Male harassment of female New Zealand sea lions, *Phocarctos hookeri*: mortality, injury, and harassment avoidance

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Abstract: Sexual aggression by male pinnipeds during breeding can lead to female injury and death, affecting reproductive success, fecundity, and increasing the cost of mating for females. Thus, females that employ strategies to minimize the probability of being injured will be at an advantage. Here we investigate the extent of injuries and the number of deaths attributed to male harassment, and test the hypothesis of whether the arrival and departure behaviour of female New Zealand sea lions (*Phocarctos hookeri* (Gray, 1844); NZSL) at Sandy Bay, Enderby Island, the Auckland Islands, is adapted to reduce the chance of injury or death from encounters with male NZSLs. During the breeding season, harassment by non-territorial male NZSLs causes mortality in adult female NZSLs, approximately 5 in every 1000 females breeding each year. Permanent scars from male bites are observed on 84% of adult females. This mortality and visible injury rate only represents the direct impacts on female NZSL from male harassment. Indirect impacts, such as the time and energy cost of avoidance behaviour, pup separation, and pup injury and death, can have as significant long-term effects on individuals and the population. We find that male harassment can influence the behaviour of individuals in NZSL breeding harems.

Résumé : L'agression sexuelle par les pinnipèdes mâles durant la période de reproduction peut causer des blessures et même la mort aux femelles, ce qui affecte le succès de la reproduction et la fécondité et augmente le coût de la reproduction chez les femelles. Les femelles qui utilisent des stratégies pour minimiser leur probabilité de blessure sont donc avantagées. Nous évaluons ici l'importance des blessures et le nombre de décès attribuables au harcèlement des mâles chez des lions de mer de Nouvelle-Zélande (*Phocarctos hookeri* (Gray, 1844); NSZL) femelles à Sandy Bay, île d'Enderby, îles Auckland; nous évaluons l'hypothèse selon laquelle les comportements d'arrivée et de départ des femelles sont des adaptations pour réduire la probabilité de blessure ou de mortalité consécutive à des rencontres avec les mâles. Durant la saison de reproduction, le harcèlement par les mâles non territoriaux est responsable d'une mortalité annuelle d'environ 5 femelles NZSL sur 1000 reproductrices. Des cicatrices permanentes de morsures par les mâles s'observent chez 84 % des femelles adultes. Cette mortalité et ce taux visible de blessure ne représentent que les impacts directs du harcèlement des mâles sur les femelles NZSL. Les impacts indirects, tels les coûts en temps et en énergie des comportements d'évitement, la séparation des petits de leur mère, ainsi que les blessures et la mort de petits, peuvent avoir des effets significatifs à long terme sur les individus et la population. Nos résultats démontrent que le harcèlement par les mâles peut influencer les comportements individuels dans les harems de reproduction du NZSL.

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Introduction

In sexually dimorphic, polygamous pinnipeds, such as New Zealand sea lions (*Phocarctos hookeri* (Gray, 1844); NZSL), breeding females interact with males that outweigh them, that possess dangerous weapons (large teeth), and that aggressively pursue interactions/copulation. Sexual aggression by males, predominantly non-territorial, can lead to female injury and death in pinnipeds (Marlow 1975; Campagna et al. 1988; Cassini and Vila 1990; LeBoeuf and Mesnick 1990; Smuts and Smuts 1993; Galimberti et al. 2000, 2000*a*, 2000*b*; Cassini and Fernandez-Juricic 2003), and consequently is a significant cost of mating for females of some species. Mortality and visible injury only represents the direct impacts on females from male harassment. Indirect impacts, such as the time and energy cost of avoidance

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behaviour, pup separation, and pup injury and death, can have significant long-term effects on individuals and the population (Le Boeuf and Mesnick 1990; Campagna et al. 1992; Hiruki et al. 1993; Cassini 1999, 2000). Given this, females that display strategies to reduce male harassment will be at a natural adaptive advantage. Responses of female mammals to potentially dangerous sexual liaisons include a range of behaviours that differ in energy expenditure (e.g., evasion, resistance, receptivity, eliciting protection from dominant males, grouping of females) or morphological adaptations (Smuts and Smuts 1993).

