

South American Sea Lions (*Otaria flavescens*) Avoid Killer Whale (*Orcinus orca*) Predation

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Abstract

South American sea lions (*Otaria flavescens*) are predictably preyed on by killer whales (*Orcinus orca*) at their breeding colonies in Peninsula Valdés, Argentina. Captures occur in shallow waters along the coastline. Killer whales strand in the surf where sea lion pups practice their swimming skills. Being slow and apparently unaware of danger (nonvigilant), pups are the most vulnerable prey (87% of captures). Adult sea lions escaped most attacks by increasing their swimming speed, changing directions swiftly, grouping, and hauling out of the water. In our observations, predator avoidance behaviours were contextual and based on the presence of killer whales and the degree of risk in the areas used by sea lions during their movements between rookeries. Swimming speed increased in sites where the risk of predation was highest and when killer whales were present. Vigilance and escape manoeuvres were recorded at these dangerous sites, characterized by deeper water and a sloping beach, which allowed the killer whales to strand or approach the coast safely. Predictability of the killer whales in space and time facilitates the South American sea lions in developing a reliable antipredation behaviour. Killer whales become more proficient at being predators, and adult sea lions become better at avoiding being preyed upon as they accumulate experience. The inexperience of the sea lion pups is the currency that sustains the killer whale's high rate of take.

Key Words: South American sea lion, *Otaria flavescens*, killer whale, *Orcinus orca*, predator avoidance, feeding strategies, Patagonia, Argentina, antipredation

Introduction

Although descriptive reports of predator-prey interactions involving marine mammals are relatively common (e.g., Weller, 2002, and references

therein), quantitative details are often difficult to record. Reports most often identify the participating species and provide a behavioural description, including some antipredator responses (Anderson & Prince, 1985; Whitehead & Glass, 1985; Jefferson, 1987; Würsig et al., 1997).

The quintessential marine mammal predator, the killer whale (*Orcinus orca*), is known to prey on at least 36 species of marine mammals (Hoyt, 1984; Jefferson et al., 1991). A dozen more species are suspected to be vulnerable to its attacks (Weller, 2002). Along the Patagonian coast of Peninsula Valdés, Argentina, killer whales prey on, at least, South American sea lions (*Otaria flavescens*), southern elephant seals (*Mirounga leonina*), and, more rarely, southern right whales (*Eubalaena australis*) (Thomas & Taber, 1984; López & López, 1985; Hoelzel, 1991). Killer whales intercept sea lions and seals in the water, but they have also developed a stranding technique to capture pinnipeds resting on the beach or swimming near the surf. Exposing most of their body out of the water, killer whales attempt to grasp a sea lion or an elephant seal with their teeth while moving quickly back into deeper waters assisted by the incoming breaking waves along the coastline (López & López, 1985; Hoelzel, 1991). A comparable, although less dramatic behaviour was described for killer whales preying on young southern elephant seals in Possession Island (Guinet, 1991).

The intentional stranding of killer whales at Peninsula Valdés occurs, predictably, in late summer (February-March) after the South American sea lion breeding season is over and at the time when pups spend a considerable amount of time in the surf (Campagna & Le Boeuf, 1988). Pups are born on land and remain close to their mothers during their first week after birth, but soon adult females go to sea to forage and alternate periods of nursing on land with foraging trips at sea which last a few days each (Werner & Campagna, 1995; Campagna et al., 2001). Pups have to develop their swimming abilities and, while doing so, are vulnerable

to killer whale attack. Previous research estimates that about 5% of the pups born in some rookeries are preyed on by killer whales during their first few months of life. Adult South American sea lions are also attacked but with a lower predation efficiency because this more experienced age class exhibits a variety of anti-predatory behaviours. For example, adults can swim in shallow areas inaccessible to killer whales, increase their swimming speed, porpoise along the coast, or haul out of the water for the safety of land (Hoelzel, 1991). Developing swimming abilities is a critical skill for pups to avoid predation—a skill which can be learned either by direct experience or by passive observation.

The purpose of this study was to analyze in depth the predator-prey interaction, particularly from the perspective of predator avoidance behaviour in a quantitative way. Since the risk of predation varies by location and time, we were able to observe and quantify the behaviour of South American sea lions in contexts of different predation dangers and to describe the contextual repertoire of responses by sea lions to killer whale predators. We discuss learned co-adaptation processes on both sides of the predator-prey interaction. The co-evolution of prey and predator shapes the behaviour of the prey usually as a trade-off concerning foraging or reproduction (Lima & Dill, 1990). This study suggests that for South American sea lion pups, the critical trade-off is between being directly exposed to predation while learning critical swimming skills vs indirectly learning predator avoidance through observations of other sea lions.

Materials and Methods

Study Area

Observations were conducted at the South American sea lion breeding rookery of Punta Norte, Peninsula Valdés, Argentina. Records covered 127 d during four breeding seasons (February–April 1991 to 1994; 14 to 62 d/period). The study area was a 5-km stretch of coastline where three sea lion breeding groups occurred: (1) Ensenada (ENSM), (2) Faro (FNOR), and (3) Reserve (RES) (Figure 1) (Campagna, 1985; Crespo & Pedraza, 1991). Breeding sea lions gather on pebble beaches that slope gradually towards the sea (*ca* 20° slope for about 100 m). Beaches merge into compact sandstone platforms that extend seaward an additional 300 to 400 m. The continuity of the sandstone platforms is broken by long channels or tidal pools, running perpendicular to the coast. Tidal range is about 5 m. At high tide, the sandstone shelves and part of the beach remain under water, and most sea lions rest along the shore or

swim in the surf. At low tides, the water retreats hundreds of meters from the animals and a wide extension of the platform is exposed. Even at low tide there are areas along the coast where sea lions have access to open waters through 200- to 300-m long, perpendicular channels that remain flooded. These channels link the beach to the ocean, are 5 to 12 m wide, and are 1 to 3 m deep at low tide (depth at high tide is then 6 to 8 m, according to places and tidal wave). From the many dozen channels in the study area, two—Orca Channel and Reserve Channel—are wider (40 to 70 m at the mouth) and deeper (4 to 5 m at low tide).

