Significance of wounding to female reproductive success in Hawaiian monk seals (*Monachus schauinslandi*) at Laysan Island

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We studied reproductive rate, length of lactation period, pup survival, and mortality of injured and uninjured female Hawaiian monk seals (*Monachus schauinslandi*) on Laysan Island, northwestern Hawaiian Islands, in 1983–1989. The severity and timing of nonfatal injuries were influential in determining their effect on female reproductive success. There was a tendency towards a shorter mean lactation period and lower survival rate of pups for females with major injuries than for uninjured females. Females with minor injuries were similar to uninjured females in terms of reproductive rate, length of lactation, and pup survival. For females injured shortly before the birth of their pup or during lactation, pup survival was lower than for uninjured females, whereas for females injured during the year prior to pupping, measures of reproductive success were not significantly different from those for uninjured females. Immature (aged 4–8 years) females entering the reproductive population were injured by adult male seals significantly more often than females aged 0–3 years, but at a similar rate to adult females. The major effect of injuries on female reproductive success is an increase in female mortality: 87.5% of the adult females (n = 16) that died on Laysan Island in 1983–1989 sustained injuries from adult male seals.

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Nous avons étudié le taux de reproduction, la durée de l'allaitement, la survie des petits et la mortalité des femelles blessées et saines dans une population de Phoques-moines (*Monachus schauinslandi*) sur l'île Laysan dans le nord-ouest de l'Archipel hawaïen de 1983 à 1989. L'effet des blessures non mortelles sur le succès de la reproduction des femelles dépendait de l'importance de la blessure et de la période où elle se produisait. Les femelles portant des blessures graves avaient tendance à allaiter moins longtemps en moyenne que les femelles saines et leurs petits avaient un taux de survie moindre. Les femelles n'ayant que des blessures superficielles avaient un taux de reproduction, une période d'allaitement et un taux de survie de leurs petits qui ne différaient pas de ceux des femelles saines. Les femelles blessées peu avant la mise bas ou durant la période d'allaitement avaient plus tendance à perdre leurs petits que les femelles saines; toutefois, une blessure reçue un an avant la mise bas n'affectait pas de façon significative le taux de reproduction. Les femelles immatures, âgées de 4–8 ans, qui commençaient leur vie reproductive, recevaient plus de blessures de la part des mâles adultes que les femelles âgées seulement de 0–3 ans, mais tout autant que les femelles adultes. L'effet principal des blessures sur la reproduction est lié à la mortalité des femelles : 87,5% des femelles adultes mortes sur l'île Laysan en 1983–1989 (n = 16) portaient des blessures causées par des mâles adultes.

[Traduit par la rédaction]

Introduction

In recent years, efforts to identify factors contributing to a decrease in the survival and productivity of Hawaiian monk seals (*Monachus schauinslandi*) have increased as part of an overall recovery plan (Gilmartin 1983, 1988). Counts of monk seals have declined from about 1000 in 1959 to approximately 580 in 1987 (Johnson *et al.* 1982; Gilmartin 1988). In this situation, even a slight decrease in female survival or productivity could have a significant negative impact on population dynamics, as the net growth of a pinniped population is dependent on, and most sensitive to, female survival and, to a lesser extent, female reproductive success (Eberhardt and Siniff 1977; Eberhardt 1985). Wounds inflicted on adult females by males during mating attempts are the most common type of injury observed in monk seals (Hiruki *et al.* 1993). Consequently, the occurrence of such injuries and their potential effect on reproductive success have become matters of concern (Gilmartin 1983).

Female reproductive success (i.e., the number of viable offspring produced by a female during her lifetime) can be subdivided into several components, such as survival of the female to breeding age, reproductive life-span, and the production and survival of offspring (Clutton-Brock 1988), all of which

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could be influenced by injuries. In long-lived animals such as monk seals that can reproduce until at least 25 years of age (Johanos *et al.* 1990), longevity is a significant component of the lifetime reproductive success of females (Le Boeuf and Reiter 1988; Thomas and Coulson 1988), particularly if only one offspring is produced per year. If injuries increase the mortality of female monk seals, their lifetime productivity will be reduced.

