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9. Sexual Dimorphism and Aggressive Use of Callosities in Right Whales *(Eubalaena australis)*

Abstract

From a long-term study of a population of southern right whales (*Eubalaena australis*) wintering in the waters of Península Valdés, Argentina, we have evidence from 20,000 photographs that individuals are distinguishable by differences in the pattern of their callosities. Determining the sex of these animals has been a problem. Whereas it is easy to identify a mature female (the only consistent companion of a calf), we only rarely get a ventral view of a male to confirm his sex. Nevertheless, we have been able to study sexual dimorphism in this species. We have compared our known females with a group of whales that contains the few known males plus other animals that are more likely males, a judgment based on behavioral characteristics of males. By examining photographs of their heads, we find that these probable males have statistically more and larger callosities than the females. Another external feature that differs significantly between the sexes is the occurrence of temporary scrape marks on the body. Males have more scrape marks than females. We suggest that the scrape marks are caused by the callosities of conspecifics and that callosities function as weapons for intraspecific aggression.

Introduction

Callosities, the raised, thickened patches of skin on the heads of right whales, are relatively smooth in fetuses and calves but become rougher with age (Lönnberg 1906). In adults the true color of most callosity tissue is gray, but from a distance callosities usually appear white due to a partial covering of cyamids, ectoparasitic amphipod crustaceans (see Payne 1976, p. 334 for a color photograph). The variability of callosity patterns is sufficient to make recognition of individual whales possible (Payne, Brazier, Dorsey, Perkins, Rowntree, and Titus 1983).

The function of callosities has been a matter of speculation for years. One hypothesis is that callosities act as a substrate to promote large populations of cyamids and that the cyamids benefit the whales by roaming over their bodies and removing larval stages of sessile organisms which, if they matured, might cause more biological damage to the whales than do the cyamids themselves (Lönnberg 1906). However, numerous underwater observations of free-ranging right whales by ourselves and others indicate that in daylight, at least, cyamids rarely leave the callosities. Furthermore, during a long-term study of southern right whales along the coast of Argentina (Payne, in press), we gained the impression that callosities were larger in males than in females. We describe here 1) our method of testing this suspicion in free-ranging animals, 2) the results, confirming our suspicion of sexual dimorphism, and 3) further results that led to a new hypothesis for the function of callosities -- that callosities function as weapons in intraspecific fights and that these fights occur primarily between males (probably for access to females).

Methods and Results

Data Base

Our principal data base, described by Payne et al. (1983), is about 20,000 aerial photographs of right whales taken over the nearshore waters of Peninsula Valdés, Argentina. Observations were also made from shore, from small boats, by diving underwater, and by examining beached corpses. From 1971 through 1977, 557 whales were identified, 411 of which were seen 2 or more (up to 18) times.

Studying Sexual Dimorphism When Only One Age Class of One Sex Can Be Determined

In order to test our impression of larger callosities in male right whales, we needed to know the sex of as many whales as possible, and we wished to do this in a benign way (their endangered status, furthermore, makes any take illegal). Mature females were easy to recognize by their close association with calves, but the situation with males was much more difficult. Because we have seen occasional reversals of expected copulatory roles both by males and by

females, the only certain indicator of a male's sex is anatomical evidence obtained from a ventral view (see below for a description). Adult males rarely roll over except in active mating groups, where it is very difficult to connect with certainty a clearly sexed ventral view of a whale with a dorsal view of the same whale, showing its callosity pattern.

When we started our comparison of callosity patterns of females and males, we knew for sure the identity (i.e., the callosity pattern) of only nine males, not a large enough sample to compare with our many known females. We got around this problem by selecting probable males ("males") to add to the known males. Probable males were whales with no evidence of being female and with behavioral indications of maleness pieced together from our long-term study of this population of right whales (presented below). We reasoned that a statistical comparison of 50 definite females with 50 "males" that included only a few definitely sexed males would uncover any obvious sexual differences. The error introduced by the accidental inclusion of females on the "males" list would always be in the same direction, causing the impression that the differences between the sexes are less than they actually are. The presence of females on the "males" list could never support the conclusion that the sexes were more different than they actually are or, for example, that males had structures that are missing in females.

We feel that this approach could be used to study sexual dimorphism in field studies on other species in which it is difficult to determine one of the sexes. In fact, if it were possible to know members of only one sex, with none of the opposite sex being recognizable, one could compare a selection of animals of the single known sex with a list of animals of unknown sex and discover any prominent sexual dimorphism if the sex ratio was not strongly skewed away from the unknowable sex. It would be important in such a situation to try to compare animals within the same age class, as much as possible, so as not to confuse any developmental changes with sexual differences.

In our population of southern right whales, however, we did not know the sex ratio, so we attempted to weight our list of probable males as heavily as possible toward actual males.

Sexing Free-Ranging Right Whales

Anatomical Field Marks. While right whale females are slightly larger than males, there is broad overlap, so size alone is an ambiguous determinant of sex (see Omura 1958 for discussion). A male can be immediately recognized by a penis, but it is rare to see one. Ventral apertures are visible more often, and their configurations are unambiguously

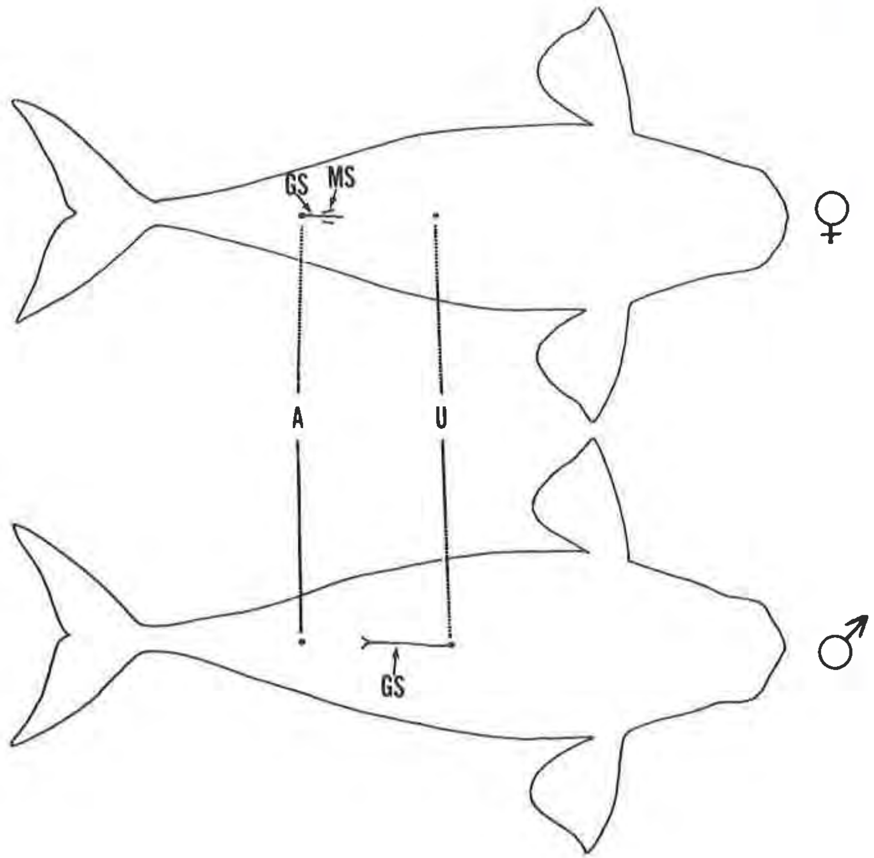


Figure 1. Comparison of anogenital configuration of female and male right whales. A=anus, GS=genital slit, MS=mammary slit, U=umbilicus.

different in males and females (Figure 1; Matthews 1938; Omura 1958). The male's ventral slit is more than twice as long as the female's and is located further forward, originating at or near the umbilicus. The male's ventral slit also bifurcates into a Y at the posterior end, whereas the female's does not (Figure 2). Relative lengths of the genital slits and their positions on the body are often difficult to determine, however, under field conditions. In our experience, the most useful indicator of male sex, outside of a penis, is a visible, separate anus, because the anus, in males, is separated from the genital slit by a distance about equal to the length of the genital slit (Figure 2). In females, on the other hand, the genital slit is more caudal, and the anus is not distinct from the genital slit, but appears to be part of the same continuous opening.