Study Subjects and the Predation Scenario

Observations occurred during the critical period in the annual cycle of South American sea lions. From late December to early February, a total of at least 1,000 pups are born at the three rookeries of Punta Norte (Campagna, 1985; Crespo & Pedraza, 1991). By mid-February, most females have given birth, harem structure is dissolved, adult males have departed on foraging trips, and lactating females spend time on land nursing their pups and move to the sea to forage (Campagna & Le Boeuf, 1988; Werner & Campagna, 1995; Campagna et al., 2001). By mid-March, about 800 to 1,000 adult females, their pups, and a few hundred 4- to 7-y-old males (here referred to as subadults) remain in the study area distributed in several groups of 200 to 400 individuals each. At this time, pups spend most of the day swimming in the surf, channels, and tide pools.

As killer whales hunt close to the coast, exposure of South American sea lions to predation varies with tidal level and coastline topography (López & López, 1985; Hoelzel, 1991). In areas where deep-water channels are present, predators may have access to sea lions at virtually all tide levels. Killer whales take advantage of the accessibility offered by these channels and spend most of their time hunting inside these areas (Hoelzel, 1991). Sea lions in the water can then be intercepted during high tides along most of the coast, and during low tides in the deep channels. Animals ashore are safe if they are away from the surf or in areas where the sandstone platform precludes killer whales from approaching the beach at most tidal conditions. Several areas had a higher risk of predation (i.e., access to sea lions by killer whales could occur at almost all tidal condition) (Figure 1): Ensenada de Medina (ENSM), Faro of Punta Norte (FNOR), Reserve Channel (RES), Piratas (PIR), and Orca Channel (OC). Four sites showed low risk (i.e., killer whales only have access to them during high tide) (Figure 1): Antiguos (ANT), Tronco (TR), Orca Channel North (OC-N) and South Bay (SB).

Recording Behaviour

Observations were based on the predicted presence, location, and behaviour of killer whales as described by López & López (1985) and Hoelzel (1991). The behaviour of South American sea lions was recorded during a total of 1,016 h, out of which killer whales were present 328 h (mean = 82 h/season, range = 25 h in 1994 and 210 h in 1992, respectively). Killer whale presence was defined as any killer whale observed within the limits of the study site. The behaviour of sea lions was recorded at four focal sites consisting of 40- to 70-m-wide stretches of coastline. Boundaries of focal sites were kept constant, regardless of tide level. Markers were placed along the coast as references for high tide observations when topographic features remained under water.

Crossing of a focal site was defined as an individual or a group traversing the location by swimming along the coast, typically within 10 m of the surf line. Observations of South American sea lions were conducted from blinds, and the sea lion's direction of travel and the time in seconds

to cross the focal site (using the markers placed at the beach as boundaries to start and end time measurements) were recorded. Crossing speed was derived from crossing time divided by the distance crossed in OC, OC-N, ANT, and TR focal sites (Figure 1). Crossing time reflected the availability of potential prey as it was determined from the instant the first individual entered the site (crossed its boundary) to the moment the last individual left it. Two observers were required to record data, one at each extreme of the focal site.

The composition of sea lion groups crossing the focal site was recorded, particularly the presence of pups among the group. We discriminated between groups of mature/subadult animals and groups of or with pups (pups only or mixed mature/subadult individuals and pups). Prey availability was estimated as the number of sea lions that crossed ENSM (1993 and 1994), FNOR (1992 to 1994), and OC (1992 to 1994) during sampling periods. Other focal sites (RES, PIR, and TR) were less appropriate for an estimate of prey availability due to their proximity to the rookeries

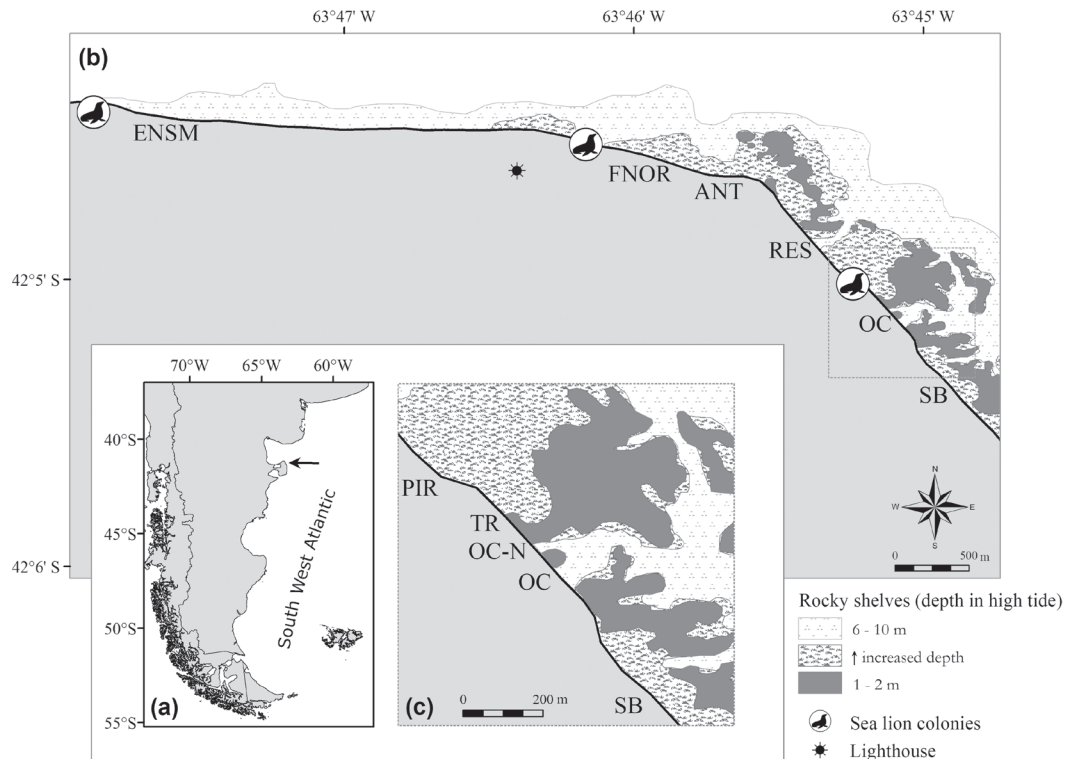


Figure 1. (a) Study area at Punta Norte, Península Valdés (Argentina), showing the location of focal observation sites; (b) Ensenada Medina (ENSM), Faro of Punta Norte (FNOR), Antiguos (ANT), Punta Norte Reserve (RES), Piratas (PIR), Tronco (TR), Orca Channel North (OC-N), Orca Channel (OC), and South Bay (SB); and (c) sample areas surrounding the OC focal site.

and the high rate of animals entering and leaving the water at all times, which made it difficult to count accurately.