NZSLs come ashore to breed in colonies on New Zealand's sub-Antarctic islands from mid-November to mid-January (austral summer; mean pupping date late December; Gales 1995). Adult and subadult males are present on Sandy Bay, Enderby Island, from mid-November until mid-January, with females arriving from early December, usually just days before parturition (Cawthorn et al. 1985). Male harassment of females occurs predominantly during female departure and arrival attempts (Marlow 1975). Male harassment is predominantly from adult and large subadult males that are non-territorial and harassment includes the following strategies: detainment (chest to chest contact stopping females from moving forward); lunging (open mouthed thrust at females); biting; charging (swift movement by males resulting in body contract); and compression beneath a male that may result in suffocation or drowning, depending on circumstances.

Female NZSLs are vulnerable to serious injuries while arriving and departing the breeding harem because (*i*) males outnumber females during harem development, (*ii*) competition to mate among males is intense, and (*iii*) the pressures of maternal investment means that females must make regular excursions to and from the harem, increasing their interactions with non-territorial males.

In this study, we investigate the extent of injuries and the numbers of deaths attributed to male harassment, and test the hypothesis that the arrival and departure behaviour of female NZSLs is adapted to reduce the chance of injury or death from violent encounters with non-territorial males. Our study represents the first quantitative analysis of harassment and possible reduction behaviours during the breeding season on any otariid species.

Methods

This study was conducted at the Sandy Bay breeding colony, Enderby Island, Auckland Islands (50°30′S, 166°17′E; Fig. 1), over the two breeding seasons of (December–January) 2002–2003 and 2003–2004. The Sandy Bay colony is the second largest breeding colony of NZSLs, with approximately 400–500 pups born per year (Gales and Fletcher 1999). Female NZSLs come ashore 1–3 days before giving birth from early December to early January. Mothers give birth to a single pup and remain with it for 5–10 days before returning to sea to forage (Cawthorn et al. 1985). During this postnatal period females come into oestrous and are mated. They then alternate between feeding trips at sea (1–5 days) and nursing of pups ashore (1–3 days) until pups are weaned at approximately 9 months of age (Cawthorn et al. 1985). Therefore, it is considered that the majority of arrival and

Fig. 1. North–East Auckland Islands showing Sandy Bay, Enderby Island (shaded; 50°50′S, 166°28′E). Inset: New Zealand's sub-Antarctic. Shaded area indicates the current distribution of New Zealand sea lions, *Phocarctos hookeri* (NZSL), and the location of the Sandy Bay breeding colony, Enderby Island, Auckland Islands (50°30′S, 166°17′E).
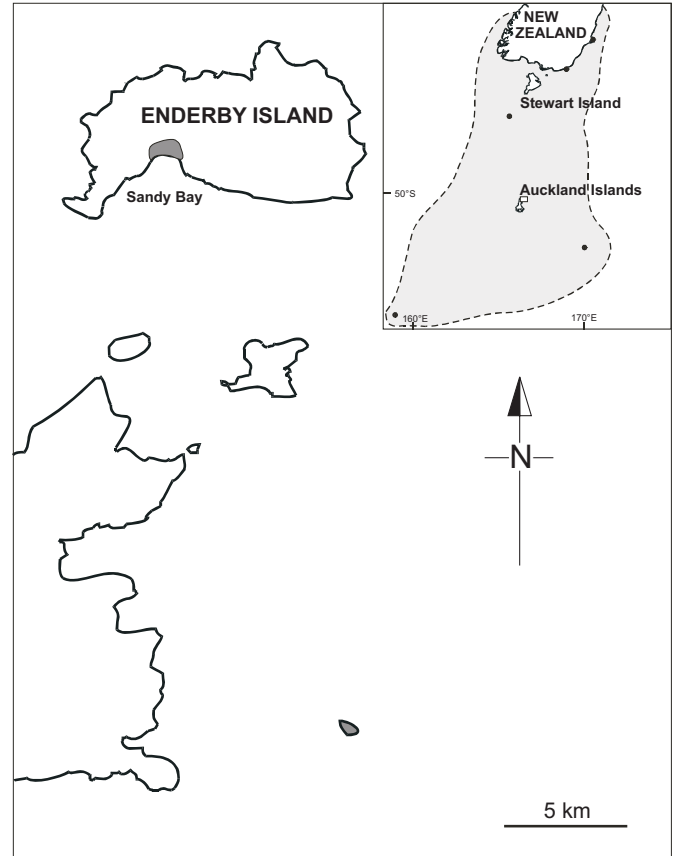
depart events of females are when females are either pregnant when first arriving or have been inseminated and are usually not in oestrous when departing.

