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"Mobbing" in Hawaiian Monk Seals (*Monachus schauinslani*): The Value of Simulation Modeling in the Absence of Apparently Crucial Data

ANTHONY M. STARFIELD,* JAMES D. ROTH,* AND KATHERINE RALLS†

*Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, U.S.A.
†National Zoological Park, Smithsonian Institution, Washington, DC 20008, U.S.A.

Abstract: *Several small populations of Hawaiian monk seals* (Monachus schauinslani) *exhibit male-biased adult sex ratios and "mobbing," an aggressive behavior in which adult males injure and often kill adult females and immature seals of both sexes during mating attempts. Mobbing appears to be limiting the growth of some populations of this endangered species. The frequency of mobbing deaths appears to increase as a population's sex ratio becomes increasingly male-biased, although the exact relationship between these two variables (the mobbing response) is unknown. We developed a stochastic demographic model of a small Hawaiian monk seal population using several different assumptions about the mobbing response. We used the model to explore the origins of male-biased sex ratios in monk seal populations and to determine whether it was possible, given the lack of data on the mobbing response, to evaluate the probable effects of alternative management strategies to address the mobbing problem. Small populations (100 to 200 seals) and those with slower growth rates were more likely to develop male-biased adult sex ratios. Almost all of our modeling scenarios supported the immediate removal of males from populations where mobbing occurs. Our conclusions were relatively unaffected when the assumptions regarding the mobbing response were varied. Thus, a model was helpful even when apparently crucial data were unavailable.*

"Mobbing" en las focas Hawaianas: el valor de la modelación de simulación en la ausencia de datos aparentemente cruciales

Resumen: *Varias poblaciones pequeñas de focas hawaianas* (Monachus schauinslani) *exhiben proporciones de sexos sesgadas hacia los machos y un comportamiento sexual agresivo "mobbing" en el cual machos adultos hieren y muchas veces matan hembras adultas y focas inmaduras de ambos sexos durante intentos de apareamiento. Este comportamiento parece estar limitando el crecimiento de algunas poblaciones de esta especie en peligro de extinción. La frecuencia de las muertes por comportamiento sexual agresivo parece aumentar a medida que las proporciones de sexos se hacen más y más sesgadas hacia los machos. Sin embargo, la relación exacta entre estas dos variables (la respuesta al comportamiento sexual agresivo) es desconocida. Desarrollamos un modelo demográfico estocástico de una pequeña población de focas hawaianas usando varios supuestos distintos acerca de la respuesta al comportamiento sexual agresivo. Usamos el modelo para explorar los orígenes de las proporciones de sexos sesgados hacia los machos en poblaciones de focas y para determinar si, ante la falta de datos sobre la respuesta al comportamiento sexual agresivo, era posible evaluar los posibles efectos de estrategias de manejo alternativas para enfrentar el problema originado por este comportamiento. Poblaciones pequeñas (100 a 200 focas) y aquellas con tasas de crecimiento más lentas fueron más proclives a desarrollar proporciones de sexos adultos sesgados hacia los machos. Casi todos los escenarios que consideramos con nuestro modelo apoyaron la remoción inmediata de machos de aquellas poblaciones donde ocurre comportamiento sexual agresivo. Nuestras conclusiones fueron relativamente poco sensibles a cambios en los supuestos acerca de la respuesta de comportamiento sexual agresivo. Por consiguiente, el modelo fue útil aún cuando datos aparentemente cruciales no se encontraban disponibles.*

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Introduction

The endangered Hawaiian monk seal, *Monachus schauinslani,* occurs in the Northwestern Hawaiian islands, with major breeding populations at French Frigate Shoals, Laysan Island, Lisianski Island, Pearl and Hermes Reef, and Kure Atoll. At Laysan and Lisianski, "mobbing" appears to be limiting population growth (Hiruki et al. 1993*a*; 1993*b*; Johanos et al. 1994). Mobbing is an aggressive behavior in which groups of adult males injure and often kill adult females and immature seals of both sexes during mating attempts (Johanos et al. 1994).