Several South American sea lion behaviours were quantified during the crossing of OC, OC-N, ANT, and TR sites (Figure 1) by individuals and by groups. One individual engaging in an avoidance behaviour (e.g., escape manoeuvres such as porpoising or leaving the water) was sufficient to record the occurrence of an antipredator behaviour for the entire group. Avoidance was any behaviour that would decrease the chances of being preyed upon by a killer whale (see Hoelzel, 1991).

Presence of predators was defined as one or more killer whales in a hunting context (near-shore milling, patrolling, pursuing, close approaching, and stranding) at about 100 m from the coast within the limits of the focal sites (after Hoelzel, 1991). Three additional focal sites were included to conduct observations of killer whales (Figure 1): RES, PIR, and SB. Killer whales also used these sites for hunting. Individual killer whales were identified by natural marks and assigned to a pod based on long-term observations conducted in the area (López & López, 1985; Hoelzel, 1991; Iñiguez, 2001).

An attack or predation attempt was defined as a *close approach*, *pursuit*, or *intentional stranding* aimed at a potential prey (see Hoelzel, 1991). A successful predation was a capture of a South American sea lion. Individual killer whales were identified for each predation attempt. The prey category and age class were recorded as was the location of the attack. Predation rate was the number of captures over the total number of hours of observations with killer whales present in the study area. Predatory efficiency was estimated as successful captures over the total number of predation attempts or attacks.

Statistical Analysis

The effects of focal site and sea lion age on availability as prey were analyzed with a two-way ANOVA (significance level of α 0.05). Data were

log transformed to obtain normality and homogeneity of variances. Mann-Whitney tests were used to examine differences in swimming speed among South American sea lion age classes. A nonparametric test was used because we could not assume normality. Two-way comparisons of frequencies were done by contingency chi-square (χ^2) tests. Neck-stretching occurred in the absence and presence of predators and at a similar rate; thus, samples in different predatory contexts were pooled together. All values are presented as means \pm standard error ($\chi \pm$ SE). Due to the large number of statistical comparisons (swimming speed and avoidance behaviours in different locations and predation scenarios—killer whale present or absent, sea lion group composition, and/or risk of the area), the significance level was adjusted to control the overall probability of a type-one error. A significance level of α equals 0.01 was used. Thus, any test that results in a p -value of less than 0.01 would be considered statistically significant; and probability values greater than 0.01 (including those between 0.01 and 0.05) were considered nonsignificant.

Results

Availability of Prey

Prey availability at ENS, FNOR, and OC focal sites (Figure 1) was similar throughout the years. Availability of prey was age-specific and changed according to focal site (Table 1). The mean time that elapsed between consecutive crossings by an individual or a group was lower for adults than for pups (two-way ANOVA: $F = 21.5$, $df = 1$, $p < 0.001$). Prey availability increased from ENSM to OC ($F = 30.4$, $df = 2$, $p < 0.001$). The highest availability of adult South American sea lion prey was at OC, with individuals crossing the site at a rate of one animal every 5.7 min. The OC was also the area with larger availability of pups, with an average of one pup every 17.6 min (Table 1). The availability of sea lions was also influenced by an interaction between place and age (place vs age interaction: $F = 4.2$, $df = 2$, $p < 0.05$).

Table 1. Prey availability expressed as mean time in min \pm SE and n (number of observations) that elapsed between consecutive crossings of South American sea lions for three focal sites (see Figure 1 for location and “Materials and Methods” for a description of sites). *Adults* refers to experienced animals of both sexes; *Pups* includes newborns and yearlings.

| Age class | Breeding colonies | | |
|-----------|------------------------|------------------------|------------------------|
| | Ensenada | Faro | Orca Channel |
| Adults | 26.4 \pm 5.5 (21) | 13.9 \pm 1.5 (62) | 5.7 \pm 0.7 (83) |
| Pups | 35.5 \pm 8.3 (14) | 30.6 \pm 5.2 (52) | 17.6 \pm 2.4 (74) |

Table 2. Successful killer whale captures by prey category and by breeding season; predation rate is the number of South American sea lions taken by killer whales per hour.

| Season | Observation dates | No. of attacks | Successful captures | | | | | Predation rate | |
|--------|------------------------------|----------------|---------------------|-------------------|---------------|----------------|-------------------|----------------|------|
| | | | Pups | 1-y-old juveniles | Adult females | Subadult males | Age-class unknown | | |
| 1991 | 12 March – 10 April (29 d) | 59 | 18 | 1 | 0 | 0 | 0 | 19 | 0.32 |
| 1992 | 7 February – 10 April (62 d) | 414 | 46 | 1 | 1 | 1 | 4 | 53 | 0.25 |
| 1993 | 3 April – 17 April (14 d) | 38 | 5 | 0 | 0 | 0 | 0 | 5 | 0.15 |
| 1994 | 4 March – 26 March (22 d) | 74 | 8 | 0 | 0 | 0 | 3 | 11 | 0.44 |
| Total | | 585 | 77 | 2 | 1 | 1 | 7 | 88 | 0.27 |

Predation

A total of 585 attacks were recorded in 328 h of observations with killer whales present in the study area, with 88 successful captures (predatory efficiency = 15%; Table 2). Five individual killer whales belonging to three pods performed 94% of the attacks (adult males B1 and B2, adult female C1, subadult male A3, and subadult female A5).