Injuries to adult female monk seals could affect the production of pups in several ways. A wounded female may be less likely to breed because her resources are needed to ensure her own survival, or if she does breed, her pup may be aborted. Injured female northern elephant seals (*Mirounga angustirostris*) did not copulate in the year that they were injured and thus did not pup in the year following the injury (Le Boeuf *et al.* 1982).

The survival of pups born to wounded females may also be reduced. If an injured female has a pup, the amount of energy she is able to invest during the nursing period may be less than that of an uninjured female. Energy stored for lactation or for development of her pup might be redirected towards recovery from the injury (Ainley *et al.* 1981). Similarly, a pregnant female recovering from an injury might not be in as good condition at parturition as an uninjured female. Female Hawaiian monk seals fast during the entire nursing period (Kenyon and Rice 1959), as do most other phocid seals (e.g., northern elephant seals (Riedman and Ortiz 1979); harp seals, *Phoca groenlandica* (Lavigne *et al.* 1982); grey seals, *Halichoerus grypus* (Anderson and Fedak 1987)). If a female monk seal is in poor condition when her pup is born, she may be more likely to have a smaller pup or to wean her pup prematurely, because she is not feeding and cannot replenish her energy stores during lactation. A low weight at weaning may reduce the pup's probability of survival through its first year of life.

This paper examines the influence of injuries on four components of female reproductive success (reproductive rate, maternal investment, survival of pups, and mortality of adult females) to test the hypothesis that injuries inflicted by adult males negatively affect survival and reproduction. We also evaluate the significance of injury to the recruitment of young females into the breeding population.

Methods

The reproductive histories and injuries of female Hawaiian monk seals were analyzed from data collected at Laysan Island, a low coral and sand island located northwest of the main Hawaiian Islands (latitude 25°42′N, longitude 171°44′W), during 24 April – 21 July 1983, 30 March – 6 August 1984, 6 March – 1 December 1985, 1 May – 4 August 1986, 6 April – 22 July 1987, 28 February – 21 June 1988, and 30 March – 14 July 1989. Females were identified by temporary marks applied with commercial bleach at the beginning of the field season, by natural markings or scars, or by flipper tags applied in previous years (e.g., Stone 1984; Hiruki *et al.* 1993). For each female with a pup, the date of parturition, weaning date, and the pup's permanent identification number were also recorded. Pups were tagged after they had been weaned (Johanos *et al.* 1987; Johanos and Austin 1988; Alcorn and Buelna 1989; Johanos *et al.* 1990). Data recorded for each injured female included identification number, size class, location of the seal, and description of the injury, as detailed in Hiruki *et al.* (1993).

Female monk seals were classified as adult or immature on the basis of estimated age. Because reproductive success might be affected by age rather than injury status, seals that matured during the study period were excluded from the analysis of reproductive success. Adults were seals classed as being of breeding size in 1983, according to their length, girth, pelage appearance, and scarring (Stone 1984), or seals that had a pup in 1983 or earlier. Immatures were seals seen as juveniles or subadults in 1983 or 1984, or seals that were born in 1983 or later.

To evaluate the impact of injuries on reproductive success, adult female monk seals were divided into three categories in each year: *uninjured*: females that did not sustain any injuries prior to parturition or in the previous year; *currently injured*: females injured during the current year, before parturition or while still nursing the pup; and *previously injured*: females injured in the previous year, usually after weaning the pup of that year. The last category also included females that were injured in the previous year and were not observed with a pup.