Also, in males, the anus is at the summit of a slightly raised pedestal, reminiscent of the crater of a low volcano (Figure 2f). When whales are in active social groups, one sometimes gets a glimpse just of the anus without seeing a genital slit. Such sightings are definite males. The converse (a glimpse of a genital slit with no obvious anus nearby) is not reliable evidence that the animal is a female unless the observer can be certain that a separate anus, if present, would definitely have been seen.

Mammary slits flank the genital slits of females and are easy to see. They are a good indicator of sex even though they are reported to be present in some males (Slijper 1962, p. 380), because they are, in our experience, invariably inconspicuous in males under field conditions. The nipples themselves are seen only in reproductively mature females and may protrude prominently even after a calf is weaned. One nipple may be noticeably larger than the other (Figure 2e), perhaps indicating that calves nurse more on one teat than the other.

Many whales have a white ventral blaze into which the forward end of the ventral slit extends. Because ventral slits are harder to see against white skin (Figure 2b), inexperienced observers may fail to notice the full length of a genital slit, and under such circumstances, score a male as a female. When a blaze is present, the genital slit can still be used to determine sex by looking for its Y-shaped posterior end. Finally, in males, the margins of the genital slit are smoother and more uniform than in reproductive females, which often have margins that are uneven and somewhat scalloped in appearance.

Unfortunately, we have only rarely been able to identify the callosity pattern of a whale whose ventral side we have seen and sexed. Using anatomical criteria, we have been able to sex only 23 males definitely from all data through 1977.

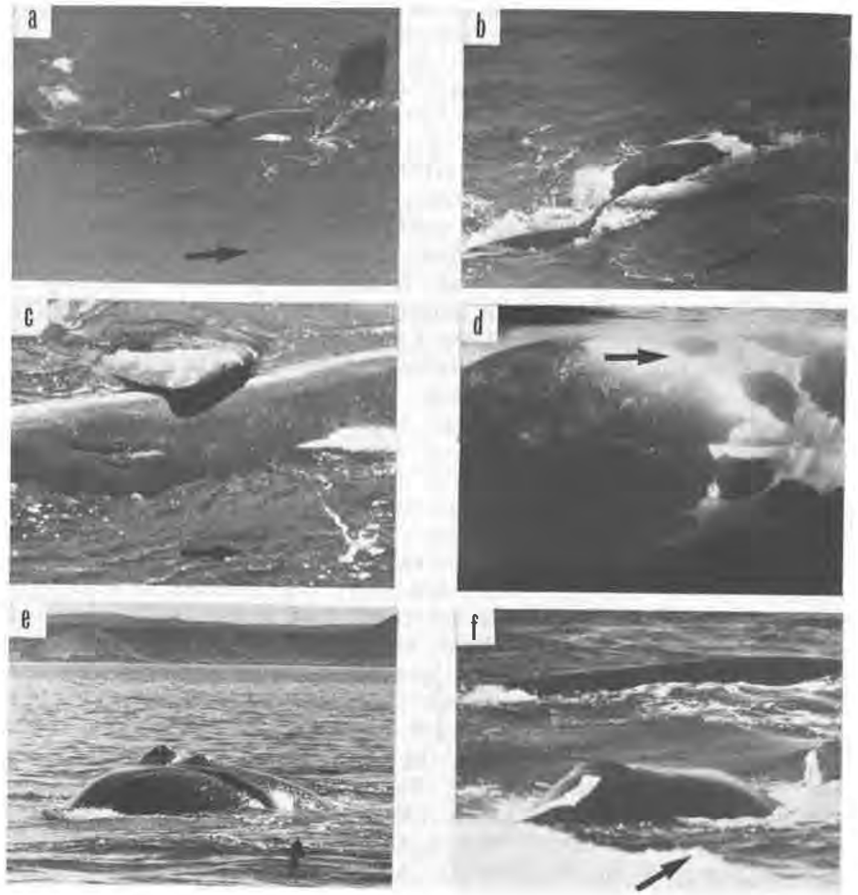


Figure 2. Anatomical features useful for sexing right whales in the field (see also Figure 3). (In all cases the arrow points anteriorly.)
a) Female, showing genital slit, mammary slits, and no separate anus;
b) Male, showing more anterior genital slit and separate anus;
c) Close-up of female genital slit, showing nipple slits flanking it;
d) Close-up of male ventral slit, showing origin of genital slit at umbilical scar and bifurcation at posterior end;
e) Partially everted nipples on a female; the one on the left (the female's right) is larger. A male is pressed against her side (his erect penis can be seen lying on her abdomen;
f) Raised anus of a male.

Behavioral Cues. When we did not have a good ventral view of an animal to indicate sex, we resorted to behavioral indicators of sex. Reproductive females are easy to know by their association with calves. First-year calves are invariably accompanied by an adult, and the adult-calf pairs stay close to shore, often travelling very little, with the adult frequently turning ventral side up either in play or to avoid nursing. On every occasion when we could see the configuration of the ventral slits of such adult companions of calves (more than 100 occasions, but usually with unidentified individuals), we found the adults to be females, often with obviously enlarged nipples.

Furthermore, calves appear to stay with the same adult. Whenever we could positively identify both adult and calf on more than one occasion in the same year, we found that both members of the pair were always the same (29 pairs with up to 7 sightings per pair). We assume that the accompanying female is the calf's mother. Out of 557 known whales, we had evidence that at least 124 of them were mature females from this kind of association with calves.

The situation with males was less straightforward. Our first behavioral indicator of maleness involves the number of consecutive years a whale has been seen as an adult without a calf. When an apparently full-grown right whale has been seen for three or more consecutive years without a calf, we consider it a likely male. Several lines of evidence support this judgment. First, after a female gives birth, she is rarely filmed on a survey flight for the rest of the year without her calf, and she is often seen repeatedly in that year (because she is so often in shallow water). So the chances are very slim that a whale filmed without a calf does in fact have a calf in that year. Secondly, mature females tend to bear calves every three years (Payne, in press). Finally, mature females tend to be seen in the years that they bear calves and not in other years (Payne, in press). In our data, only 11 out of 94 known mature females have been seen for three consecutive years, while 6 out of 17 known mature males have been seen for three consecutive years, a statistically significant difference (chi-square = 6.197, df = 2, $p<0.05$). A full-grown whale seen for three or more consecutive years without a calf, therefore, is more likely to be a male than a female.