**Figure 2.** An intentional stranding of a killer whale attempting to prey upon an adult South American sea lion that avoided the predator by increasing swimming speed and porpoising

Adult male B2 captured 51% of the 88 prey items, followed by subadult male A3, with 32%.

Most common attacks (69%) represented interceptions at sea (patrol, pursuit, and close approach), while 31% involved intentional strandings (Figure 2). Strandings resulted in more captures than interceptions (64 of the 184 strandings vs 24 of 401 interceptions; $\chi^2 = 81.9$, $df = 1$, $p < 0.001$).

Killer whales preferentially targeted pups. Pups were the most common prey item (77 of the 88 captures; Table 2), followed by juveniles and mature animals of both sexes. For seven captures, the sex and age category of the South American sea lion could not be determined. The rate of total successful predation was one sea lion captured every 3.7 h of observation with killer whales in the area. The rate for pups was one capture every 4.3 h.

Attacks and successful captures occurred at all focal sites (Table 3), with a high representation of the OC (33 of 88 captures). However, predation rates were higher at RES (1.8 prey/h) and PIR (0.7 prey/h) than at OC (0.4 prey/h).

Table 3. Number of South American sea lions captured by breeding season and the predation rate as a function of focal site (Figure 1); predation rate is the number of sea lions taken by killer whales per hour.

| Season | Focal site | | | | | | | Total |
|----------------|------------|-----------|-----------|-----------|---------|--------------|-----------|-------|
| | Ensenada | Faro | Reserve | Piratas | Tronco | Orca Channel | South Bay | |
| 1991 | 1 | 2 | 5 | 0 | 1 | 10 | 0 | 19 |
| 1992 | 4 | 6 | 6 | 15 | 0 | 18 | 4 | 53 |
| 1993 | 1 | 0 | 0 | 0 | 1 | 3 | 0 | 5 |
| 1994 | 5 | 2 | 0 | 2 | 0 | 2 | 0 | 11 |
| Total (%) | 11 (12.5) | 10 (11.4) | 11 (12.5) | 17 (19.3) | 2 (2.3) | 33 (37.5) | 4 (4.5) | 88 |
| Predation rate | 0.24 | 0.22 | 1.83 | 0.74 | 0.03 | 0.43 | 0.11 | |

Predator-Avoidance Behaviours

Group Size—South American sea lion group size tended to be larger at times when predators were present (Figure 3). Sea lions were in groups in 63% of the crossings ($n = 558$) when killer whales were within the limits of the study area, while 55% of them were in groups in 2,046 crossings without predators ($\chi^2 = 11.1$, $df = 1$, $p < 0.01$). Mean sea lion group size with killer whales present was 2.90 ± 0.11 individuals ($n = 558$) vs a mean of 2.40 ± 0.04 individuals ($n = 2,046$) with predators absent (Mann-Whitney test = -4.2 , $p < 0.001$).

Swimming Speed—South American sea lions crossing high-risk areas moved in a straight line parallel to the coast. Both pup and adult groups increased swimming speed in the presence of killer whales in the OC (Figure 4). Swimming speed in a high-risk site was higher when predators were present than when they were absent, and this was observed both in adult groups (Mann-Whitney = -6.01 test, $p < 0.001$) and in mixed groups of adults and pups (Mann-Whitney test = -3.31 , $p < 0.001$). The opposite pattern was observed in low-risk areas, where mean swimming speed tended to be slower when killer whales were present for both group types (Mann-Whitney test = 1.29 and 1.05 , respectively; $p > 0.05$; Figure 4).

The presence of pups in a group slowed down the swimming speed of the entire group (Figure 4). In the presence of killer whales, groups without pups crossed the OC 1.6 times faster than groups with pups. For example, when one or more pups were part of a group of adults, mean swimming speed in OC was significantly slower, both in the presence (Mann-Whitney test = 6.72 , $p < 0.001$) and in the absence of killer whales (Mann-Whitney test = 14.64 , $p < 0.01$). This pattern was also observed in low-risk areas (Mann-Whitney test = 2.84 for killer whales present, $p < 0.01$, and 5.49 for killer whales absent, $p < 0.001$). The fastest crossing speed was recorded for groups without pups when crossing the OC in the presence of killer whales (mean = 113.2 ± 3.3 m/min), while the slowest was for groups with pups when crossing low-risk areas in the presence of predators (mean = 31.9 ± 2.7 m/min).

South American sea lions at OC-N (Figure 1) behaved differently depending on the direction they were traveling. For animals traveling south, OC-N represented the immediate site before the crossing of the high-risk OC; conversely, for animals moving north, the OC-N was the exit after a risky crossing. Adults moving into the OC-N at the end of a crossing entered the site at a significantly faster speed than those heading towards the risky context (mean = 87.4 ± 5.7 m/min, $n =$