Injuries were classified as minor or major. Minor wounds were circular wounds inflicted by cookiecutter sharks (*Isistius brasiliensis*), wounds inflicted by seals in jousting incidents, or those inflicted by the seal contacting a coral reef or debris (Hiruki *et al.* 1993). Major wounds were dorsal lacerations or gaping wounds inflicted by adult male seals during mating incidents or injuries caused by large sharks (described in Hiruki *et al.* 1993). Some of the wounds inflicted by adult males did not appear to be severe externally (e.g., Fig. 2A, 2B, Hiruki *et al.* 1993), but were classified as major because superficially minor abrasions and lacerations may mask significant subcutaneous damage (Johanos and Austin 1988), and some females die after sustaining seemingly minor wounds from adult male monk seals (Johanos *et al.* 1990; T. C. Johanos, B. L. Becker, and L. M. Hiruki, personal observations).

The reproductive rate, defined as the proportion of females that have a pup in a particular year, of uninjured females was compared with that of females injured in the previous year. The currently injured females were excluded from the analysis of reproductive rate because, by definition, they all had pups.

The parental investment period (the number of days that a female nurses and defends her pup) was calculated from the birth and weaning dates of each pup. If a range of dates was recorded for birth or weaning (e.g., 1–3 March), the last day in the range (3 March) was used to calculate the parental investment period. The lengths of completed parental investment periods of currently and previously injured females were compared, as were those of injured and uninjured females. If a female's parental investment period was cut short because her pup died or because she lost her pup to another female and did not gain another (Johnson and Johnson 1978; Boness 1990), it was excluded from the analysis, so that only complete nursing periods were considered. Females with major and minor injuries were compared independently with uninjured females to assess the effect of severity of injury on parental investment.

Pup survivorship was measured in two ways: the proportion of pups alive at the end of the nursing period and the proportion of pups alive after their first year. The survivorship of the pups of currently injured females and those of previously injured females was compared, and each was compared independently with pups of uninjured females. Pups of females with major and minor injuries were compared independently with pups of uninjured females.

The reproductive histories of all permanently identified adult female seals were examined in relation to the number of major injuries sustained per year in 1988 and 1989. The distribution of major injuries within years (number of injuries per year for each seal) was compared with a Poisson distribution to determine whether some females received a disproportionate fraction of the injuries. The number of identified female seals that died or disappeared from Laysan Island during 1983–1989 was examined to determine how many were known to have been injured by adult males.

Immature seals were divided into two classes, based on their reproductive maturity and age in 1988 and 1989. Seals aged 0–3 years were classed as prereproductive. This classification is based on 5 years being the youngest observed age of first reproduction for Hawaiian monk seals (Johanos *et al.* 1990); hence, the minimum age of first estrus appears to be 4 years, since female monk seals mate

TABLE 1. Power of tests used to compare components of reproductive success between injured and uninjured female Hawaiian monk seals at Laysan Island, northwestern Hawaiian Islands, 1983–1989, and the sample size required to determine a significant difference between the observed proportions when the power of the test = 0.80 (α = 0.05; one-tailed test)

Comparison	Test statistic	Power of test	Sample size required
Reproductive rate			
Major vs. uninjured	$G = 0.599$	0.19	783
Minor vs. uninjured	$G = 0.024$	0.10	5601
Parental investment			
Major vs. uninjured	$t = 0.981$	0.31	49
Minor vs. uninjured	$t = 0.723$	0.17	260
Survival to weaning			
Injured vs. uninjured	$G = 5.53$	0.82	137
Survival through first year			
Major			
Current vs. uninjured	$G = 2.92$	0.30	44
Previous vs. uninjured	$G = 0.002$	0.07	2953
Pooled vs. uninjured	$G = 1.01$	0.1	1043
Minor			
Pooled vs. uninjured	$G = 2.56$	0.40	138

the year before they give birth. Seals aged 4–8 years were classed as transitional, because they were starting to enter the reproductive cohort.

To determine the age-class of immature females injured most frequently by adult males, the proportions in the prereproductive (aged 0–3 years) and transitional (aged 4–8 years) classes of immature seals injured by adult males in 1988 and 1989 were compared.

For comparing two proportions, a 2 × 2 *G*-test with the Williams correction was used (Sokal and Rohlf 1981). Because of the small size of the samples tested, the power of the tests comparing injured and uninjured females was calculated. Also calculated was the sample size needed to be 80% certain of detecting a significant difference between two samples (Casagrande *et al.* 1978; Sokal and Rohlf 1981).

