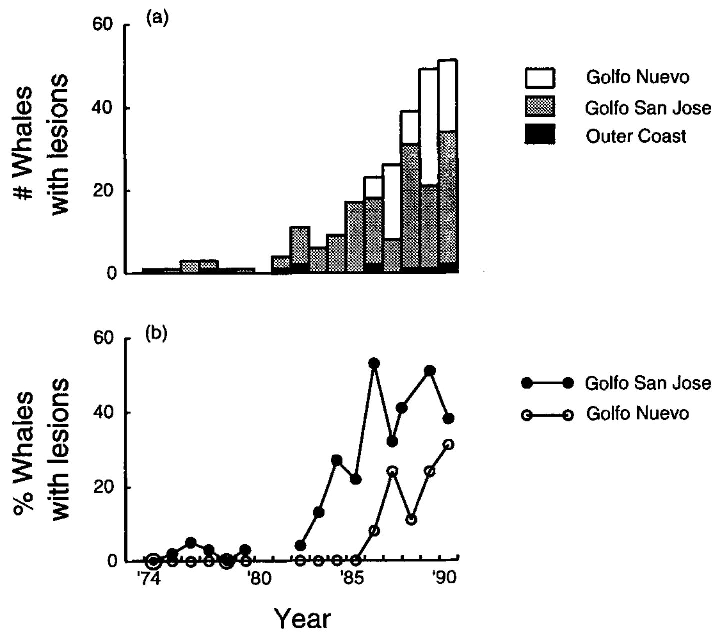

Figure 6. Temporal increase in (a) number and (b) proportion of right whales at Península Valdés with lesions on their backs. Whales with lesions did not appear in Golfo Nuevo until 1986 (1980 and 1981 excluded because of poor survey coverage).

attack or recovering from attack. Because of gull attacks, mothers spend 3.7 times more of their daylight hours traveling at medium and fast speeds than they otherwise would. Gull attacks influence whales in ways other than increasing their swimming speed. For example, some whales change their posture to keep their backs underwater, while others remain underwater for prolonged periods (Thomas 1988). One whale in 1995 responded to attacks by keeping its head and tail (areas seldom attacked by gulls) high above the water for long periods while sharply depressing its back below the surface.

The increase in time spent traveling at relatively high speeds may deplete blubber reserves that mothers normally use to feed their calves and to migrate back to major feeding grounds. Because there is little opportunity for mothers to feed on the nursery ground, it is difficult or impossible for them to recover the costs of fleeing gull attacks. Thus calves may either be growing less, spending less time in play and other forms of behavioral development, or migrating prematurely. Calf survivorship may also be declining. It seems possible that gull harassment could eventually drive right whales from the area.

The white lesions on the whales' backs are similar in appearance to human and dolphin skin lesions caused by viruses, pollutants, and UV-B radiation (Simpson and Gardner 1972, Greenwood *et al.* 1974, Geraci *et al.* 1979, Morison 1989, Haebler and Moeller 1993). Delphinids appear to develop an immunity to pox viruses (Van Bressem and Van Waerebeek 1996). The appearance of additional lesions on three right whales after a two-to-three-year period suggests that the whales do not develop an immunity to the factor causing the lesions. Similar lesions have not been seen in the right whale populations off South Africa, the eastern United States or southern Australia (P. Best, P. Hamilton, S. Burnell, personal communication). We conclude that kelp gulls are probably causing the lesions, or are at least responsible for enlarging small pre-existing lesions, because (1) the gulls often aim their attacks at the lesions, (2) the ragged edges of the lesions look as if they could have been made by a gull's bill, (3) Thomas (1988) saw gulls enlarge a lesion on one whale's back by attacking it repeatedly during the nursery season, and (4) the lesions occur almost exclusively on parts of the whales' backs that are above water when the whales surface to breathe.

If gulls are causing the lesions, then the geographical distribution of whales with lesions (Fig. 6a) shows that gull-attack behavior became established in Golfo San José before it appeared in Golfo Nuevo. It seems likely that the behavior originated in Fracaso, the bay in Golfo San José where Thomas saw most of the gull attacks in 1984 and where the attack frequency was highest in 1995. The rapid increase in the proportion of whales with lesions in the 1980s (Fig. 6b) probably reflects an equally rapid rise in the level of harassment during this period.

Gulls have probably fed on the skin of whale corpses and on sloughed (dead) skin of living whales for millenia. But feeding on skin and blubber gouged from the backs of living whales appears to be a new development among the kelp gulls at Península Valdés. The fact that juvenile gulls are also involved in attacking the whales indicates that the behavior is spreading through imitation of birds that have already learned the technique. The history of the gull attack behavior is similar to the classic example of natural learning shown by British tits. These birds learned to tear foil and cardboard from the tops of milk bottles so they could feed on the milk inside (Fisher and Hinde 1949). The behavior was originally observed in 1921 and spread from several centers through imitation. By 1947 it had become widespread and was used by at least eleven different species of birds.