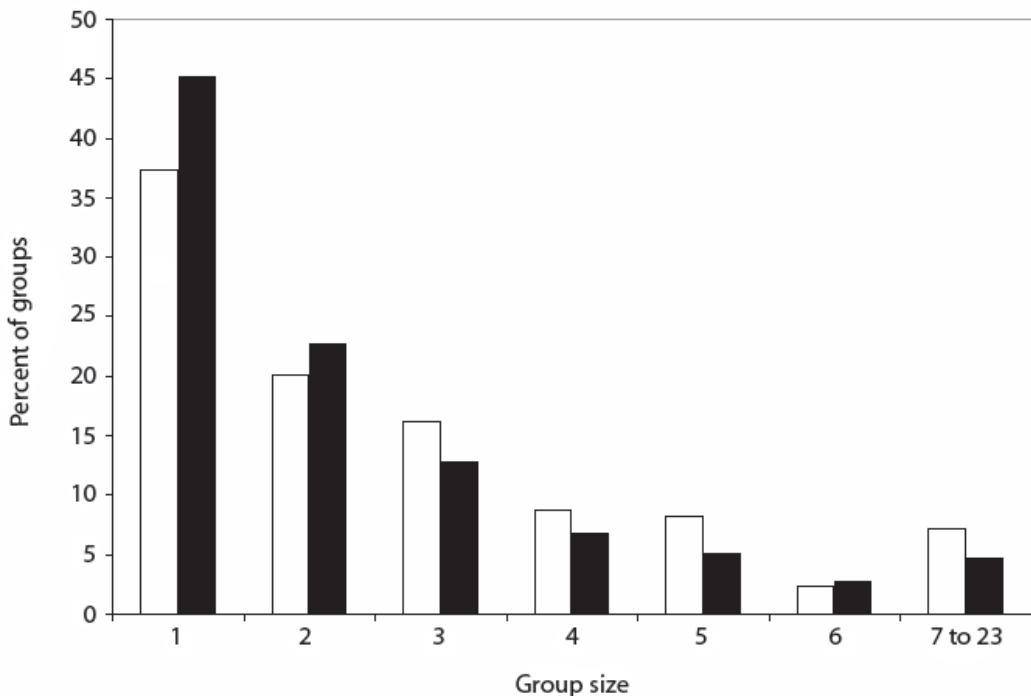


Figure 3. Group size of South American sea lions as a function of the presence (white) or absence (black) of killer whales

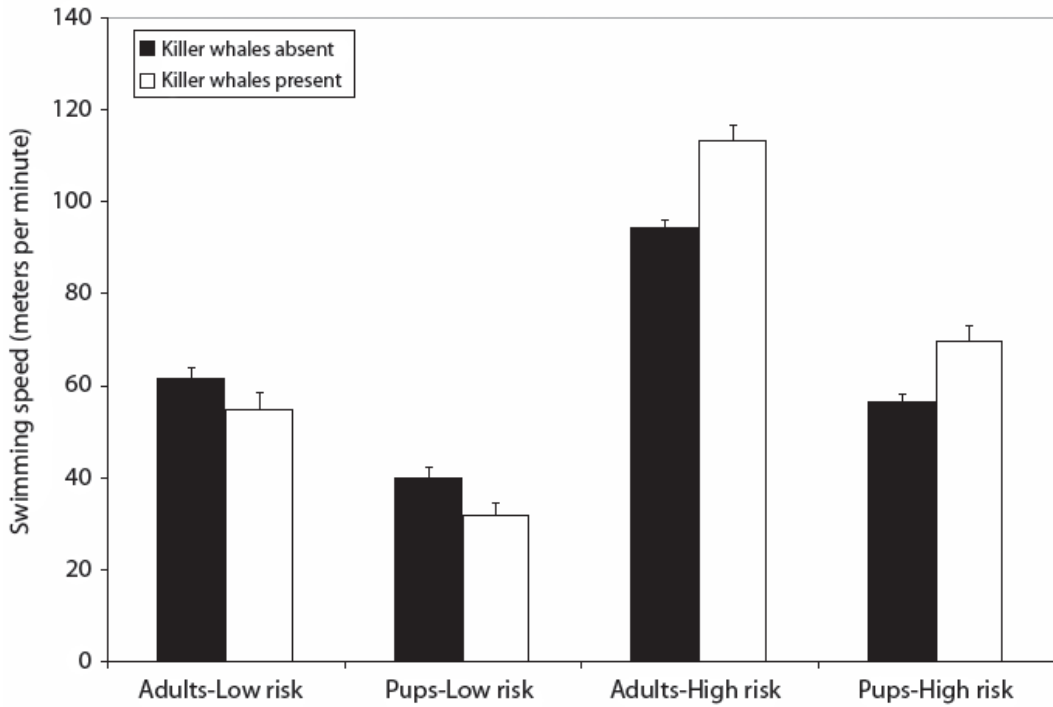


Figure 4. Comparative mean swimming speed (m/min ± SE) of South American sea lions in low- and high-risk focal sites with killer whales present/absent

62 vs mean = 49.3 ± 2.3 m/min, $n = 234$; Mann-Whitney test = -6.4, $p < 0.001$). Groups with pups travelled at a similar speed before and after crossing the OC (mean = 53.8 ± 3.5 m/min, $n = 47$, and mean = 49.9 ± 3.6 m/min, $n = 79$, respectively; Mann-Whitney test = -0.99, $p > 0.05$). These different predation contexts also had behavioural parallels. Adults ready to cross the OC spent time at the OC-N area. They surfed the waves, swam back and forth, and stretched their necks to glance in the direction of the OC. Conversely, adult sea lions exiting the OC continued to swim at a similar speed when crossing the OC-N area.

Porpoising—This behaviour was associated with high-speed swimming. South American sea lions exposed their body almost completely out of the water, reentering the water with almost no splash (Figure 2). Porpoising was virtually restricted to high-risk sites. At the OC, porpoising occurred (1) in adults as frequently in the presence as in the absence of killer whales ($\chi^2 = 0.6$, $df = 1$, $p > 0.05$; Table 4); (2) more frequently when adult sea lions were moving away from the channel than when they were entering it (13 times for 89 groups that crossed the OC vs 16 of 264 groups before entering the site; $\chi^2 = 6.5$, $df = 1$, $p > 0.01$).

Table 4. Percent of South American sea lions exhibiting different antipredation behaviours while crossing a high-risk site (Orcas Channel, Figure 1) as a function of age and presence/absence of killer whales; adults include experienced animals of both sexes, and pups include newborn pups alone or mixed with experienced individuals.

| | Killer whales present | | Killer whales absent | |
|-------------------------|-----------------------|------|----------------------|------|
| | Adults | Pups | Adults | Pups |
| Number of crossings | 289 | 234 | 895 | 620 |
| % porpoising | 15.6 | 4.3 | 17.5 | 3.5 |
| % spot predators | 16.6 | 8.1 | 17.7 | 2.4 |
| % move out of the water | 20.1 | 44.4 | 3.6 | 8.7 |
| % change direction | 22.1 | 44.4 | 4.2 | 20.6 |

but did not change in relative frequency in groups with pups ($\chi^2 = 2.5$, $df = 1$, $p > 0.05$); and (3) more frequently when a group was composed of adults only than when pups were part of it (Table 4), both in the presence and absence of killer whales ($\chi^2 = 68.8$, $df = 1$, $p < 0.001$, and $\chi^2 = 17.5$, $df = 1$, $p < 0.001$, respectively).