Males sometimes injure or kill females during mating attempts in a variety of other mammalian species (reviewed in Le Boeuf & Mesnick 1990), and a male-biased adult sex ratio is thought to increase the probability of these behaviors (Le Boeuf & Mesnick 1990). Male-biased adult sex ratios exist or existed recently in three of the five major breeding populations of Hawaiian monk seals, although male and female pups are born in approximately equal numbers (National Marine Fisheries Service, unpublished data). The reasons for the frequent occurrence of male-biased sex ratios in this species are unknown, but small population size may be a contributing factor. Mobbing is relatively common in monk seal populations, such as those at Laysan and Lisianski with male-biased adult sex ratios, but it is unknown or rare in those where sex ratios are approximately equal (Hiruki et al. 1993*a*). The current sex ratio at Laysan is about 1.3 males per female, and 14 of the 16 adult females found dead there in 1983–1989 were fatally injured by adult male seals (Hiruki et al. 1993*b*).

Intervention to equalize the sex ratio at Laysan and/or Lisianski in the hope of reducing mobbing mortality has been discussed by various concerned groups and advisory bodies for several years. But uncertainties regarding the exact relationship between a given male-biased adult sex ratio and the number of mobbing deaths (the mobbing response), and thus the probable results of various management interventions, have made it difficult to reach agreement on a management plan.

Simulation modeling may help resolve such management problems (Starfield & Bleloch 1991). Several general stochastic demographic models exist (Burgman et al. 1993), as well as a stochastic model of Mediterranean monk seals, *M. monachus* (Durant & Harwood, 1992). However, this situation requires a model specifically designed to fit the problem of mobbing in Hawaiian monk seals. We therefore developed a stochastic demographic model of a small monk seal population using several different assumptions about the mobbing response. We used this model to identify factors likely to facilitate the development of male-biased adult sex ratios in monk seal populations and to determine whether uncertainty about the mobbing response prevents an evaluation of the probable success of alternative management strategies for addressing the mobbing problem.

Methods

The adult sex ratios and demographic parameters of monk seals vary among islands, and the population at each island is considered a separate unit for research and management purposes (Ragen 1993; Gilmartin et al. 1995). We therefore developed a model that would approximate the population at Laysan, a site where mobbing is a problem. The model is based on data collected during the past 10 years, mostly at Laysan, by personnel of the National Marine Fisheries Service (NMFS).

Demographic Parameters

The mean annual birth rate at Laysan is 0.558 pups per adult female (Johanos et al. 1994), with a mean sex ratio at birth of 1:1. Females first give birth at approximately 6 to 7 years (Johanos et al. 1994). We assumed that 25% of females of age 6, 75% of females of age 7, and 100% of females of age 8 and older could potentially give birth. We assumed all males become sexually mature at age 7.

The annual survival rates for pups at Laysan are 0.82 for males and 0.87 for females (Gilmartin et al. 1993). Annual survival rates of older individuals have not been reported. We used 0.91 for juveniles (1–2 years) and subadults (females 3–5 years and males 3–6 years) and 0.95 for all adults. These values do not include mortality from mobbing and were chosen to give a population growth rate of 1.06, a value considered appropriate for a healthy phocid population (Eberhardt & Siniff 1977) and consistent with the observed growth rate of the Hawaiian monk seal population at Pearl and Hermes Reef, where mobbing has not been observed (NMFS, unpublished data). We truncated the population so that no individual survived beyond age 30.

Description of the Model

We developed two versions of the model: a stochastic model without mobbing mortality and a stochastic model with mobbing mortality. Both versions operate on a time interval of one year and simulate the structure of the population immediately after pups are born. Both males and females are divided into 31 age classes, from age class 0 for newborn pups to age class 30. The annual sequence of events is births (the model calculates the number of newborn male and female pups), mobbing deaths (if applicable), management intervention (if applicable), and natural survival (each year those seals that survive are promoted from one age class to the next). Because the populations are currently well below historical levels and we are projecting only 20 to 25 years

into the future, it is not necessary to model density-dependent feedbacks.

The purpose of the without-mobbing model was to investigate whether demographic and environmental stochasticity alone (without deaths due to mobbing) might lead to male-biased sex ratios in small monk seal populations. Demographic stochasticity was modeled by interpreting birth and survival rates as probabilities (Burgman et al. 1993). Newborn pups are similarly assigned sexes through generation of a random number from a uniform distribution (in the interval 0 to 1) for each individual: if the random number is less than 0.5, the pup is male; otherwise it is female. Historical records indicate that monk seal birth rates are drastically reduced in some years, probably due to environmental variation (Wirtz 1968; Johanos et al. 1994). We incorporated this environmental stochasticity into the model as a 0.17 probability that the birth rate would be halved in any year (on average once in 6 years).