The Sandy Bay breeding beach is a 450 m long white volcanic/calcareous sand beach, maximum width 50 m at low tide, with extensive grassy sward areas to the north and east of the beach (Fig. 1). The width and sand cover on the beach varies considerably with tide, including neap and spring tides, and weather conditions, specifically storms, making the proximity of the harem to water from 5 to 40 m. Males are resident on the beach before females arrive for an unknown period thought to be between 1 and 2 weeks.

Data on female deaths directly caused by, or precipitated by, male harassment were taken from necropsy records of all NZSL deaths on Sandy Bay, Enderby Island, from 1999 to present (P. Duignan, unpublished data). Records of sea lion bite wounds (identified by characteristic scarring caused by the canine teeth) on adult females were collected while individuals selected for telemetry studies (B.L. Chilvers, unpublished data; *n* = 64) were under general anaesthesia during the 2002–2003 and 2003–2004 seasons. Behavioural observations were made from an elevated position within 10 m of the harem for 4 h each day between 0800 and 2000 (12 December – 12 January) in both seasons and between

2300 and 0100 every 3rd night during the 2003–2004 season. Night observations were made using Night Mariner binoculars (ITT Night Vision Equipment, Roanoke, Virginia), with 1× magnification and a 40° field of view. Female arrivals and departures were observed ad libitum within all observation periods. Between 14 January and 15 February, 18 females (in 2003) and 24 females (in 2004) had VHF tags attached to monitor their attendance patterns through an automatic receiver and logger (Model R2000; Advanced Telemetry Systems Inc., Isanti, Minnesota). These data were analysed to determine unobserved female arrival and departure times. For the analysis, arrival and departures were grouped into six 4-h blocks: 0000–0400, 0400–0800, 0800–1200, 1200–1600, 1600–2000, and 2000–2400.

The following information was recorded for each event. For arrivals, we recorded the following: date; time; female arrival behaviour; the straight-line distance between the point of exiting the sea and the point of entry to the harem; and the outcome of the female's behaviour defined as whether she (*i*) arrived into the harem unharassed, (*ii*) was harassed (i.e., chased, lunged at, or bitten), or (*iii*) "captured" (i.e., detained from reaching the harem by being chased, pinned by the body mass of a male, or bitten). Female arrival behaviour was categorized into four non-mutually exclusive categories: (1) female is observed to travel up and down the shoreline just behind the breakers before leaving the sea; (2) female comes straight in from the sea and heads directly to the harem; (3) female sits on the beach water's edge for >5 s before heading for the harem area; and (4) female interacts (i.e., snarls, lunges, or bites) with males in the harem/beach area. The last category (4 or "defence behaviour") was analysed separately from the other three categories. We scored four category combinations: A = 1; B = 2; C = 1 and 3; and D = 2 and 3. The probability of harassment given any arrival behaviour was analysed using χ^2 test.

For departure, we recorded the following: date; time; distance to water from harem exit point; number of males present in the area of departure (i.e., the number of males within 10 m of the point females entered the water); number of females attempting to depart at the same point (i.e., a female "departure group" was classified as a group of females at the outer seaward side of the harem that were clumped and actively "moving" towards the water, although this movement may have occurred over various time periods); number of females successfully departing; and the outcome of the departure attempt defined as for arrivals (i.e., (*i*) unharassed, (*ii*) harassed, and (*iii*) captured). Weather information (cloud cover, wind strength and direction, still air temperature, and wind chill) and shortest straight-line distance between harem and water were recorded every 0.5 h during observations regardless of whether female arrival and departure events were recorded.