Porpoising was site-related and occurred at OC more often than at TR (Figure 1), both when killer whales were absent or present (no killer whales: 18% of 895 crossings of the OC by adult groups vs 3% of 109 crossings of TR; $\chi^2 = 15.9$, $df = 1$, $p < 0.001$. With killer whales: 16% of 289 vs 2% of 47 crossings for OC and TR, respectively; $\chi^2 = 6.2$, $df = 1$, $p > 0.01$).

Neck-Stretching—Adult South American sea lions near high-risk areas stretched their necks, reaching as far out of the water as possible, looking in either direction where killer whales were located or towards the area that the focal animal was going to cross (Figure 5). Neck-stretching at the OC was performed by adults equally often no matter the presence of predators ($\chi^2 = 0.2$, $df = 1$, $p > 0.05$; Table 4). Neck-stretching was recorded in 17% of 1,184 occurrences of OC crossings by adults, both as solitary individuals or in a group. Neck-stretching was less common in pups crossing the OC: in 4% of 854 crossing episodes of pup groups or mixed groups with pups, we

recorded at least one individual neck-stretching (comparison with adults alone: $\chi^2 = 85$, $df = 1$, $p < 0.001$). Neck-stretching by adults was more common before crossing than immediately after exiting the OC. In 58% of the 264 crossings, at least one adult performed a quick neck-stretching before crossing, glancing towards the middle of the channel, vs 17% of the 89 crossings for which we recorded data after the crossing ($\chi^2 = 44.3$, $df = 1$, $p < 0.001$). Neck-stretching occurred infrequently outside high-risk areas—only in 6 (4%) of 173 crossings of the TR site, which included adults and pups both in the presence and absence of killer whales. Neck-stretching also occurred when sea lions were at the beach and killer whales were swimming along the coast in the vicinity of the rookery.

Escape Manoeuvres—South American sea lion groups chased by killer whales quickly dispersed and swam fast in different directions. While some animals swam back to safe areas, others engaged in evasive manoeuvres, changing directions unpredictably until they crossed the high-risk area.

Groups with pups or adults only in the OC changed swimming direction more frequently when killer whales were present than when they were absent (Table 4). Of 289 groups of adult South American sea lions that crossed the OC in the presence of killer whales, 22% were involved



Figure 5. Vigilance response (neck-stretching) by South American sea lions before crossing the risky Orca Channel (OC-N; Figure 1)

in escape manoeuvres (vs 4% of 895 groups when killer whales were absent; $\chi^2 = 88.9$, $df = 1$, $p < 0.001$). Changes in swimming direction also occurred in groups of pups and mixed groups ($\chi^2 = 48.6$, $df = 1$, $p < 0.001$). Comparatively, changes in the direction of swimming occurred infrequently outside high-risk areas—only in 11 (4%) of 248 crossings of ANT site, which included adults and pups both in the presence and absence of killer whales.

Close Contact with Pups—Females crossing high-risk or low-risk areas always remained almost at body contact with a pup assumed to be their offspring. They also were often in vocal contact. In 63% of 120 records of mother-pup crossings of the focal sites, pups were positioned between the mother and the coast. The pup was almost on top of the mother while crossing in 21% of these episodes; and in 7%, the pup was in the middle of a group of adults. Pups crossed in vulnerable positions only in 11 (9%) of the 120 observations.

Haul Out of the Water—Some South American sea lions moved ashore when threatened by the proximity of the killer whale. They remained ashore for a few minutes immobile and then continued the crossing by walking along the coast. The behaviour was unusual in the absence of killer whales (4% of OC crossings by adults without predators) (Table 4), but the proportion increased significantly to 20% when killer whales were present ($\chi^2 = 84.6$, $df = 1$, $p < 0.001$). In groups that included pups, individuals left the water for the coast more often with killer whales present than when they were absent ($\chi^2 = 143.9$, $df = 1$, $p < 0.001$; Table 4).

Leaving the water was also recorded in the OC-N, before entering the high-risk area, and at a higher frequency when killer whales were inside the OC (19% of 69 vs 3% of 195 adult crossing episodes with and without predator in the OC; $\chi^2 = 21.3$, $df = 1$, $p < 0.001$). For groups with pups, the frequency of leaving the water before starting the crossing tended to be similar when killer whales were present or absent in the OC (10% of 21 episodes vs 12% of 66 episodes, respectively). Hauling out of the water was not observed in low-risk areas, even when killer whales were present (37 and 59 crossing episodes of ANT and TR sites, respectively).

Discussion

South American sea lions showed a repertoire of behaviours to avoid killer whale predation adapted to the likelihood of a predator being present and the degree of risk at a particular site. Predator avoidance patterns were fully developed in mature sea lions. Adult sea lions, even when ashore, were

visually aware of the presence of killer whales. Experienced sea lions that crossed high-risk sites adopted a vigilant behaviour even when killer whales were not in the vicinity.

The scenario of hundreds of inexperienced pups in the surf during the annual breeding season sets a predictable yearly cycle of killer whales being nearby South American sea lion colonies. Killer whales live long, have relatively constant home ranges, and spend decades in an area. Thus, they can learn about good foraging sites and the biological cycles of their prey. In contrast, sea lion pups seem to be unaware of danger as they swim in the surf where killer whales may see and hear their movements and target them. The agility and endurance of swimming by pups is somewhat constrained, and improving swimming skills requires being in the water, exposing themselves to predators. Safety may increase when pups are part of groups with adults. Pups often follow adults and move from rookery to rookery, and mothers search for them, exposing themselves to predation. Very young pups do not venture too far, however; they remain at one place in the surf and represent almost nonmovable targets for killer whales.