Many species of gulls have varied diets (Pierotti and Annett 1990). Although the natural diet of kelp gulls consists of mollusks and other intertidal invertebrates, their diet is extremely flexible and varies with available food sources, often including those created by human activities (Murphy 1936). For example, in the early 1900s kelp gulls fed on carcasses at shore whaling stations and slaughter houses, and they were hated in Patagonia for attacking young lambs (Murphy 1936). The apparent reduction in gull attacks at times when feeding areas in the intertidal zone are free of water suggests that the attacking gulls take foods other than whale skin and blubber. We suspect that the synchrony with tide cycle is real because it is consistent with observations of other gulls and shorebirds, where feeding rates increased on exposed intertidal areas at low or low and rising tides (Burger *et al.* 1977; Burger 1983, 1984; Puttick 1984). A mussel bed near the Cliff Hut observation site regularly attracted gulls when it was exposed during low phases of the tide cycle.

Kelp gull populations at Península Valdés have grown rapidly in the last

15 yr (Bertellotti *et al.* 1995; P. Yorio, M. Bertellotti, P. Gandini and E. Frere, personal communication). Nesting pairs at the colony nearest to Fracaso nearly tripled between 1979 and 1994 (from 1,920 to 5,397 pairs) (Bertellotti *et al.* 1995). The human population on the nearby mainland also grew during this time, supported by an aluminum factory, three fish-processing plants, and a thriving ecotourism industry based in part on right whales. Foods provided by humans can be of major importance to many species of gulls (Mudge and Ferns 1982, Spear 1988). Daily movements of gulls to and from waste-disposal sites near the Península suggest that human refuse may have contributed to the growth of gull populations (Yorio, Bertellotti, Gandini and Frere, personal communication). The increase in number of gulls is unlikely to be the sole cause for the observed increase in harassment because the rate of harassment has increased faster than the size of the gull population (attack epidodes/whale-hour increased 4.8 times in 11 yr while the gull population increased 2.8 times in 15 yr). The proportion of whales with lesions increased thirtyfold in the 1980s. This disproportionate increase in gull harassment could be caused by particular individual gulls spending more time attacking whales or by a larger proportion of the gull population feeding on whales. In either case it remains unclear why the rate of attack has increased. The kelp gull population could have outgrown its food supply, or mussel beds could have declined. Increased competition could be driving younger or less competitive birds to seek new food sources.

Right whales are not the only species in Patagonia being affected by kelp gulls. Imperial cormorants, cayenne terns, South American flamingos, Magellanic penguins and hooded grebes are all subject to greater or lesser degrees of harassment (W. Conway, personal communication). We do not know the proportion of gulls involved in harassing the right whales. In many species of gulls, individuals often specialize on particular food types (Pierotti and Annett 1990 and references therein). It remains true, as noted by Thomas (1988), that the number of gulls attacking whales at any given time is a small fraction of the gulls that are visible. To design an effective management program, it will be important to establish the proportion of gulls involved in attacking right whales.

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Appendix A

Nineteen "follows" of individually identified mother-calf pairs seen on two or more days. "Follows" are identified by the number given to each whale, the observation site, the date in 1995, and the time the "follow" began. Five-minute intervals without gull attacks are indicated by a period. Intervals with gull attacks are indicated by an X.

Mother-calf pairs followed on more than one day

```
200 CH 0916 1300 ....................x.............
200 FR 0926 1035 xxx..
200 FR 0928 1345 ....xx.....
200 FR 1009 1720 xxxxx.xxxxxxxxxxxxxxxxxx.
200 FR 1016 1725 x...x.......

201 CH 0914 1040 .....................
201 CH 0916 1335 ............xxx.x...
201 CH 1001 1235 ............x..xxxx...............
201 FR 1017 1220 ........

202 CH 0919 1500 .........
202 FR 0926 1300 .....xx..

203 CH 0911 1650 xxx.x.
203 CH 0916 1355 ........xxxxx...

204 CH 0920 1130 x.x.x........xx.x......xx...x.xx.x...
204 CH 0929 1035 ...x.......xx......x..........................

205 FR 0928 1215 ...xxx.....xx.xxxx..
205 FR 1010 1405 .x............xxx...xxx.x...

206 GN 0916 1115 .xx................xx............................x.
206 GN 0924 1605 ..x...............
```

Appendix B

"Follows" of lone mother-calf pairs that were not individually identified. "Follows" are grouped by observation site. Individual "follows" are identified by the date and time the "follow" began. Five-minute intervals without gull attacks are indicated by a period. Intervals with gull attacks are indicated by an X.