Data were analysed using SPSS® version 10 (SPSS Inc. 2004). Logistic regression models were used to analyse female behaviour (categories A, B, C, and D), time of day, defence behaviour, and environmental factors to predict the binomial outcome of female arrivals against females being harassed (category *ii* and *iii*) or not (category *i*), and for those females that were harassed, whether they were captured (category *iii*) or not (category *ii*). Similarly for departures, logistic regression models were used to analyse time of day, the number of females attempting to leave, distance to water, the number of males between the water and the departing females, and environmental factors to predict the binomial outcomes of female departures being harassed (categories *ii* and *iii*) or not (category *i*), and for those females that were harassed, whether they were captured (*iii*) or not (*ii*). This technique provides a measure of the significance of each variable in the model (Wald's χ^2) and the slope of the effect. Values are reported as means ± SE.

Departure was also measured in terms of success, i.e., the percentage of females that successfully departed relative to the number attempting to depart. These data were analysed using a univariate general linear model (GLM), examining the relationships between success and distance to water, number of females attempting to depart, and number of males between departing females and water.

In each year, mark–recapture estimates for the number of pups born at Sandy Bay harem were conducted between 15 and 16 January. On 15 January, 200 caps were glued to the heads of pups within the harem. On 16 January, three observers counted capped verse uncapped pups three times each to obtain a capped to uncapped ratio, which allowed the use of the Peterson–Lincoln index (closed population) mark–recapture estimate.

Results

Harem development

In both years of observation, the harem grew gradually from a small founding group of between four and six females that came ashore in early December. Once the harem was fully formed (mid-December), it consisted of a maximum of 346 females on the beach on any 1 day (271 ± 15 (mean ± SE), n = 28), with a maximum of 47 adult males holding harem territories and 33 adult males holding peripheral territories within 10 m of harem females (B.C. Robertson, and B.L. Chilvers, unpublished data). The maximum number of adult males was 210 (141 ± 4) and subadult males was 40 on the breeding beach on any single day, with a maximum of another 90 of each (adult males and subadult males) on the sward/grass area adjacent to the breeding beach.

Death and injury from male harassment

During the 2002–2003 season, one female died after a male bit her head, perforating the cranium and cerebrum. Three females were killed by males during the 2003–2004 season; one was pinned beneath a male in the surf zone and drowned, while the deaths of two pregnant females were attributed to male harassment (i.e., severe internal injuries sustained from crushing by males; P. Duignan, unpublished data). From a calculation of mark–recapture estimates and known pup deaths, 488 and 507 pups were born at Sandy Bay in the 2002–2003 and 2003–2004 season, respectively. These numbers represent the minimum number of reproductive females who were present in the area during each breeding season (12 December – 12 January). Based on these estimates of female numbers, total mortality of breeding females owing to male harassment each season was approximately 0.2% and 0.6%, respectively (Table 1). In the 2000–2001 and 2001–2002 seasons, four and two female deaths

Table 1. Yearly female mortality of New Zealand sea lion, *Phocarctos hookeri*, attributed to male harassment calculated from yearly pup mark–recapture estimates, representing minimum number of breeding females present at Sandy Bay breeding rookery, Enderby Island, and number of female deaths attributed to male harassment.

Year	Pup mark–recapture estimate	Female deaths attributed to males	Calculated yearly mortality (%)
2000–2001	562	4	0.7
2001–2002	403	2	0.5
2002–2003	488	1	0.2
2003–2004	507	3	0.6
Overall	1960	10	0.5

were attributed to male harassment, giving a level of mortality of 0.7% (562 pups/breeding females) and 0.5% (403 pups/breeding females), respectively (Table 1). Over the last four breeding seasons, the approximate mortality rate of females attributed to male harassment was 0.5% ± 0.1% per year or 5 females in every 1000 breeding females. No deaths of adult females were attributed to male harassment outside of the pupping period (12 December – 12 January; P. Duignan, unpublished data).