The second behavioral indicator that we use to select likely males is participation in mating groups. A mating group is an active group of three or more non-juveniles separated by less than an adult whale length. Most of the action is at the surface and there is much white water. It is caused by rolling, rapid turning and diving, rubbing of bodies and stroking of flippers. Within these groups, there is frequently a whale that lies belly up, at the surface, for long periods. If the sex of this individual can be determined, it is seen to be a female. She may often have another adult whale beneath her, also belly up and holding its breath for long periods. When she rolls into a position to breathe, with her back uppermost, other adults approach the female from behind, swimming on an even keel. As they pull along side and parallel to her, they may stroke along her back with a flipper, perform a roll, and sink under her to try to mate. Occasionally an unsheathed penis can be seen in the midst of all the action. In these groups, as the bellies are turned up, they show male after male, so we have concluded that these groups are composed of more males than females. Because of the confusion in these groups, however, we have been able to identify by callosity pattern only a very few of the males. A whale seen in a mating group, therefore, is more likely to be a male than a female.

This contention was supported by an examination of the individuals found in the mating groups. In 39 mating groups, we identified 98 individual whales, some of which were seen in two or three such groups. For 29 of these 98 whales, we could assign a sex, either certain or likely. (For this analysis, a certain male was known anatomically, and a likely male was a whale that had been seen for three or more consecutive years as an adult without a calf). The 29 sexed participants in mating groups consisted of 16 certain or likely males and 13 certain or likely females, or 55.2% males. Because of the difficulty of identifying males, however, only 21.2% of all sexed whales at the time were males (33 certain or likely males in 156 sexed whales). The percentage of males in mating groups was significantly greater than the percentage of males in the overall population (arcsin-transformed t-test for comparing percentages: $p=3.549$, $df=183$, $p<0.0001$). Thus the identified male:female ratio in the mating groups was 4.6 times that ratio in the total identified population.

The third behavioral indicator of maleness is close companionship to a known male in a non-mating situation. There is reason to believe that males tend to associate with other males. When females are spaced along the coastline, each with a calf, we have observed small groups of whales move from female to female; when a female does not repulse them, one or more members of the group may try to mate with her before the group moves on to the next female. These groups are apparently composed of males travelling together. We have often observed such groups from the shore, where we can determine the sex of participants but cannot see their head patterns well enough to identify them. In such cases, most members of these groups have proven to be males. In addition to this, we know that females with calves usually stay relatively isolated from other whales, while mature females in non-calf years are usually not seen in the areas. Therefore, we felt that any full-grown whale seen close to a known male in a non-mating context was more likely to be a male.

An analysis of the whales seen with the known males outside of mating situations supported this belief. We identified 29 companions of known males, adult whales photographed within their body length of a male where there was no evidence of mating. 13 of these could be sexed: 7 (53.8%, as above) were certain or likely males (as above). Comparing this figure to the percent of males in all sexed whales at the time (21.2% of 156 sexed whales), we found that the incidence of males among the non-mating companions of known males was significantly higher (arcsin-transformed t-test for comparing percentages: $t=2.390$, $df=167$, $p<0.02$).

We list in Table 1 the categories we have used in determining the sex of animals, in decreasing order of certainty. Each category in this list is graded from A to C, with A being at or close to certainty and C being a good guess.

Applying the criteria in Table 1 to our data from 1971 through 1977, we have 106 females of grade A, 29 of grade B and 3 of grade C; we also have 23 males of grade A, 27 of grade B and 17 of grade C.

Sexual Dimorphism in Callosities

In order to compare the callosities of males and females, we took 50 grade A females and selected for comparison the most definite males that we had at the time - 9 grade A males, 12 grade B males and the 29 best grade C males. These whales are listed by identification number and sex grade in Figure 3. The callosity pattern of each whale was scored for 61 features by close examination of our best photographs of it. These features refer to number, approximate size, and shape or configuration of the major callosities -- bonnet, rostral islands, lip patches, mandibular islands, coaming, nostril islands, and post-blowhole islands. For the locations and typical shapes of these callosities, see Figure 4; for a more complete description, see Payne et al. (1983). Appendix 1 defines in detail the callosity features included in Figure 3.

A solid circle in Figure 3 indicates definite presence of a feature and an open circle indicates possible, but not certain, presence. Because we were conservative in ascribing certainty, we suspect that most features indicated by open circles were actually present. As an example of how we scored the callosity patterns, lip patches (the callosities occuring along the upper margin of the lower lip) could be

Table 1. Sex grades for female and male right whales. The categories were derived from long-term observations and are in decreasing order of certainty.

FEMALE SEX GRADES

A1: Photograph shows short genital slit without a separate anus or with nipple slits or protruding nipples.

A2: Field notes indicate definite female from ventral slit configuration.

A3: An adult-sized whale seen on three different days in the same year, each time alone with a calf.

A4: An adult-sized whale seen on two different days in the same year, each time alone with a calf.

A5: An adult-sized whale seen on two days in the same year with the same identified calf.

A6: An adult-sized whale seen once accompanied by a calf in water so shallow (as indicated by a shadow or the observer's notes) that it can definitely be stated that no other adult is out of sight underwater within the immediate vicinity.

B1: An adult-sized whale seen on two different days in the same year with a calf, one sighting including another adult.

B2: An adult-sized whale seen once with a calf late in the season (after November 10).

B3: A whale seen alone with a calf in two different non-consecutive years, during both of which it was at adult size.

B4: An adult-sized whale seen once alone with a calf.

C1: An adult-sized whale seen once with a calf, either not alone or with behavior that makes the relationship uncertain.

C2: A whale, sub-adult size or larger, obviously avoiding mating attempts, e.g. lying belly-up at the surface with another adult-sized whale belly up beneath it or chasing it.

Table 1 (continued).

MALE SEX GRADES

A1: Photograph shows a penis, or a separate anus, or an anteriorly placed ventral slit with a forked posterior end.

A2: Field notes indicate definite male from anogenital configuration.

B1: A whale seen for four or more consecutive years at adult size without a calf.

B2: A whale seen for three consecutive years at adult size without a calf and seen on three or more occasions when there were social indicators of maleness: (a) or (b) below.

B3: A whale seen for three consecutive years at adult size without a calf and seen on one or two occasions when there were social indicators of maleness: (a) or (b) below.

B4: A whale seen for three consecutive years at adult size without a calf.