The purpose of the with-mobbing model was to investigate, given various assumptions about the nature of the mobbing response, the likely effects of various management interventions in a population exhibiting an initial male-biased sex ratio and deaths due to mobbing. The mobbing component of the model was based on the hypothesis that mobbing-related mortality increases in some way as the adult sex ratio (number of adult males/number of adult females) becomes increasingly male-biased.

We modeled the mobbing response in several different ways. In the simplest case, we assumed that mobbing deaths are a linear function of the adult sex ratio (linear model). For each of the seals most susceptible to mobbing (defined below), the probability of death due to mobbing is 0 when the adult sex ratio is less than or equal to one and increases linearly with the sex ratio to a maximum of 0.30. The maximum probability of 0.30 was based on the observation that the greatest extent of known mobbing deaths and injuries in adult females observed at Laysan in a single year is 12.1% killed and 24.2% injured (NMFS, unpublished data). Sensitivity analyses indicated that varying the maximum probability of mobbing mortality between 0.20 and 0.50 had little effect on the model's output (population growth rate, number of seals killed by mobbing, and so forth), perhaps because the sex ratio rarely increased to the point where this maximum was applied. We also varied the slope of the line, which did have an effect on the model output.

We also modeled a "fuzzy" relationship between mobbing deaths and the adult sex ratio to simulate a trend of increased mobbing with higher sex ratios accompanied by a large variance in the incidence of mobbing (fuzzy model). ("Fuzzy" indicates an imprecise relationship between variables [Zadeh 1965; Mendoza & Sprouse 1989]). For sex ratios less than 1.0, there is no mobbing. For any sex ratio between 1 and 2, the probability of mobbing for the most susceptible seals is generated by a random number drawn from a uniform distribution between 0 and 0.15. For sex ratios between 2 and 3, the probability of mobbing is a random number between 0.075 and 0.375. For any sex ratio greater than 3, the mobbing probability is a random number between 0.10 and 0.40. On average this version of the model is roughly but not exactly equivalent to the linear model with a slope of 0.15 and a maximum of 0.25.

The risk of being mobbed varies across age and sex classes of seals. Mobbed seals are often adult females, but immature seals of both sexes are also mobbed (Hiruki et al. 1993*a*). Subadults are mobbed as often as adult females but significantly more often than juveniles (Hiruki et al. 1993*b*). Older adult females (over 12 years), which may have learned to avoid situations likely to lead to mobbing, seem to be mobbed less frequently than younger adult females (NMFS, unpublished data).

Based on these data, we modeled deaths due to mobbing as follows: if x is the probability of mobbing mortality determined by either the linear or the fuzzy model, then mortality for females 3–12 years is x; mortality for females over 12 or between 1 and 2 years is $x/2$; and female pup mortality is $x/4$. Adult males suffer no mortality from mobbing. Male pups and subadults experience the same probability of mobbing mortality as a female of the same age. Mobbing mortality was applied stochastically using the same approach as for birth and survival rates.

In age-structured modeling it is important to differentiate between short-term and long-term scenarios, relative to the life span of the organism. In short-term scenarios the initial age structure of the population strongly influences the population's growth patterns. The initial age structure is irrelevant, however, for investigating long-term scenarios. Both versions of our model address short-term problems, so an appropriate initial age structure is essential. (However, when we used a deterministic, age-structured model to calculate the long-term growth rate resulting from various combinations of demographic parameters, it was appropriate to start with an arbitrary age structure.)

To investigate how a "normal" population might develop a male-biased adult sex ratio required an estimate of the age and sex structure of a healthy monk seal population. We therefore incorporated the age structure that emerged from a long-term deterministic model (whose the adult sex ratio was 0.80) into the "no mobbing" version of the stochastic model. We varied the size of the initial population and considered three scenarios: a healthy population with a growth rate of 1.06, reduced pup survival leading to a growth rate of 1.03, and a combination of reduced pup and adult survival leading to a stable population (growth rate = 1.00).

In the with-mobbing version of the model, we were

concerned with populations that had already developed a male-biased sex ratio and a mobbing problem. We therefore started simulations with the actual age and sex structure on Laysan in 1991 (Becker et al., 1995) and projected the population forward for 20 years. We replicated each experiment 1000 times.

In view of the uncertainty in demographic parameters and the mobbing response, we investigated each management strategy in eight different ways. We assumed two population growth rates (1.06 and 1.03), each with four assumptions regarding the mobbing response: three different slopes (0.1, 0.15, and 0.2) for the linear mobbing response model and the fuzzy model.