The number of females with injuries sustained by male harassment was difficult to assess from behavioural observations alone. Nevertheless, all female arrivals and departures scored as captured (10% arrivals and 14% departures) sustained obvious bite injuries (i.e., broken skin and bleeding). Observations from 64 anaesthetized females showed that 84% (54/64) had permanent sea lion bite marks on their bodies, indicating that at sometime they had been bitten by other sea lions whose bites had broken the skin. Harem observations indicate that females rarely bite each other (B.C. Robertson and B.L. Chilvers, unpublished data); hence, the majority of these injuries must have been caused by males, either adults or subadults.

Behaviour

A total of 208 h of behavioural observations distributed evenly between 0800 and 2000 were collected between 12 December and 12 January in the 2002–2003 and 2003–2004 seasons (104 h each season). Twenty hours of night observations were made during the 2003–2004 season between 2300 and 0100. A total of 478 arrival events (224 in 2002–2003 season and 254 in 2003–2004 season) and 76 departure events (37 in 2002–2003 season and 39 in 2003–2004 season) were recorded over both seasons. All arrival events recorded were of individual females, whereas the number of females departing in a group was from 1 to 34 animals (7.5 ± 1.1, n = 76). The proportion of the group successfully departing (success rate) was 81% ± 5%. Of all arrivals, 55% were recorded entering the harem without harassment, 35% were harassed (i.e., chased, lunged at, or bitten), and 10% were captured and bitten. Of all the departure events (groups), 58% were not harassed, 28% were harassed, and 14% were captured. Of the four female arrival behaviours recorded, 67% of females came straight in from the sea and headed for the harem without stopping (category A); 29% of this group were harassed on arrival and 8% were captured. Of all arrivals, 14% were observed to travel back and forth along the beach area in the sea just behind the breakers before leaving the sea (category B); 43% of this group were

harassed on arrival and 14% were captured. Of all female arrivals, 12% came straight into the beach but then sat on the water's edge for >5 s (category C); 51% of this group were harassed and 17% were captured. Similarly, 7% of all arrivals travelled back and forth along the beach area before coming ashore and then sitting on the water's edge for >5 s before heading for the harem area (category D); 56% of this group were harassed and 9% were captured. There was a significant difference between arrival behaviour and harassment probability, with females displaying category A behaviours having the lowest likelihood of being harassed, followed by females displaying category B behaviours (χ^2 = 29.76, df = 3, $p < 0.001$). There was no difference in the levels of harassment verse capture by arrival behaviour (χ^2 = 1.26, df = 3, $p = 0.76$).

The number of female arrivals was significantly lower during darkness hours (2300–0100) than daylight hours (one-way ANOVA, $F_{[3,474]} = 11.2$, $p = 0.002$; Fig. 2); however, there were no significant differences within daylight hours (0800–2000). From the VHF data collected over the two seasons, 293 arrivals and 295 departures from 42 animals were recorded. Although there was variation in the number of arrivals and departures when analysed in four hourly blocks, there was no significant difference (one-way ANOVA; arrival: $F_{[5,287]} = 1.07$, $p = 0.41$; departure: $F_{[5,289]} = 0.66$, $p = 0.65$; Fig. 3). There was also no significant difference between the number of arrivals observed at high water and those observed at low water (one-way ANOVA, $F_{[1,477]} = 0.006$, $p = 0.95$).

The number of attempted departures differed significantly during the day (one-way ANOVA, $F_{[3,72]} = 8.9$, $p = 0.004$; Fig. 2), with late afternoon/early evening (1600–2000) having significantly higher numbers of departures recorded per hour than any other time of day (Fig. 2). This pattern was repeated when the number of females attempting to depart in each departure attempt was considered (one-way ANOVA, $F_{[3,566]} = 3.8$, $p = 0.045$; Fig. 2).

Higher numbers of departure attempts occurred during high water than low water (high: 0.39 ± 0.034 attempts/h, 61 h; low: 0.2 ± 0.032 attempts/h, 44 h; one-way ANOVA, $F_{[1,74]} = 17.2$, $p = 0.05$). However, there was no significant difference in the number of females departing per hour at high or low water when the group size of departures was considered (one-way ANOVA, $F_{[1,568]} = 1.72$, $p = 0.31$).