Results

Data were available on 55 individually identified adult female seals and 10 untagged and 99 tagged immature female seals. Thirteen adult and 2 untagged immature female seals were identified in all years from 1983 through 1989. Only partial records were available for the remaining 42 adult and 8 untagged immature females. All tagged animals were easily identifiable between years; seals identified only by means of minor scars or marks applied with bleach were not consistently identified between years.

Power of tests

The power of most tests used to examine the differences between injured and uninjured females was low (Table 1). Given the proportions compared, the sample sizes required to detect a significant difference between injured and uninjured females were substantial.

Reproductive rate and pup survivorship

No effect due to severity of injury on the reproductive rate of females injured in the previous year was detected (Table 2). The reproductive rates of females with major injuries ($n = 25$; $G = 0.599$, df = 1, $p = 0.474$) and those with minor injuries ($n = 7$; $G = 0.024$, df = 1, $p = 0.892$) were similar to that of uninjured females ($n = 201$).

Of the six pups that died prior to weaning, two had uninjured mothers, two had mothers with a major injury, and two had mothers with a minor injury. No significant difference was detected in survivorship to weaning of pups of females with major injuries, currently ($n = 7$) and previously ($n = 13$; $G = 0.25$, df = 1, $p = 0.687$). Survival to weaning was similar for pups of females with major injuries ($n = 18/20$) and those with minor injuries ($n = 9/11$; $G = 0.361$, df = 1, $p = 0.585$). When the major and minor injury classes were pooled, pup survival to weaning ($n = 27/31$) was significantly lower than that of pups of uninjured females ($n = 119/121$; $G = 5.53$, df = 1, $p = 0.027$).

Survival through the first year of life did not differ significantly for pups of females with major injuries currently ($n = 7$) and previously ($n = 13$; $G = 1.98$, df = 1, $p = 0.229$, Table 2). Pups of currently injured females had slightly lower survival than pups of uninjured females ($n = 121$; $G = 2.92$, df = 1, $p = 0.091$), though the difference was not statistically significant. Pups of females previously with major injuries had survivorship similar to pups of uninjured females ($G = 0.002$, df = 1, $p = 0.965$). Survivorship of pups of injured females (currently and previously injured classes pooled) did not differ significantly from that of pups of uninjured females ($G = 1.01$, df = 1, $p = 0.401$).

Survival through the first year was similar for pups of currently ($n = 7$) and previously ($n = 4$) injured females with minor injuries ($G = 0.045$, df = 1, $p = 0.874$). No difference was detected between the survivorship of pups of females with minor injuries (currently and previously injured classes pooled) and uninjured females ($G = 2.56$, df = 1, $p = 0.126$).

Parental investment

Females with major injuries did not appear to invest significantly less in their pups than did uninjured females. The parental investment period of previously injured females with major injuries ($n = 6$, $\bar{x} = 38.8 \pm 5.6$ d) was similar to that of uninjured females ($n = 74$, $\bar{x} = 41.1 \pm 3.8$ d; Mann–Whitney normal approximation, $t = 0.918$, $p = 0.179$). Currently injured females with major injuries ($n = 2$) invested the same amount of time in their pups ($\bar{x} = 40 \pm 1.0$ d) as previously injured females (Mann–Whitney *U*-test: $U = 6.5$, $p > 0.5$). When both currently and previously injured classes were combined, females with major injuries ($n = 8$) invested a similar amount of time in their pups ($\bar{x} = 39.13 \pm 4.8$ d) to uninjured females (Mann–Whitney normal approximation: $t = 0.981$, $p = 0.163$).