Group size had no effect on the attack rate by killer whales (Hoelzel, 1991), but it represents a contextual feature of relevance for South American sea lions. Learning about predation risks and avoidance, either as part of a group or as an individual, is critical for pup survival during the first few months of life. Pups are almost always in groups when attacked by a killer whale. When a capture occurs during an intentional stranding, a pup is grabbed during the last instant of the attack. Being in a group benefits a pup due to the Dilution Effect or Safety in Numbers (Hamilton, 1971), but it also is a way of acquiring information about predator avoidance based on what happened to them and to others.

Suboptimal antipredator behaviors by sea lion pups could be due to a variety of factors, including the inability to recognize predators and a lack of physical attributes to escape. Efficiency in avoiding predators increased with experience through learning in social groups (e.g., Griffin, 2004). In a few months, sea lion pups progressed from being apparently unaware of danger to being vigilant and fast-moving with adult groups. Furthermore, the capture efficiency of yearlings by killer whales was lower than of pups (Hoelzel, 1991; this study). As they develop their behavioral repertoire, they are almost always in groups, apparently aware of each other, and are often attacked by predators, escaping by chance.

Results from this study were similar to those reported by Hoelzel (1991) on prey availability and predator avoidance behaviours. For example,

the rate of South American sea lion pups crossing the OC was one every 17.6 min in this study and one every 17.3 min in Hoelzel (1991). Consistency over time is another interesting comparative result that applies to availability of sea lion adults in the OC, group sizes of sea lions, heterogeneity of areas used by killer whales, prey choice, and hunting effort concentrated where the capture rate was greater. A scenario that is predictable (López & López, 1985; Hoelzel, 1991; this study) suggests an opportunity for co-adaptation of learning for both killer whales and sea lions.

Avoidance of Predation by Other Marine Mammals

Reports of killer whale avoidance and protective behaviour by marine mammal prey are often limited to anecdotal or opportunistic observations, despite the great range of species that this superb predator is capable of attacking, from small seals to large whales (Hoyt, 1984; Jefferson et al., 1991; Weller, 2002). The variety of behaviours that may represent antipredation encompasses a mother swimming close to her calf in dusky dolphins (*Lagenorhynchus obscurus*) (Würsig & Würsig, 1980) and southern right whales (Thomas & Taber, 1984), the fleeing by rapid swimming or by hiding in the surf zone or tidal shallows in dusky dolphins (Würsig et al., 1997); an increase in swimming speed in Dall's porpoise (*Phocoenoides dalli*) (Jefferson, 1987); fleeing the presence of a predator in dugongs (*Dugong dugon*) (Anderson & Prince, 1985); and fluke trashing, turning, and rolling in humpback whales (*Megaptera novaeangliae*) (Whitehead & Glass, 1985). A recent study has classified the responses of baleen whales to predatory advances and attacks by killer whales into two distinct categories: the fight and flight strategies (Ford & Reeves, 2008). The fight strategy consists of active physical defense, while the flight strategy consists of rapid directional swimming away from killer whales.

Thomas et al. (1987) reported that Antarctic Weddell seals (*Leptonychotes weddellii*) in breeding colonies abruptly decrease their underwater vocalization rate from nearly 75 sounds/min to silence when killer whales are first heard nearby. Predator avoidance also has been proposed as an evolutionary shaping factor of the sonar signals of nonwhistling odontocetes to be at frequencies above the upper hearing limit of the killer whale (Madsen et al., 2005). Furthermore, Mossbridge & Thomas (1999) documented that when the killer whale and leopard seal (*Hydrurga leptonyx*) were sympatric predators in an area, killer whales changed the frequency range and frequency modulation of their calls to avoid acoustic competition with leopard seals.

There is evidence that supports a direct relationship between predation risk in different

habitats, predator presence, and habitat use by prey (Festa-Bianchet, 1988; Berger, 1991; Taber & MacDonald, 1992a, 1992b; Cowlshaw, 1997; Altendorf et al., 2001; Creel et al., 2005; Winnie & Creel, 2007; Baldi, 2007). Prey would perceive predation risk in an area and respond accordingly. Indian Ocean bottlenose dolphins (*Tursiops aduncus*) select deep waters when tiger sharks (*Galeocerdo cuvier*) are present in productive, but dangerous, shallow habitats of Western Australia. Bottlenose dolphin groups are also larger in more dangerous shallow habitats. These findings suggest that the distribution of foraging dolphins reflects a trade-off between the danger of being exposed to predators and food availability (Heithaus & Dill, 2002).

The array of avoidance behaviour by prey discussed above acts as a selective force resulting in the development of skillful predators. This study confirms previous observations of differential individual success by killer whales in the capture rate, particularly for the intentional stranding technique (López & López, 1985; Hoelzel, 1991). Predation on sea lions by killer whales in the study site had an indisputable practice component. Some killer whales are particularly skillful at profiting from a bounty of food available for a short period of time (see also Guinet, 1991). But skills seem to be maintained by practice and may also be facilitated by observing the performance of others. Killer whales, including juveniles, have been seen intentionally stranding in solitary beaches of Peninsula Valdés where prey is absent (López & López, 1985; Hoelzel, 1991; pers. obs.).

Comparative Aspects of Predator Avoidance in Mammals

Examples of antipredator behaviours in mammals include most of the aspects reported for the sea lion-killer whale interaction: vigilance (Elgar, 1989; Lima & Dill, 1990; Roberts, 1996), grouping (Hamilton, 1971; Fitzgibbon & Lazarus, 1995; Frid, 1997; Creel & Winnie, 2005), and avoidance of risky areas (Abramsky et al., 1996; Cowlshaw, 1997; Heithaus & Dill, 2002; Creel et al., 2005). The risk of predation depending on habitat configuration was suggested by several authors (Cowlshaw, 1997; Heithaus & Dill, 2002; Creel et al., 2005), sex and age of the prey (Fitzgibbon, 1990b; Fanshawe & Fitzgibbon, 1993; Toigo, 1999; White et al., 2001), and physical condition of the prey (Bachman, 1993; Sinclair & Arcese, 1995; Winnie & Creel, 2007). Juvenile mammals are usually at greater danger than adults (Holmes, 1984; Longland & Jenkins, 1987; Fanshawe & Fitzgibbon, 1993; Ross & Jalkotzy, 1996). Protection against predators is often related to acquisition of risk information through learning

from others and from individual experiences (Griffin, 2004).