Harassment during arrival

Although there was a significant difference in arrival behaviour and level of harassment within each behavioural

Fig. 2. The mean (±SE) number of groups and individual female arriving or departing per hour of observation at Sandy Bay, Enderby Island, NZSL harem between 12 December and 12 January during the 2002–2003 and 2003–2004 seasons. || indicates a break in observation times.
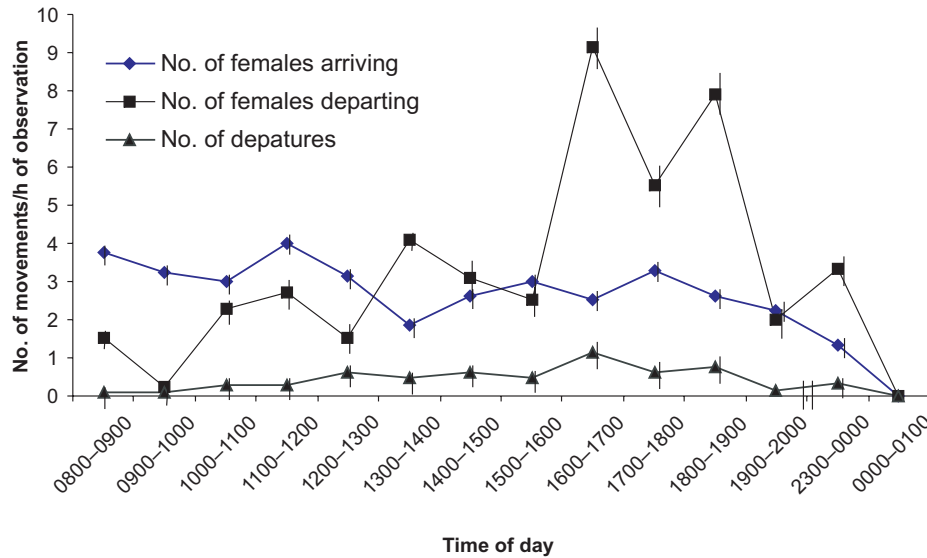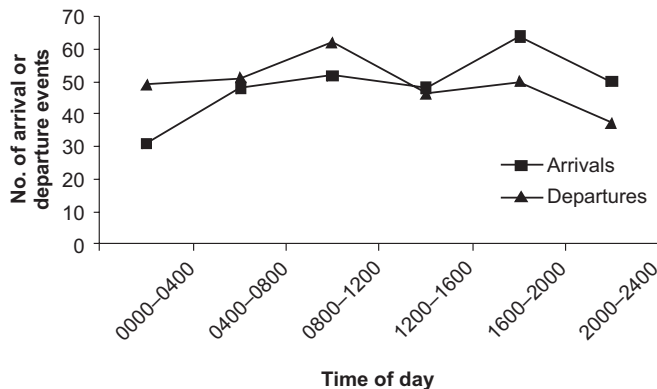

Fig. 3. The time of day for arrival and departure records for 42 VHF-tagged female NZSLs between 14 January and 15 February during the 2002–2003 and 2003–2004 seasons.

group, the probability of being harassed during arrival was only significantly related to distance between water's edge and harem when all other factors were considered (outcome predicted $R^2 = 68\%$). The closer the water's edge to the harem and, therefore, the closer the female was to the harem when leaving the water, the less likely she was to be harassed (Wald's $\chi^2 = 15.82$, $p = 0.0001$, slope = 0.145). Similarly, for those females that were harassed, distance between water and harem was the only significant factor determining whether a female was caught and bitten or simply harassed (outcome predicted $R^2 = 78\%$; Wald's $\chi^2 = 7.87$, $p = 0.005$, slope = 0.161). We found no significant correlations between any environmental factor (i.e., wind strength, time of day, or temperature) and female harassment on arrival.

"Defence" behaviour showed a significant difference between the probability of being harassed and not being harassed. By definition, however, females did not have to defend themselves if they were not harassed; therefore, all non-harassed females showed no defence behaviour. There was a trend that those females who fought were less likely to get caught and bitten than those that did not (Wald's $\chi^2 = 3.13$, $p = 0.07$, slope = –0.071).