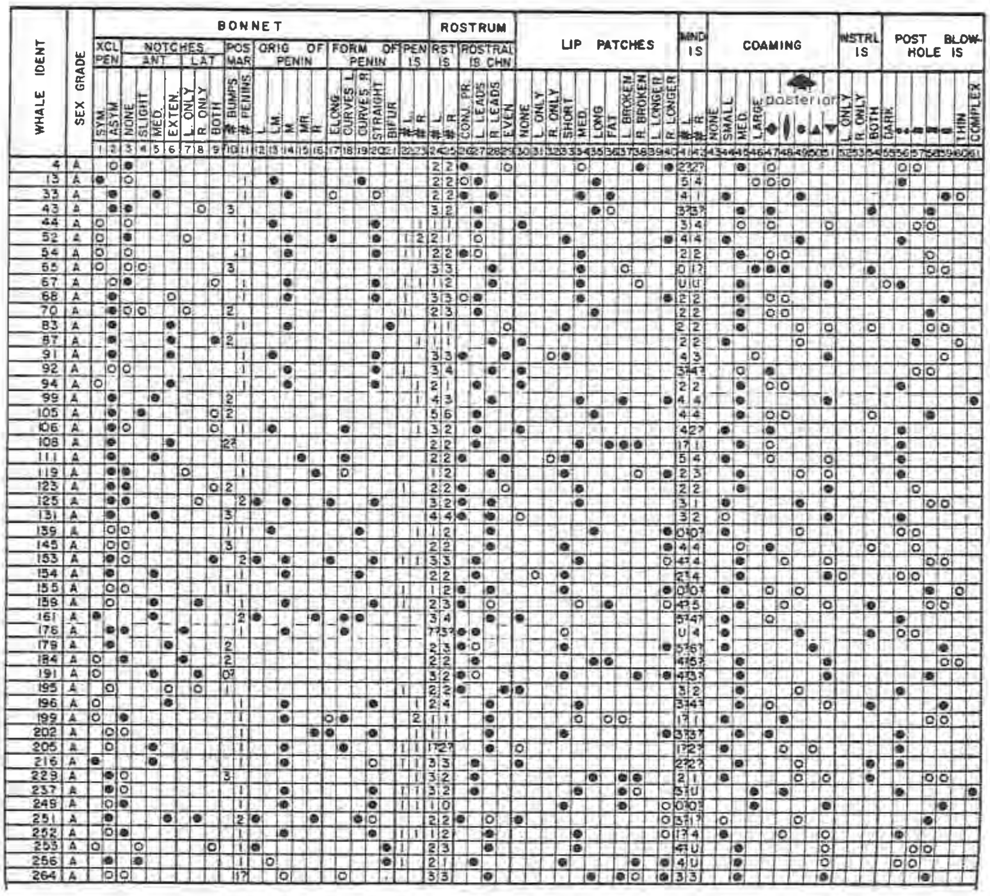
C1: A whale seen for two consecutive years at adult size without a calf and seen on one or more occasions when there were social indicators of maleness: (a) or (b) below.

SOCIAL INDICATORS OF MALENESS

(a) Seen in a mating group

(b) Seen within one adult body length of an adult-sized male of sex grade A when there is no evidence of mating.

FEMALES



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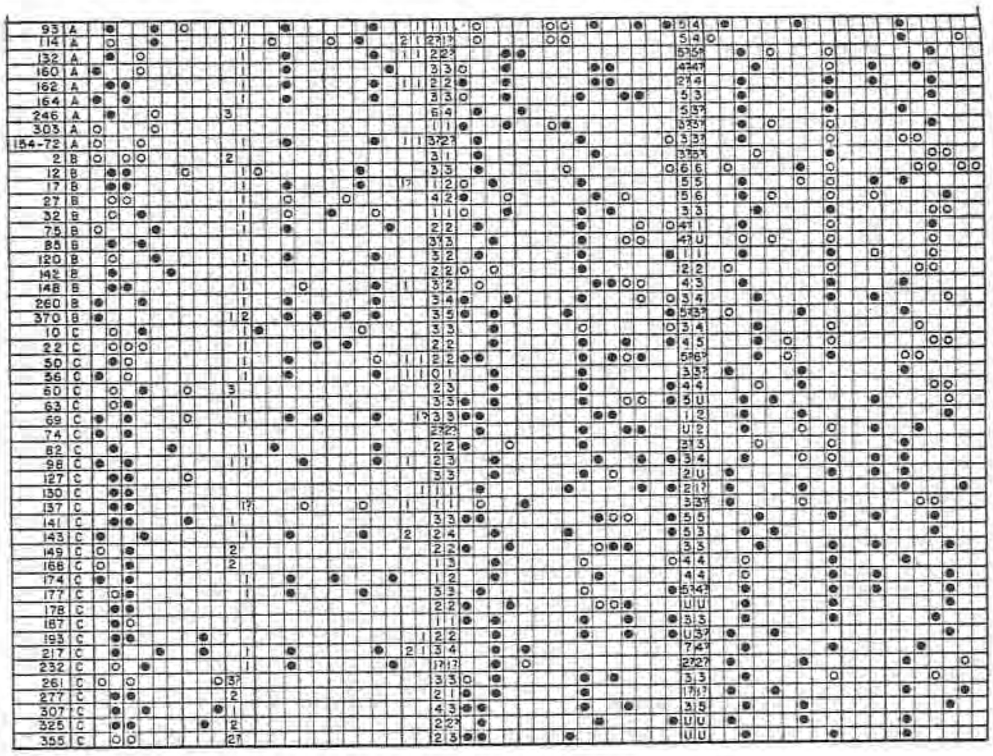

Figure 3. Callosity features in 50 female and 50 "male" right whales. See Table 1 for an explanation of the sex grade. See Appendix for an explanation of the callosity features and how they were scored. See Figure 4 for a sketch of typical callosities and their names. ● = feature definitely present, O = feature probably present, no symbol = feature not present, ? = number undetermined because obscured by water. See Tables 2 and 3 for statistical analysis.

absent entirely, present on only one side, short or medium or long, longer on one side than the other, unusually wide or not, and discontinuous (broken) on one or neither side or both sides.

Since completing the analysis of the data in Figure 3 (presented below), we have acquired more information on the sex of seven males graded B or C. For six of them, we have definite anatomical confirmation of sex and all six are indeed males. The sex of the seventh (a grade C male in Figure 3) is still uncertain, but the whale is now classified as a grade B4 female. Thus we appear to have been successful in skewing our selection of probable males toward true males on the basis of behavioral evidence.

To test for sexual dimorphism in callosities, then, we analysed callosity features one at a time (e.g. size of coaming or frequency of one coaming shape), using either the chi-square test of independence or, where categories were ordered, the Wilcoxon rank sum test. In this latter test, corrections were made for ties, since there were always many, and the levels of significance used were all two-tailed, because we were looking for any difference between the sexes. We treated the uncertain entries in Figure 3 ("o" and "?") in two different ways. In one case, we considered them to be positive entries ("o" = "•") and included them in the calculations. In the other case, we considered them to be undeterminable entries ("o" = "u") and omitted them from the calculations.

The results of these tests are presented in Table 2. We found differences between males and females, at significance levels ranging from $p<0.10$ to $p<0.005$, in 10 of the 25 callosity features analysed and in a total of 17 of the 19 tests possible on those ten features. Of the 17 results suggesting sexual dimorphism, 14 were at a significance level of $p<0.05$, and 7 of those were highly significant at a level of $p<0.01$. We have chosen to consider and report all results where $p<0.10$, rather than the more usual $p<0.05$, because of the probability that our sample of males is diluted with some females.

Of the callosity features showing evidence for sexual dimorphism, the first four in Table 2 concern the bonnet, the largest and most anteriorly placed callosity. There is, first, a tendency for males' bonnets to be more symmetrical than the females'. Secondly, the males have fewer anterior notches in their bonnets than the females do, this at a high level of significance. The males also have bonnets with significantly smoother posterior margins than the females do. And lastly, the males have significantly fewer peninsula islands, while having the same frequency of peninsulas as the females. The form and origin of peninsulas do not differ between the sexes. Most of the observed differences in the bonnet suggest that males tend to have a bonnet that is more

filled in than the females, resulting in a smoother bonnet outline.