Experience is relevant in developing antipredator responses (Berger, 1998; Hunter & Skinner, 1998), with juveniles exhibiting less acute responses than adults (Seyfarth & Cheney, 1980; Fitzgibbon & Lazarus, 1995; Arenz & Leger, 1997). Differential juvenile vulnerability due to lack of experience or inability to recognize predators has been proposed for some species (Caro, 1987; Longland & Jenkins, 1987; Fitzgibbon & Lazarus, 1995). A period of transition in the abilities to escape predation and a high mortality of "poor runners-swimmers" was described for Thomson's gazelles (*Gazella thomsoni*) (Fitzgibbon, 1990a). Lack of physical attributes or experience necessary to prevent attacks have been suggested for yearling moose (*Alces alces*) (White et al., 2001), while delayed detection of potential threats and longer escape times were mentioned for hoary marmot juveniles (*Marmota caligata*) (Holmes, 1984).

Immature animals may derive antipredator benefits simply from association with other individuals (Lima & Dill, 1990). In the present work and other studies (e.g., Caro, 1994), mothers provide information relevant to predator recognition and avoidance. Experienced sea lion mothers swim close to a pup and apparently place themselves between the predator and their pup. When speed or relative position fail and the attack occurs anyway, mothers were observed calling to their pups and leaving the waters at any spot during the crossing of a dangerous site. Constantly traveling close to the mother has been suggested as defensive behaviour for dusky dolphins (Würsig & Würsig, 1980) and southern right whales (Thomas & Taber, 1984), but the sea lion pups spend many days alone unattended on the beach while their mothers forage at sea (Campagna & Le Boeuf, 1988; Werner & Campagna, 1995; Campagna et al., 2001). From mid-February on, at least 30 to 40% of the females may be in the water while pups are left waiting (Campagna & Vila, unpub. data).

Vigilance is one of the most common behaviours by which prey detect and avoid predators (Lima, 1987; Lima & Dill, 1990; Quenette, 1990). Adult sea lions' increased neck-stretching in risky areas or before crossing an area suggests vigilant behaviour. Predation risk influences vigilance in other species (Illius & Fitzgibbon, 1994; Molvar & Bowyer, 1994; Hunter & Skinner, 1998; Altendorf et al., 2001; Wolff & Van Horn, 2003). That vigilance is advantageous has also been shown for Thomson's gazelles (Fitzgibbon, 1989).

Vigilance is influenced by group size (Pulliam, 1973; Pulliam et al., 1982; Elgar, 1989; Lima &

Dill, 1990; Roberts, 1996). As others become part of the group, the chances of detecting a predator are improved. This effect has been proposed for pinnipeds exposed to land predation (da Silva & Terhune, 1988). The large number of sea lions performing neck-stretching simultaneously made it difficult to determine the relationship between group size and vigilance. However, the observation of sea lions in rookeries spotting predators from safe locations ashore suggests that being in a group could increase the acquisition of information on risks from others (Griffin, 2004).

Potential prey may also benefit from being in a group by confusing the predator or by diluting their chances of being chosen (Hamilton, 1971; Bertram, 1978). We report an increase in group size, porpoising, and escape manoeuvres in risky contexts, suggesting that group size may be a response to predation pressure in sea lions. Porpoising and changes in direction could be helpful to confuse killer whales as it was suggested for stotting and leaping while fleeing in Thomson's gazelles (Caro, 1986) and impalas (*Aepyceros melampus*) (Jarman, 1974), respectively. Stotting also has been suggested as a behaviour to avoid predation in Patagonian hares (*Dolichotis patagonum*) (Taber & MacDonald, 1992a). Predators would have more difficulty in following a prey moving fast and in an unpredictable direction (Humphries & Driver, 1967).

Hoelzel (1991) proposed a passive listening mechanism in killer whales that attack sea lions. Visual detection of prey would be difficult in shallow waters due to the turbulence of the surf, and active acoustics or echolocation is likely to be less efficient in very shallow waters due to the scattering of the clicks off the surface and bottom (Thomas & Taber, 1984; Hoelzel, 1991; Heithaus & Dill, 2002). If the reflective surface of the water and substrate amplify the sound of pinnipeds swimming against stones (Hoelzel, 1991), sea lions that are porpoising may confuse killer whales. For short intervals while in the air, as if mimicking dolphins, sea lions would disappear as a signal. Pups have rarely been seen porpoising during their first weeks of life.

Sea lion pups are a relatively small meal for an adult killer whale or for a pod of them. Most pups weighed 14 to 20 kg during the periods after the breeding season when this study took place. Maximization of food intake would then require more attacks and stranding risks than preying upon adults. The pattern of targeting young is widespread in nature, however. It has been observed in killer whales (Jefferson et al., 1991; Baird & Dill, 1995; Gaydos et al., 2005; Mehta et al., 2007), and it was also reported in terrestrial mammals. African wild dogs (*Lycaon pictus*)

prefer young Thomson's gazelles and wildebeest (*Connochaetes taurinus*), which are easier to catch than mature animals (Schaller, 1972; Fitzgibbon & Fanshawe, 1989). Likewise, the success of cheetahs (*Acinonyx jubatus*) hunting gazelles decreases as the age of the prey increases, which may explain why these predators selected immature gazelles in greater numbers than predicted on a representational basis in the population and despite smaller sizes (Fitzgibbon & Fanshawe, 1989). Baird & Dill (1995) also suggested that harbour seals (*Phoca vitulina*) may be more difficult to catch during the winter months when more experienced pups are likely to detect killer whales and assess the associated danger.

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