The parental investment period of currently injured females with minor injuries ($n = 6$, $\bar{x} = 41.8 \pm 4.2$ d) did not differ significantly from that of previously injured females ($n = 2$, $\bar{x} = 41.5 \pm 3.5$ d; Mann–Whitney *U*-test: $U = 11$, $p > 0.05$). Injured females (currently and previously injured classes combined, $n = 8$, $\bar{x} = 41.75 \pm 3.8$ d) and uninjured females had similar investment in their pups (Mann–Whitney normal approximation: $t = 0.723$, $p = 0.235$).

Frequency of injury and mortality of females

Thirty-seven of 55 adult female seals (67%) did not sustain a major injury in 1988 or 1989 (Table 3). The distribution of the number of major injuries per year for adult female seals did not differ significantly from a Poisson distribution ($G = 1.87$, df = 1, $p > 0.1$).

Eight of 55 permanently identified adult female monk seals

TABLE 2. Survivorship through the first year of life of pups of injured and uninjured female Hawaiian monk seals, Laysan Island, northwestern Hawaiian Islands, 1983–1989

	Females with major injuries		Females with minor injuries		Uninjured females
	Current[a]	Previous[b]	Current[a]	Previous[b]	
No. of pups that survived	2 (29)	9 (69)	3 (43)	2 (50)	79 (65)
No. of pups that did not survive	4 (57)	4 (31)	4 (57)	2 (50)	33 (27)
No. of pups with fate unknown	1 (14)	0 (0)	0 (0)	0 (0)	9 (8)
Total no. of pups	7	13	7	4	121
Total no. of females	7	25	7	7	201
% of females with pup	100	52	100	57	60

NOTE: Numbers in parentheses are percentages.
[a]Seals injured before or during parental investment.
[b]Seals injured in the previous year after the end of parental investment, or during a year in which they were not seen with a pup.

TABLE 3. Number of major injuries per year for adult female Hawaiian monk seals at Laysan Island, northwestern Hawaiian Islands, 1988 and 1989

No. of injuries per year	Number of female monk seals 1988	1989	Pooled	Expected frequency
0	25	12	37	34.28
1	5	7	12	16.21
2	1	3	4	4.43
3	2	0	2	
Total	33	22	55	

NOTE: Expected frequencies are generated from a Poisson distribution.

TABLE 4. Numbers of immature female Hawaiian monk seals injured in the transitional (T; aged 4–8 years) and prereproductive (P; aged 0–3 years) classes at Laysan Island, northwestern Hawaiian Islands, 1988 and 1989

	1988		1989		Pooled	
	P	T	P	T	P	T
No. of females injured	4	4	3	12*	7	16*
Total no. of injuries	4	7*	3	15*	7	22*
No. of females not injured	46	23	41	20	87	43
Total no. of females	50	27	44	32	94	59

*Significant difference between transitional and prereproductive classes.

died in 1983–1989. All eight had sustained injuries inflicted by adult male monk seals shortly before their death. Two unidentified adult females died of unknown causes, perhaps age-related, in 1983; however, one had two small punctures on her back and the other carcass was being mounted by an adult male seal. Six unidentified females died in 1983–1989; all had sustained injuries inflicted by adult male monk seals. Of the uninjured females, three (two in 1983, one in 1988) that were easily identified by natural marks were not seen in any subsequent years. Thus, 14 of 16 adult females that died had been injured by adult males shortly before their death.

One untagged immature female and 4 of 26 females aged 3–6 years died after sustaining injuries from adult male seals. Two immature females identified from flipper tags disappeared after sustaining adult male inflicted injuries, and were not seen in subsequent years.

Effect of injuries on recruitment of immature females

In 1988, no significant difference was detected in the proportion of transitional immature female seals aged 4–8 years (n = 4/27) and prereproductive females aged 0–3 years (n = 4/50; $G = 0.78$, df = 1, $p = 0.442$; Table 4) that were injured by males. Although the difference between the two classes was not statistically significant, wounding of transitional females (15% of the class) was almost double that of prereproductive females (8% of the class), which is consistent with the results from 1989, when a greater proportion of transitional than prereproductive immatures was injured (n = 12/32 and 3/44, respectively; $G = 10.86$, df = 1, $p < 0.001$). Moreover, many females in the transitional class, but none in the prereproductive class, were injured more than once (Table 4). The number of injuries per female was significantly greater for the transitional class than for the prereproductive class in both years (1988: $G = 4.16$, df = 1, $p = 0.043$; 1989: $G = 16.56$, df = 1, $p < 0.001$). The proportion of immature females in the transitional class that were injured by adult males in 1988 and 1989 (n = 16/59; Table 4) was similar to that of adult females (n = 18/55; Table 3; $G = 0.42$, df = 1, $p = 0.494$).