The number and conformation of rostral islands and the number of nostril islands show no differences between the sexes, but the mandibular islands do. The males have significantly more of these islands than the females.

Another dimorphic feature is the size of the lip patches. The males have significantly longer lip patches than the females and show a tendency to have wider ones as well.

The last callosity feature showing sexual dimorphism concerns the coaming, or splash barrier, just in front of the blowholes. Although there is no significant difference between the sexes in the size of this callosity, one of the shapes, wide in back and narrow in front, occurs more often in males than in females, at a high level of significance. Concomitantly, two other coaming shapes, diamond-shaped and thin, occur less often in males than in females.

The four areas of callosity dimorphism on the whales are thus the bonnet, the lip patches, the mandibular islands and the coaming. But rather than just listing the features that show sexual dimorphism, we found it was more instructive to look at the kinds of differences we were finding between the sexes. We found that the callosity features considered fell naturally into 3 categories: degree of coverage, shape (or configuration), and complexity of bonnet outline (Table 3). Only two out of seven features pertaining to shape differed between males and females, whereas five out of nine measures of degree of coverage proved to be different, always with males showing greater coverage. In two out of five measures of bonnet outline complexity, males had bonnets whose outline was less complex -- i.e. more filled in, suggesting again that the male bonnets may be larger.

Since many of our results indicated larger and more callosities in males, we decided to test that possibility by another approach. We measured the differences in the percent of the head covered by callosities in males and females, using high quality aerial photographs of their heads. In order to avoid the distortions of foreshortening, we selected the photographs so as to insure a consistent angle between the photographer's line of sight and the top of the whale's head. In order to achieve this we took advantage of the fact that the eyebrow callosities of surfacing right whales show up clearly in most aerial photographs even though they are near the bottom of the head and thus usually seen through more than a meter of water. In aerial photographs taken from a point within that vertical plane which includes the whale's long axis, both eyebrow callosities can be seen. If a line is drawn between these callosities, the point (in a photograph) at which it intersects with the

Table 2. Statistical analysis of sexual dimorphism in southern right whale callosities, from data presented in Figure 3.

CALLOSITY FEATURE		predominant in which sex	test	o = ● result	o = ● level of significance	o = u result	o = u level of significance
BONNET	symmetry	♂	χ^2	-	.25<p<.50	+	.05<p<.10
	anterior notch	♀	rs	**	p=.0096	**	p=.0014
	side notches	-	rs	-	p=.1362	-	p=.3844
	smooth posterior margin	♂	χ^2	*	.025<p<.05	**	.005<p<.01
	frequency of peninsulas	-	χ^2	-	.25<p<.50	-	.25<p<.50
	frequency of bumps	-	χ^2	-	.75<p<.90	-	.25<p<.50
	origin of peninsulas	-	χ^2	-	.10<p<.25	-	.10<p<.25
	form of peninsulas	-	χ^2	-	.75<p<.90	-	.75<p<.90
	# of peninsula islands	♀	rs	*	p=.0348	*	p=.0220
ROSTRAL ISLANDS	number	-	rs	-	p=.6384	-	p=.4472
	freq. of conj. pairs	-	χ^2	-	.10<p<.25	-	.25<p<.50
	evenness of chains	-	χ^2	-	.50<p<.75	-	.10<p<.25
LIP PATCHES	length	♂	rs	*	p=.0178	*	p=.0300
	width	♂	rs	+	p=.0574	+	p=.0734
MAND. IS.	number	♂	rs	**	p=.0034	*	p=.0114
COAMING	size	-	rs	-	p=.1676	-	p=.1286
	frequency of ◆ shape	♀	χ^2	*	.01<p<.025	-	.25<p<.50
	frequency of ● shape	♀	χ^2	**	.001<p<.005	/	
	frequency of ● shape	-	χ^2	-	.75<p<.90	-	.10<p<.25
	frequency of ▼ shape	♂	χ^2	**	.001<p<.005	**	.005<p<.01
NSTR. IS.	number	-	χ^2	-	.25<p<.50	-	.10<p<.25
POST-NOSTRIL ISLANDS	frequency of ● ● shape	-	χ^2	-	.50<p<.75	-	.75<p<.90
	frequency of ●● shape	-	χ^2	-	.50<p<.75	/	
	frequency of ●● shape	-	χ^2	-	.75<p<.90	-	.75<p<.90
	frequency of ⬬ shape	-	χ^2	-	.75<p<.90	-	.50<p<.75

**: highly significant difference between the sexes (p<.01)
* : significant difference between the sexes (.01≤p<.05)
\+ : tendency without usually accepted statistical significance (.05≤p<.10)
\- : no difference between the sexes (p≥.10)
/ : sample size too small to do test
rs: Wilcoxon rank sum test, corrected for ties, at two-tailed level of significance
χ^2: chi-square test of independence
callosity features: abbreviations and explanations as in Figure 3.
o = ●: uncertain entries are treated as certain and included in totals
o = u: uncertain entries are treated as undeterminable and excluded from totals
p : the probability of the observed distribution occurring by chance assuming the null hypothesis of no difference between males and females

Table 3. Sexual dimorphism results from Table 2 with callosity features grouped into 3 categories. Note that some features fall into two different categories. ●●● = highly significant (p<0.01), ●● = significant (0.01≤p<0.05), ● = tending toward significance (0.05≤p<0.10), - = not significant (p≥0.10)

DEGREE OF COVERAGE	
Anterior Bonnet Notch	●●●
Side Bonnet Notch	-
# Peninsula Islands	●●
# Rostral Islands	-
# Mandibular Islands	●●●
# Nostril Islands	-
Length of Lip Patches	●●
Width of Lip Patches	●
Size of Coaming	-
SHAPE	
Form of Peninsula	-
Origin of Peninsula	-
Rostral Islands: Frequency of Overlapping Pairs	-
Rostral Islands: Evenness	-
Shape of Coaming	●●●
Shape of Post-Blowhole Islands	-
Symmetry of Bonnet	●
COMPLEXITY OF BONNET OUTLINE	
Anterior Bonnet Notch	●●●
Side Bonnet Notch	-
Frequency of Smooth Posterior Bonnet Margin	●●●
Frequency of Peninsulas	-
Frequency of Bumps	-

midline of the head depends on how the whale was holding its head. Unless the whale was on an even keel with its body held straight, the head may have been nodded (moved about its pitch axis) or twisted (moved about its roll axis). We could ensure that all pictures showed the head in the same orientation relative to the camera by requiring that all photographs met two criteria: 1) the eyebrow-to-eyebrow line passed through the nostrils (corrects for pitch of head), and 2) a line passing from the tip of the snout to the center of the coaming bisected the eyebrow-to-eyebrow line, within about 10 percent (corrects for roll of head).

We chose 15 known females and 15 known or suspected males for which we had high quality photographs meeting these criteria. As before, the list of males may have included some females, but 11 of the 15 "males" were sex grade B or better, the rest were grade C. Each acceptable photograph was greatly enlarged in area (2000X-3000X) and traced onto paper. We defined a consistent measure of total head area as the area enclosed by four lines connecting the centers of each of the eyebrows and each of the chin callosities. The area of each callosity and the total area of the head were then measured using a surveyor's compensating polar planimeter (Keuffel and Esser Co., model 620010). The planimeter contributed a negligible error to the data, measurements being reproducible to about 0.05%. Larger errors were introduced by the enlarging procedure (reproducibility about 2%), and by the angle from which the photograph had been taken (12% or slightly more). These were considered to be random errors.