Harassment during departure

The probability of being harassed during departure was significantly related to female group size and the number of males between the departing group and the sea (outcome predicted $R^2 = 70\%$). The smaller the group of females attempting to depart the more likely they were to be harassed (Wald's $\chi^2 = 4.53$, $p = 0.03$, slope = –0.156). The larger the numbers of males between the departing group and the shore, the more likely the females were to be harassed (Wald's $\chi^2 = 8.53$, $p = 0.003$, slope = 0.251).

Departure success (the proportion of females successfully departing to sea) was significantly related to the group size of females departing and the interactions between (*i*) female group size and number of males between the departing group and the water's edge, and (*ii*) female group size and distance to the water's edge of the departing group. The smallest (1–5 females) and largest (>20 females) groups of departing females had the greatest success at departing (univariate GLM, $F_{[7,28]} = 3.65$, $p = 0.01$), although as seen above smaller groups were more likely to be harassed during departure. The significant interactions were that large groups of females had higher success when closer to the water's edge ($F_{[10,28]} = 2.9$, $p = 0.006$), while high numbers of males between the water's edge and the departing female groups reduced the success of small and medium-sized female groups (<20, $F_{[10,28]} = 1.7$, $p = 0.1$). There was a trend for higher numbers of males between the water and the departing group that reduced departure success; however, this was not significant ($F_{[5,28]} = 1.7$, $p = 0.1$). We found no significant relationships between any environmental factor (i.e., wind strength, time of day, or temperature) and female harassment or success levels.

Discussion

Harassment deaths and injuries

Male harassment of female NZSLs at the Sandy Bay colony caused an appreciable level of mortality and injury. Male harassment was responsible for the mortality of 10 adult females in the last 4 years, resulting in a mean mortality rate of 0.5% per year or 5 in 1000 breeding females. This level of mortality, directly attributable to male harassment, has not previously been quantified for NZSLs or any other otariids. The extent of females with injuries sustained from male harassment was difficult to assess from behavioural observations alone. The reason for this is that bites do not always result in skin lacerations that are visible through the pelage. Thus, the external signs of trauma may be subtle, but subcutaneous contusion and deep soft tissue laceration may be severe (P. Duignan, unpublished data). Nevertheless, all female arrivals and departures that were scored as captured (10% arrivals and 14% departures) sustained obvious bite injuries from males (i.e., broken skin and bleeding), and from observations on anesthetized females, 84% showed previous sea lion bite scars.

Male harassment and injury of females from nonterritorial males is common among pinnipeds. Male-inflicted injuries are a cause of female mortality for Northern elephant seals, *Mirounga angustirostris* (Gill, 1866), during the breeding season (Le Boeuf and Mesnick 1990). Male-induced female deaths during harem breeding at Año Nuevo Island are estimated to be 1 in 1000. Such a rate is believed to have had a significant selection pressure in shaping the behaviour and morphology of females to reduce harassment (Endler 1986; LeBoeuf and Mesnick 1990). In South American sea lions, *Otaria flavescens* (Shaw, 1800), groups of subadult males injure and kill females during abduction raids on harems (Campagna et al. 1988; Cassini and Vila 1990). Northern fur seal, *Callorhinus ursinus* (L., 1758), males compete for females on the border between territories with two males occasionally seizing a female with their teeth, resulting in injury or death from being pulled in opposite directions (Gentry 1997). On Año Nuevo Island, adult male Steller sea lions, *Eumetopias jubatus* (Schreber, 1776), have been observed to kill females during copulation attempts (R. Gentry, personal communication, in Le Boeuf and Mesnick 1990).

Death and injury are quantitative consequences of male harassment on females. Indirect impacts of male harassment are less obvious but can have significant long-term and short-term effects, including increased energy cost to females, disruption to their activity rhythms and time budgets, affect their pup's survival, energy budget, and disrupt maternal care (Le Boeuf and Mesnick 1990; Campagna et al. 1992; Hiruki et al. 1993; Cassini 1999, 2000). Based on necropsy data on pups born at Sandy Bay since the 1999–2000 season, males were responsible for the death of over 15 pups each breeding season, usually approximately 25% of all deaths recorded for pups aged between birth and 3 months (P. Duignan, unpublished data). Males (including territorial, peripheral, and subadult) kill pups through biting, shaking, crushing, and suffocation. The combination of direct and indirect effects of male harassment on females is likely to influence female breeding behaviour and could lead to the lowering of the overall reproductive success of individual females, and hence, productivity at the population level (Le Boeuf and Mesnick 1990; Campagna et al. 1992; Hiruki et al. 1993; Cassini 1999, 2000).