Cliff Hut (CH)

```
0908 1430 ........
0908 1505 ......
0908 1510 ..xx.
0908 1630 .........
0908 1630 ..............xx...
0908 1630 ..x.........x......
0908 1630 .x...........x.....
0908 1715 .....x..
0909 1550 ......x..
0909 1640 xxxxx.....
0909 1800 ...............
0910 1105 ...........x.....
0910 1105 ...........xx.....xx...........x.....xxx...
0910 1305 xxxx
0910 1400 ..........x.xxxx......
0910 1600 ..xx...
0910 1720 ....
0911 1550 ...
0913 1015 ..........xxx..xxx.
0913 1025 ...
0913 1155 ..........
0913 1215 .xxx...
0913 1430 ....
0913 1430 ...................xx.....
0913 1650 .........
0914 0930 ....................................
0914 1410 ...............
0914 1520 ...........xx.x.
0914 1610 .x.x.xx..xxxxxxxxxxx.x.....xx...
0916 1115 .......x......x
0916 1515 ................x....xxx.
0918 1115 x..x.....
0918 1125 ....x...
0918 1205 ...
0918 1205 ..xxx........
0918 1225 ...xx.xxx...
0918 1615 ......
0918 1700 ....
0919 1030 .....
0919 1040 .......xx........
0919 1050 .........
0919 1140 x.x.....x...
0919 1315 ..x...
0919 1325 x...x...x.........x.
0919 1500 xx..xxxxx
0919 1635 xxxxx.x....
0919 1645 ...x....
0920 1130 ...
0920 1205 ........................................(8.)
0920 1235 ...xx.
0920 1310 ...x.....xxx......
0920 1615 xxx.x.....
0920 1640 ....
0922 0945 ............................x......
0922 1045 x...................x.........x.x.x
0922 1125 ...............
0922 1240 ......x.xx......
0922 1245 ........
0922 1425 ........
0922 1515 ...........
0922 1520 xxxx.....................x..
0922 1550 ........................
0922 1625 .................
0925 1455 ...xxx.
0925 1530 ..xx.x.xx.
0929 1030 ......................................(28.)
0929 1105 ....xx.
0929 1215 ..........
0929 1355 ............
0929 1440 ...x...
0929 1520 .....
0929 1545 ..................
0929 1640 ...
0929 1640 ...........
0929 1715 ....
1001 1205 ...x.x.
1001 1215 .................................
1001 1310 .....
1001 1455 x......
1007 1415 ..x.
```

Fracaso (FR)

```
0926 1040 xx...xxx......
0926 1100 x.xxxx....
0926 1200 xxxx.xxx..x....xxx..
0926 1200 xxxxxx
0926 1240 xxx.
0926 1315 .....xx...
0926 1410 xxxxx.xx
0926 1445 ...xx..
0926 1450 x.....xxxx..
0926 1650 ......
0926 1650 .xx
0928 1105 ...............................
0928 1225 .......xxx....x.........
0928 1405 x...x.x.
0928 1455 .x....
0928 1510 xxxx
1009 1720 xx..x.............x....xx.
1009 1730 ..........x.
1009 1735 x...
1010 1410 ...xxxxx.xx.xx.
1010 1605 x.xxxxx...xxx.....
1010 1715 ..x.
1015 0935 .x..x.x...
1015 1015 .xxx..
1015 1050 ..xx.
1015 1115 .x..........xx....
1015 1330 .xx.xxx...
1015 1420 ..x...x....x..x
1015 1535 .....xx.xx.x..xxxxxxx.xx..x.......
1015 1620 xxxx.xx.xxx
1016 1010 ....x
1016 1010 .xxxxxx..
1016 1050 x........
1016 1125 xxxxx.x
1016 1200 xxxxxxxx.x.x
1016 1355 .x..xxxx
1016 1435 xxxxx.xxx.x.x..
1016 1550 .........x.....
1016 1700 .x.x.x.xxxxx..xx.xxx.......
1017 1000 ....x
1017 1015 ..x.x.x..xx.x.....x......xxxx.....
1017 1040 x.xxx.x.
1017 1130 .......x..
```

Golfo Nuevo (GN)

```
0915 1110 ......
0915 1115 ......................
0915 1115 ......................
0915 1120 .....................
0915 1120 ......................xx.xx.........x...
0915 1140 .................
0915 1145 ................xx.x..x.
0915 1155 .....
0915 1315 x.....
0915 1330 x...
0915 1405 .....
0915 1455 .......
0915 1455 .......
0915 1455 .xx..xxxxxxxxx.x
0915 1530 ..............
0915 1630 ......
0915 1640 ......
0916 1050 ........
0916 1050 xx....x.xxxx.....x.
0916 1100 ............................
0916 1115 ............x............................(10.)
0916 1235 .x.x....
0923 1110 ..........x.....
0923 1110 ..........xx.....xxxxx..x.xx...............
             ...x....xxx.....x...........x..x.x..xxx..
0923 1110 ......x.xx..xx.xx....x.x....x.........
0923 1245 ..................
0923 1420 .........xxxxxxx...xxx.......................
0923 1430 ....
0923 1450 ...x...............
0923 1625 .....x......x.x......
0924 1055 ......................
0924 1055 ..................x.
0924 1055 .................x...........
0924 1240 ..........................
0924 1300 ............
0924 1305 ................
0924 1445 ......x....
0924 1445 ....x.x..........x.
0924 1530 xx..x.x
0924 1550 ......x...x.
0924 1705 ......xx..
```