From the planimeter measurements, the relative coverage of several kinds of callosity was calculated by dividing the area of each callosity by the total head area. The callosities studied were the bonnet, lip patches, coaming, post-blowhole islands, and rostral islands (see Figure 4). These callosities were chosen because they are at the top of the whale's head and are not distorted by water in aerial photographs, as lower callosities may be. The results are presented in Table 4. Males had a significantly larger area of their heads covered by callosities, confirming the results from Figure 3. The level of significance when all callosities are considered together ($p<0.001$) is particularly noteworthy, given that some of the "males" might be females. The percent coverage in males was greater in each of the callosities measured separately, although not all of the differences were significant.

Although, as mentioned earlier, female right whales are bigger than males, the difference in length is only about 1%. The difference we have found here in total callosity coverage is about 45%, the square root of which, to get a linear measure for comparison, is almost 7%. The males

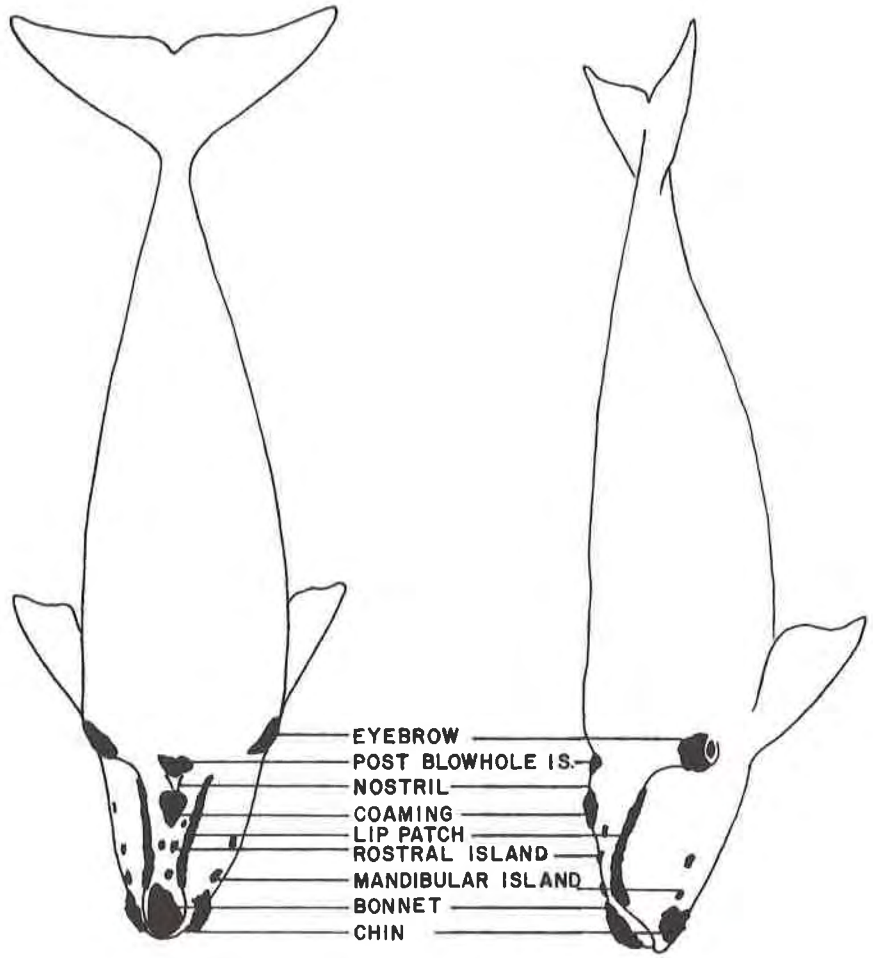

Figure 4. Diagrammatic view of a right whale showing the name, position, and form of typical callosities.

Table 4. Percent of head area covered by callosities in male and female right whales.

	MEAN PERCENT COVERAGE		t STATISTIC	p
	FEMALES n=15	MALES n=15		
ALL CALLOSITIES	11.24	16.39	3.43	.001
BONNET	5.30	5.93	1.53	.068
ROSTRAL ISLANDS	1.25	1.32	0.28	.389
LIP PATCHES	2.27	5.51	2.88	.004
COAMING	1.16	2.02	3.13	.002
POST-BLOWHOLE ISLANDS	1.26	1.63	2.12	.022

clearly have, on average, a larger absolute area of their heads covered with callosities.

Both of the analyses described above yielded results confirming our original suspicion that male right whales have more and larger callosities than females. Some of the results, like significantly different coaming shapes, were unexpected. We want to stress that the dimorphisms we have discovered are all statistical in nature rather than absolute, with considerable overlap between the sexes, like height in humans. We have not found any callosity feature that indicates sex unfailingly by itself.

Scrape Marks

In many animals, secondary sexual characters which are more developed in the males are related to fighting -- antlers in moose, horns in sheep, the mane of a sea lion, the enlarged claw of fiddler crab males, for examples. We thought that the callosities might likewise function sometimes as weapons. In this light, it may be significant that the height of callosity tissue in southern right whales varies. When viewed from the side, they can appear low and relatively smooth (Figure 5a) or jagged (Figure 5b). We do not have enough side views of animals of known sex to relate height of callosities to sex, but suspect that the unevenness increases with age, for the callosities of calves are always smooth, and very rough contours occur only in large adults. Callosities are not very hard tissue to the human touch, more like the skin of a cantaloupe than a human fingernail, for example, but the normal skin of mysticetes lacks the protection of a cornified epithelium (Ling 1974). We therefore suspect that at least the roughened callosities might be capable of inflicting injury to the skin of another whale.

Right whales at times make extensive physical contact with one another -- rubbing bodies together, stroking with flippers, and rubbing with heads. Usually they appear to take great care not to make contact with their callosities: they will slide the underside of their chin along another's back touching only with the smooth area that contains no callosities. But sometimes in active mating groups, we will see a whale turn its head over and run the dorsal side of the head against another whale, making clear contact with its callosities. The animal on the receiving end immediately twists or writhes, so as to move its body away, while the whale doing the scraping adjusts so as to keep its callosities in contact with the recipient. All indications are that the behavior is deliberate and that the result is painful. We have not seen any marks actually result from such an incident, but it would require very exceptional viewing conditions to do so. One would have to be sure that the portion of the recipient's back being scraped was originally free of any marks and that