Behavioural responses to harassment

The risk of injury and death observed for female NZSLs increases the risk and cost of breeding for females. This level of detrimental effect should impose selection pressure on female behaviour, which will favour females with behavioural responses such as arrival strategies that act to reduce this cost, as shown in other harem breeding pinnipeds (Endler 1986; Le Boeuf and Mesnick 1990).

Female NZSLs arrival and departure behaviour appear to differ if considered a strategy to avoid male aggression. Arrival behaviour of female NZSLs appears to be orientated towards evasion of males on arrival and defence when necessary to reduce possible male harassment rather than synchronization of arrival times. It is expected that the availability of prey, distance to prey source, individual variation in foraging strategies, ocean environment such as ocean currents involved in foraging, and maternal care requirements may have a greater influence on the timing of female arrival than possible avoidance behaviour towards male harassment (Chilvers et al. 2005). This hypothesis is supported by the even distribution of arrival times of females during daylight hours and the even distribution of arrival time throughout the day from the automatically logged VHF-tag data. Similar results were found for Steller sea lions, where arrivals of lactating females ($n = 534$) were evenly distributed between day and night (Trites and Porter 2002).

In contrast, departure behaviour appeared to be more adapted to the reduction of harassment via departure at high water, departing in groups, for harassment dilution effect (Hamilton 1971), and higher group departures when male numbers were low. The number and rate of female departures showed significant differences across the day, with the highest numbers of females and groups departing during late afternoon/early evening. Both the temporal and tidal variances in departure timing may arise from females departing for best timing of foraging that is related to the distance which she travels to a prey source, prey diurnal patterns, or tide strengths to specifically lower transport costs to and from foraging sites. The diving behaviours of female NZSLs show no significant temporal variation in the timing of the dive (Gales and Mattlin 1997), indicating no strong preference in diving/foraging timing that could be related to the timing of harem departure. Thus, variation in departure timing may relate to the general behavioural activity of the harem and harassment avoidance, with females leaving during a natural low in the temporal pattern of harem activity. Such a pattern has been observed within the Sandy Bay harem, with activity levels of all animals lower in late afternoon/early evening relative to any other times of the day (B.C. Robertson and B.L. Chilvers, unpublished data). Alternatively, females may be timing their departure to avoid sharks, apparently major predators on NZSLs around the Auckland Islands based on shark attack wounds observed on survivors and occasional beach cast remains of victims (B.L. Chilvers, unpublished data). Lactating Steller sea lions were found to have a similar departure pattern during their sum-

mer breeding season with NZSL females, typically departing during the evening in the summer and during daylight hours in the winter. These differences are thought to reflect seasonal differences in prey sought and relative day length between seasons (Trites and Porter 2002). This is supported by work in similar latitudes by Georges and Guinet (2000) who found that lactating female Subantarctic fur seals, *Arctocephalus tropicalis* (Gray, 1872), also departed during the late evening in the summer ($n = 4$).

Male harassment is an important factor affecting the survival, health, and reproductive success of female NZSLs, and therefore the overall fitness of the population. Mortality and injuries inflicted on female NZSLs are predominantly by non-territorial males and are combined with the observations that males cause pup deaths (P. Duignan, unpublished data), are reported to cannibalize pups (Wilkinson et al. 2000), and injure each other (McConkey et al. 2002; Marlow 1975) to demonstrate that males are an influential force which can shape the behaviour of conspecifics. Male aggression is a natural mortality factor that needs to be considered in estimating sex-specific survival rates of NZSL sexes and cohorts, and a factor that needs monitoring because it maybe affected by changing sex ratios and population demographics in this threatened species.

Acknowledgements

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