Discussion

We cannot conclude that injuries have no effect on reproductive success, though the hypothesis that injuries negatively affect female reproductive success was only weakly supported. Because the sample sizes were small, the power of the tests used to compare injured and uninjured females was low (Table 1), and the probability of committing a type II error was high. The power of a test can be improved by increasing the sample size (Sokal and Rohlf 1981); however, the sample sizes required to find significant differences between injured and uninjured females in our study were in most cases very large (Table 1). The probability of observing injuries with such high frequency in a small population of adult females (55 permanently identified seals) was very low. Despite the low power of the tests, pup survival showed some negative effects due to injury. Pups of females with major injuries appeared to survive less well than those of uninjured females. Pups of injured females (all classes pooled) had significantly lower survivorship to weaning than pups of uninjured females, and pups of currently injured females with major wounds had slightly lower survival through the first year than pups of uninjured females (Table 2). Thus, despite small sample sizes, there is some evidence that injuries affect female reproductive success.

The timing of an injury to a female could influence the amount of energy she has during lactation, which in turn could affect the pup's survival through its first year. Lactation is energetically costly for females (Young 1976). Because female phocids generally do not feed during lactation, they use a significant proportion of their energy reserves to feed their pups. For example, female grey seals use 85% of their stored energy resources while nursing their offspring (Fedak and Anderson 1982), northern elephant seals use 58% (Costa *et al.* 1986), and hooded seals (*Cystophora cristata*) use 33% (Bowen *et al.* 1987). A female in poor condition because of a recent injury may have a lower than normal supply of stored fat available for lactation, resulting in reduced pup survival.

Although the survival of pups of currently injured females was not significantly different than for pups of uninjured females (Table 2), there is some evidence that currently injured females use energy, otherwise allocated for lactation, to recover from injuries. Two female monk seals that sustained severe injuries inflicted by sharks shortly prior to pupping at French Frigate Shoals (latitude 23°45′N, longitude 166°10′W) in the northwestern Hawaiian Islands could not nurse their pups and eventually abandoned them (M. P. Craig, Honolulu Laboratory, personal communication). One female injured by adult male seals at Kure Atoll (latitude 28°25′N, longitude 178°10′W) also abandoned her pup within days of its birth (J. R. Henderson, Honolulu Laboratory, personal communication).

Poor condition of females before parturition may reduce the survival of their offspring. Female northern elephant seals arriving for the breeding season with fresh shark wounds were less successful at pupping and breeding than uninjured females (Ainley *et al.* 1981; Le Boeuf *et al.* 1982). The pups of injured female elephant seals were stillborn or abandoned soon after birth, or wounded mothers allowed other females to nurse their pups. The injuries sustained by elephant seals affected their ability to successfully wean their pups. Ainley *et al.* (1981) found that females that had raised pups successfully to weaning age in the years prior to their injury were less successful in raising their pup during the year in which they were injured. Thus, wounds that result in the condition of females being poorer than normal apparently cause reduced survival of offspring to weaning.