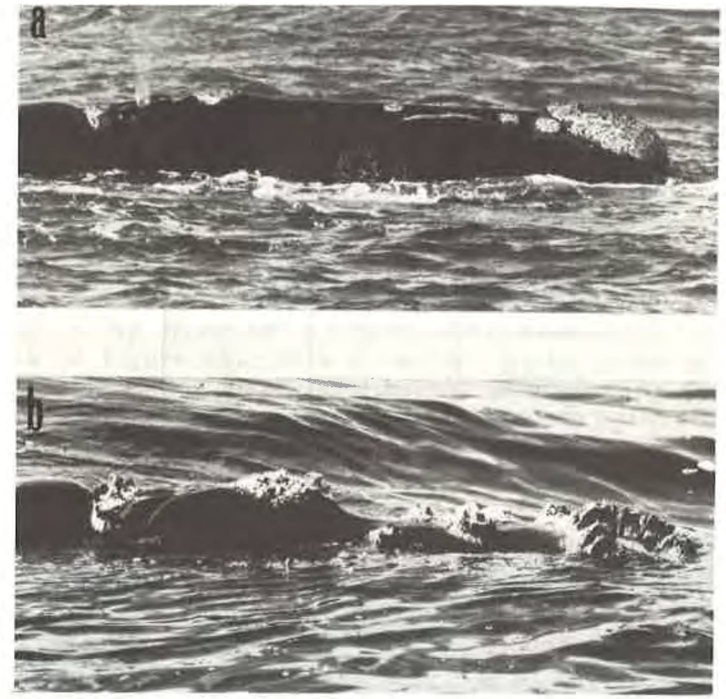

Figure 5. Side views of two southern right whale heads showing the variation in the height of the callosities. a) Low, relatively smooth callosities; b) Tall, rough callosities.

Table 5. Incidence of scrape marks by sex in adult right whales. A chi-square test of independence gave the following result: $\chi^2 = 29.014$, df=2, $p \ll 0.001$.

	males	females
scrapes present	16	14
scrapes absent	3	59

Figure 6. Scrape marks, probably caused by the callosities of another whale, on the back of a southern right whale.

what was visible immediately following contact was not streaks of foam or some other artifact.

However, we have found that many right whales carry suggestive scrape marks. Figure 6 shows a close-up of the back of a right whale. In addition to amorphous skin mottling, a few sets of gray parallel lines can be seen. These gray parallel lines are temporary marks and are distinctly different from the scars we have seen on right whales from the teeth of killer whales (Payne, in press) or sharks. The tooth scars are evenly spaced and strictly parallel lines that are deeper and much whiter and more nearly permanent than the marks in Figure 6. The gray lines in Figure 6 are irregularly spaced and not strictly equidistant within each set, and they sometimes fade in and out as though they were made by projections of irregular height bearing unevenly against the surface. We believe that these scrape marks were made by callosities of another whale -- by irregular callosity projections such as those shown in Figure 5b. Sets of scrape marks occur in widths comparable to the length of a bonnet or a coaming and never wider. We have also noted that the spacing between two or more narrower sets of scrape marks whose lines are mutually parallel is similar to the spacing between mandibular island callosities.

Another possible explanation for these scrape marks is contact with hard surfaces like rocks. We have three reasons to believe, however, that the origin of the scrape marks is not inanimate. First, the areas where whales spend the vast majority of their time at Peninsula Valdés have soft bottoms (mud or tiny, smooth pebbles). When they do get close to large rocks or cliffs, they appear to move carefully and slowly so as to avoid touching any surface. Second, when whales are most active, they move into deeper water than they stay in when they are quiet (Payne, in press). And third, the incidence of these scrape marks is highly correlated with social factors, as we will now demonstrate.

To analyze the incidence of scrape marks in Argentine right whales, we considered only photographs showing at least half of the whale's dorsal surface above water with sufficiently clear detail, proper lighting and contrast to show scrape marks if any were present. Pictures of 92 adults were scored for presence or absence of three or more parallel lines -- 73 females (sex grade B or better) and 19 "males" (2 of grade A, 16 of grade B, and 1 of grade C). Table 5 shows a comparison of scrape marks found on males and females. Most of the males had scrape marks, most of the females did not, and a chi-square test of independence shows a negligibly small possibility ($p \ll 0.001$) of these results occurring by chance if there is no sex difference.

Adult females alternate between two different social conditions. In the years that they have calves, they keep

Table 6. Incidence of scrape marks by reproductive condition in adult female right whales. A chi-square test of independence gave the fllowing results: χ^2=9.204, df=2, p=0.002.

	females with calves	females without calves
scrapes present	7	7
scrapes absent	51	8

Table 7. Incidence of scrape marks in adult right whales: males vs females in non-calf years. A chi-square test of independence gave the following result: χ^2=5.399, df=2, p=0.020.

	males	females without calves
scrapes present	16	7
scrapes absent	3	8

mostly separate from other whales and are seldom involved in mating groups. One would thus expect a difference between calf years and non-calf years for adult females in the incidence of these scrape marks, if they are acquired principally in the context of mating groups. When we analyzed the females by reproductive condition (Table 6), we found a difference in the expected direction: females without calves had significantly more scrape marks than females with calves (p=0.002).

If scrape marks are mostly the result of males fighting over females, one would expect males to direct most of their callosity attacks against other males, with the result that males would be more scraped up than the females that are probably in those groups, which are females without calves. Once again, we found a significant difference (p=0.020) in the predicted direction (Table 7).

Discussion

We have no trouble calling the interactions that produce these scrapes aggression, since they are interactions principally between males, involving physical contact which leaves marks on the skin, in a context where competition for females is to be expected. In right whales, males appear to make a much smaller investment in the care of the young than the females, because females do all of the rearing as far as we can tell (Payne, in press). From studies on other animals in which this is the case, we might therefore have expected both the greater development of a sexually dimorphic character in males and the male-to-male competition (Wilson 1975).

In odontocetes, sexual dimorphism related to male-to-male aggression is well known. A few examples are: the large size of sperm whales (*Physeter catadon*) with battles observed (Shaler 1873); the tusk of the male narwhal (*Monodon monoceros*) and the scars it leaves on other males (Silverman and Dunbar 1980; Best 1981); and the special teeth found only in males throughout the family Ziphiidae with scars that match the arrangement of those teeth (McCann 1974; Mead, Walker and Houck 1982).

In contrast, among baleen whales, we believe that our findings on right whale callosities are the first example of a sexually dimorphic structure used for intraspecific aggression. Nemoto (1962) has observed a sexual dimorphism in the shape of the upper jaw of fin whales (*Balaenoptera physalus*) and, to a lesser extent, Bryde's whales (*B. edeni*), but there is no evidence that the observed difference is related to intraspecific aggression. Humpback whales (*Megaptera novaeangliae*) are the only other baleen whales for which we know of reports of clear aggression (Tyack 1981; Darling, Gibson, and Silber 1983). We suggest that it might be interesting to look for evidence of sexual dimorphism or aggressive function for the peculiar growths found on the anterior ventral surface of the lower jaw of humpback whales, or for the knobs on their flippers or heads, or perhaps even for the size and number of barnacles on them (as well, perhaps, as on other whale species). In this light, it is not entirely unreasonable to suppose that, if cyamids eat callosity tissue, as we and others have proposed (Payne et al. 1983; Leung 1976), they may actually be of use to male right whales in keeping their weapons "sharp" or roughened.

We do not intend to imply that callosities are useful to right whales only for fighting. Because they vary so much from whale to whale, they could be used by the whales for individual recognition. Ventral blazes are also individually specific (Payne et al. 1983) and, if used by right whales in combination with the callosities, might make it possible for them to identify each other visually from every direction but the rear.

Summary

1) We have described a benign technique for studying sexual dimorphism in a free-ranging whale species when the sex of only some members of one sex can easily be determined.

2) We present evidence that the extent of callosity coverage is a sexually dimorphic character in southern right whales, with males having more and larger callosities than females.