Based on extensive discussions with personnel of the NMFS monk seal program, we simulated eight alternative management strategies:

(1) Take no action, providing the base-line prediction of what is likely to happen to the population if there is no human intervention over the next 20 years.
(2) Remove 10 males each year in which the adult sex ratio is greater than 1.2. The males in this and subsequent simulations are removed at random from the 6- to 12-year age classes.
(3) Remove 10 males each year in which there are more than three mobbing deaths.
(4) Remove 10 males each year in which there are more than six mobbing deaths.
(5) Remove 10 males if no management action was taken in the previous year and there were more than three mobbing deaths in both the current year and the previous year.
(6) Remove five males each year in which there are more than three mobbing deaths.
(7) Add 10 one-year-old females each year in which the adult sex ratio is greater than 1.2. We assumed that these relocated females would have a 0.1 reduction in survival during their first year on the island.
(8) Take no action for the first six years and then remove 10 males each year in which there are more than six mobbing deaths.

These alternatives explore the range of possible management strategies suggested by biologists familiar with the mobbing problem. We also examined the effects of introducing a delayed population response to management intervention. The model normally assumes that the population responds immediately to management intervention. Removing males, for example, reduces the adult sex ratio, which in turn produces a smaller probability of mobbing the following year. Mobbing could be a learned behavior, however, that will persist for some time after the sex ratio is reduced (W. G. Gilmartin, personal communication). We modeled this possibility using a linear mobbing response with a slope of 0.15 and a five-year "mobbing memory." That is, we based the mobbing deaths for each year on the highest adult sex ratio attained by the population during the previous five years.

Results and Discussion

To check the demographic and environmental stochasticity incorporated in the model, we ran the without-mobbing version of the model for 1000 simulations. The annual variation in pup birth and survival rates produced by these simulations (Table 1) was similar to that at Laysan (Gilmartin et al. 1993; Johanos et al. 1994). Adding mobbing to the model had no effect on birth rates but slightly decreased pup survival; the exact effect depended upon the assumption made about the mobbing response. Thus, the with-mobbing version of the model may slightly underestimate pup survival. Any underestimates would have no affect on our conclusions regarding management alternatives, however, as these proved insensitive to even very large changes in survival rates (see sensitivity analyses).

We then used the with-mobbing version to compute the number of adult females killed by mobbing. Because mobbing mortality was applied stochastically, even the linear mobbing response produced considerable variation in the number of adult females killed at a given sex ratio (Fig. 1*a*). Mobbing seemed to increase as the sex ratio increased from 1 to 1.7. Over the same range of sex ratios, the fuzzy mobbing response (Fig. 1*b*) produced even greater variation in adult female mortality for a given sex ratio but no tendency for mobbing to increase with increasing sex ratios. The large variation in mobbing mortality at a given sex ratio is consistent with observations at Laysan (NMFS, unpublished data).

As one might expect, smaller populations showed greater variation in both the final and the maximum sex ratios attained during a 25-year period (Fig. 2). Thus, stochasticity is more likely to produce a male-biased sex ratio in small populations. Male-biased sex ratios were also more likely to arise in populations with slower growth rates (Fig. 3).

Table 1. Mean and 95% confidence limits of annual pup survival and birth rates from 1000 runs of the without-mobbing model compared to those reported for Laysan Island (Gilmartin et al. 1994; Johanos et al. 1994).

	*Mean and 95% Confidence Limits**	
	Model	*Laysan Island*
Pup Survival Rate		
Males	0.82 (0.71–0.93)	0.82 (0.73–0.86)
Females	0.87 (0.78–0.96)	0.87 (0.81–0.91)
Birth Rate	0.56 (0.32–0.80)	0.56 (0.31–0.81)