After weaning, a pup fasts for a number of weeks and may therefore need a minimum amount of energy from the nursing period to survive. The postweaning period is critical because the pup is relatively defenseless and inexperienced, and must live on stored energy until it learns to feed on its own (Reiter *et al.* 1978). Hawaiian monk seal pups lose approximately 15–30% of their weaning weight in the postweaning fast (Kenyon and Rice 1959), and most of the energy used during this period appears to be from blubber accumulated during nursing. About 94% of the energy required by grey seal pups during the first month of their postweaning fast comes from blubber stored during the nursing period (Nordoy and Blix 1985; Worthy and Lavigne 1987). Similarly, harp seal pups obtain 80–90% of their energy from blubber acquired in the nursing period (Worthy and Lavigne 1983, 1987). Because of the high energetic cost of the postweaning fast, a pup weaned at a lighter than normal weight would probably be less likely to survive its first year. Consequently, the first-year survival of pups of currently injured females may be detrimentally affected by their mothers' wounds (Table 2).

In contrast to currently injured females, females injured in the year prior to parturition appear to have recovered sufficiently to store normal energy reserves. Reproductive rate, mean parental investment period, and pup survivorship of previously injured females were not significantly different from those of uninjured seals. Most pregnant grey seals do not start increasing in weight until the time of implantation of the blastocyst (approximately 3–4 months after copulation; Boyd 1984). Johnson and Johnson (1978) found that many Hawaiian monk seal females had regained most of the weight lost during lactation after 42–66 days, before undergoing an extended (20–30 d) stay on shore to moult. Monk seals appear to fast or to eat very little during the moult (Kenyon and Rice 1959). If female Hawaiian monk seals do not begin storing energy for lactation until after they moult, a previously injured female would have several months to recover from her wound before starting to deposit fat reserves for lactation, and her pup would be more likely to receive the full nutritional benefit of lactation than the pup of a currently injured mother.

A wounded female monk seal's reproductive success appears to be influenced by the severity of her injuries. Minor injuries had no detectable effect on the reproductive success of female monk seals. Reproductive rate, mean parental investment period, and survivorship of the pups of currently and previously injured females with minor wounds were the same as for uninjured females. Major injuries negatively affected the reproductive success of currently injured females with respect to pup survivorship (Table 2). Le Boeuf *et al.* (1982) monitored 11 female northern elephant seals with "moderate to severe" fresh wounds and suggested that the injured females successful in raising their pups appeared to have the least severe injuries.

Most of the female seals that died at Laysan Island sustained injuries inflicted by adult males before they died. Some of the females that died did not appear to have injuries that were serious enough to be fatal (Hiruki *et al.* 1993). In these cases, it may have been the continued harassment of the males during a mobbing incident, where several males attempt to mate with a female, that resulted in wounding sufficient to cause death. Some female seals are reinjured often enough in the same year by adult males (Table 3) that the cumulative effect may result in the death of the female. Similarly, female northern elephant seals sometimes die after being harassed by groups of subordinate males (Le Boeuf and Mesnick 1990). A female elephant seal departing from the harem may be chased by several subordinate males, all of which attempt to mount her. During this time, she receives over 20 times more blows, mounts, and copulations than normal, and if she dies, males sometimes compete over her carcass (Le Boeuf and Mesnick 1990). Female mink (*Mustela vison*) have also been known to die after being pursued by, and mating with, several males (Hatler 1972). The female sustains neck injuries during mating, but generally these are not severe enough to be fatal (Hatler 1972). Hatler (1972) has suggested that because the males pursue her frequently, she probably cannot hunt and replenish her energy reserves and dies as a result of the continued harassment.

Immature female Hawaiian monk seals were injured more often by adult males as they entered the reproductive population than when they were prereproductive (Table 4). The proportion of immature females aged 4–8 years with injuries was similar to that of adult females. Immature females sometimes die from these injuries: 4 of 26 females aged 3–6 years in 1988 and 1989 sustained fatal injuries. Mortality of young females is a serious concern with respect to population growth, as their potential productivity is never realized, thus reducing future recruitment into the population.

In summary, the major consequence of injuries for female reproductive success is the increase in female mortality, which shortens their reproductive life. The timing and severity of injuries can affect the survivorship of pups of injured females if the females do not have sufficient time to recover before parturition and lactation. However, if the females have sufficient time between sustaining injuries and parturition, there appears to be no major effect on the survival of pups to weaning and through the first year of life.

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