3) We present evidence that the callosities function at least in part as weapons for intraspecific aggression, with that aggression occurring mostly between males.

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Appendix 1

The callosity features presented in Figure 4 and the abbreviations used to describe them require explanation. For definition of terms used to describe callosities see Payne et al. (1983). For a diagram of typical callosities see Figure 5.

WHALE IDENT.

(Whale identity) Each whale is given a unique identifying number for life. Calves are given their mother's number followed by the year of their birth, e.g., 154-72 is a calf born to whale #154 in 1972.

SEX GRADE

Animals of whose sex we are certain are given an A grade, while those for which we can only guess the sex from behavioral data are given a B or C rating. (See Table 1 for explanation).

BONNET

The bonnet is the most anterior as well as the largest of the callosities and is an important clue to identity because it has a highly varied outline from individual to individual.

XCL. PEN. stands for "excluding peninsula". Although the bonnet is often rather oval in shape, there are frequently one or more projecting arms of callosity tissue called peninsulas, originating from its rear edge.

1. SYM. (symmetrical)
2. ASYM. (asymmetrical).

In these categories, we are noting whether the main body of the bonnet excluding the peninsula(s) is symmetrical or asymmetrical about the line of intersection of the saggital plane with the top of the head (i.e., the midline of the head).

NOTCHES. Notches are indentations in the periphery of the bonnet.

ANT. (anterior). Refers to a notch in the anterior edge of the bonnet. It is placed in one of the following categories depending on its size:

3. NONE (no anterior notch in the bonnet)
4. SLIGHT
5. MED. (medium)
6. EXTEN. (extensive)

LAT. (lateral). refers to notches on the sides of the bonnet.

7. L. ONLY. (left only). Present only on the left side.

8. R. ONLY. (right only). Present only on the right side.

9. BOTH. Present on both sides of the bonnet.

POS MAR. (posterior margin). Projections of more than one type can extend from the rear of the bonnet.

10. # BUMPS (number of bumps). A bump is a projection that is wider than it is long. Here we are counting the number of bumps on the posterior margin of the bonnet.

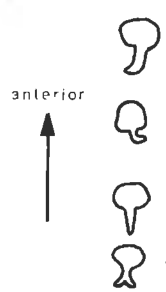
11. # PENINS. (number of peninsulas). A peninsula is a projection that is longer than it is wide.

ORIGIN OF PENIN. (origin of peninsulas). The base of a peninsula is connected with the bonnet at some point along the rear margin of the bonnet. Here we are noting whether it springs from the:

12. L. (left)
13. L.M. (left middle)
14. M. (middle)
15. M.R. (middle right)
16. R. (right)

FORM OF PENIN. (form of peninsula). Peninsulas may be classified into several shapes as follows:

17. ELONG. (elongated). The peninsula is longer than 3/4 of the length of the main body of the bonnet.



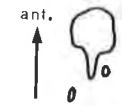
18. CURVES L. (curves left). The peninsula projects towards the left side of the whale.

19. CURVES R. (curves right). The peninsula projects towards the right side of the whale.

20. STRAIGHT. The peninsula points straight, posteriorly.

21. BIFUR. (bifurcated). The peninsula divides into a Y at its tip.

PEN. IS. (peninsula islands). Isolated callosities lying alongside the peninsula. When an island lies near the tip of the peninsula, it is considered a peninsula island (and not a rostral island) if and only if the midpoint of the island lies anterior to the most caudal point on the peninsula. In the example, the island on the right of the whale is a peninsula island, the one on the left is a rostral island.



22. # L. (number left). Number of peninsula islands to the left of the peninsula.

23. # R. (number right). Number of peninsula islands to the right of the peninsula.

ROSTRUM

The upper jaw from the blowholes forward.

RST. IS. (rostral islands). Small isolated callosities lying on the rostrum between the coaming and the rear of the bonnet. (see peninsula islands, above).

24. # L. (number left). Number of islands to the left of the midline of the head.

25. # R. (number right). Number of islands to the right of the midline of the head.

ROSTRAL IS. CHN. (rostral island chains). In many whales, the isolated callosities on the rostrum lie in lines like archipelagos or island chains stretching down each side of the head in graceful arcs. Where these chains come closest together near the midline of the head, two islands (i.e., the small isolated callosities) may touch or even partly fuse. The next category refers to a common juxtaposition of islands from the left and right chains.

26. CONJ. PR. (conjugated pair). Rostral islands which have a separation at their closest point not exceeding the width of the widest member of the pair and which are aligned such that their long axes overlap by 1/2 or more of their length. The pair on the left in the example is not conjugated, while the pair on the right is. The next three categories are concerned with how the chains are aligned along the length of the whale's head.

27. L. LEADS. (left leads). The anterior-most rostral island is on the left side of the whale's head.

28. R. LEADS. (right leads). The anterior-most rostral island is on the right side of the whale's head.
29. EVEN. The anterior-most rostral islands in both island chains lie side-by-side.

L. LEADS. R. LEADS. EVEN.

LIP PATCHES

The lip callosities are very variable and often show different degrees of development on the two sides of the head. When asymmetries are present, it is virtually always the right side which is more developed (see Payne et al. 1983). The following categories dissect out these differences.

30. NONE
31. L. ONLY (left only)
32. R. ONLY (right only)
33. SHORT
34. MED. (medium)
35. LONG
36. FAT Some lip callosities are exceptionally wide.
37. L. BROKEN (left broken). Some lip callosities are discontinuous.
38. R. BROKEN (right broken)
39. L. LONGER (left longer). The asymmetry alluded to above.
40. R. LONGER (right longer)

MND. IS. (mandibular islands)

These are small round callosities arrayed in rows along the mandibles. They are often hard to see in aerial photographs because they are usually underwater, but they show considerable variability in number and placement.

41. # L. (number on left mandible).
42. # R. (number on right mandible).

COAMING

The callosity lying just ahead of the blowhole.

43. NONE
44. SMALL
45. MED. (medium)
46. LARGE

47. ◆ (diamond-shaped)
48. ▮ (cigar-shaped)
49. ● (roughly circular)
50. ▼ (triangular with the apex pointing back and the base forward.)
51. ▲ (triangular with the apex pointing forward and the base caudal).

NSTRL. IS. (nostril islands)

Small callosities lateral to the blowholes on either or both sides of the head. They are caudal to the anterior margin of the blowholes.

52. L. ONLY (only on the left side of the head)
53. R. ONLY (only on the right side of the head)
54. BOTH (on both sides of the head)

POST BLOWHOLE IS. (post-blowhole islands)

One or two (rarely more) small callosities directly caudal to the nostrils. The diagrams show the shape of the pair and how they fuse to make a single callosity.

55. DARK. Some whales have few or no white cyamids covering their callosities. This is frequently the case with post-blowhole islands. When the cyamids are missing, the post-blowhole islands look dark and their form can be seen in only exceptionally good aerial photographs.
56. ● ● The callosities are clearly separated.
57. ●● The callosities are just touching.
58. ●-● The two callosities are fused by a narrow isthmus.
59. ▬ Callosities appear as solid band with no sign of fusion.
60. THIN. Post-blowhole callosities are sometimes very thin.
61. COMPLEX. Rarely, the post-blowhole callosities have a bizarre and complex form

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