* *Confidence limits in parentheses.*

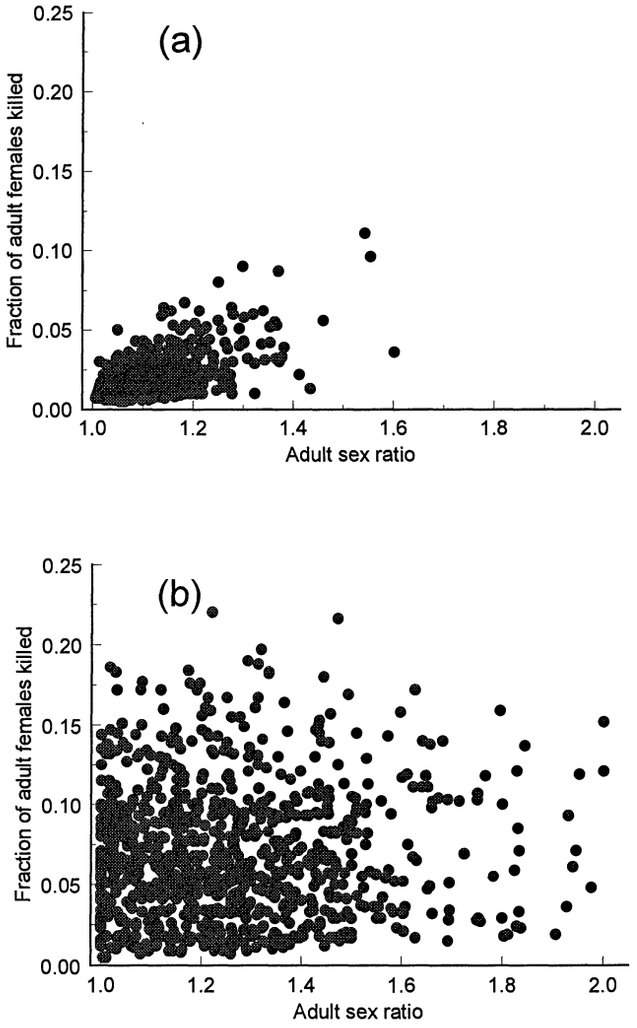

Figure 1. Simulated observations of adult female deaths due to mobbing using the linear version of the with-mobbing model with a slope of 0.15 (a) *and using the fuzzy version of this model* (b).

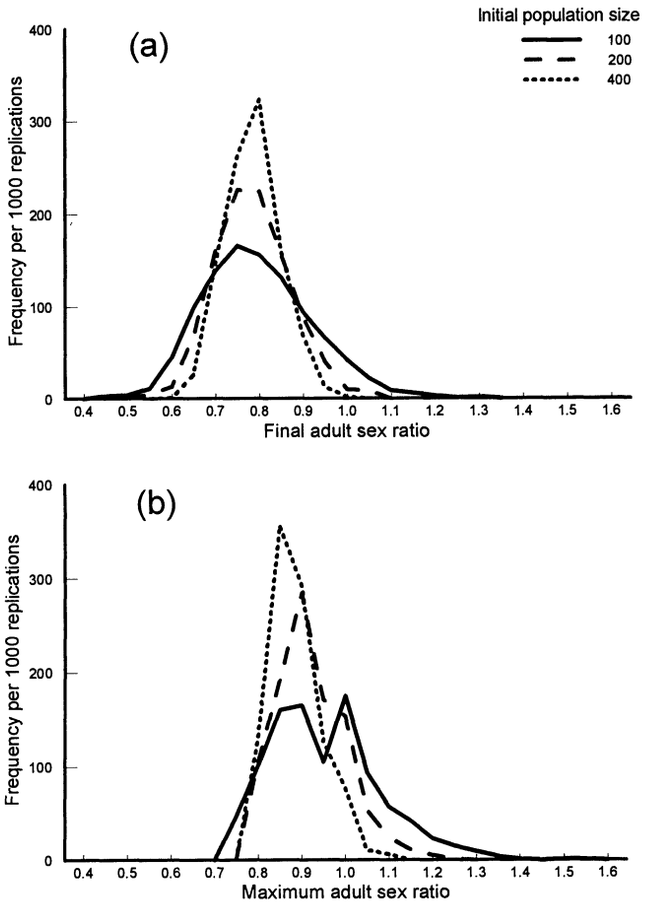

Figure 2. Effect of initial population size on final adult sex ratio after 25 years (a), *and maximum adult sex ratio reached during the same 25-year period* (b), *in both cases without mobbing deaths.*

One of the difficulties of presenting and interpreting results from a stochastic model is the huge amount of information that can be generated by the model. Figure 4 shows some sample distributions of outcomes under four of the management strategies. These distributions are often skewed and sometimes bimodal, and they change shape under different management scenarios. Summarizing the data using means and variances could therefore be misleading. We found it useful to present probabilities of specific, selected outcomes to compare the performance of the different management strategies, as in Table 2.

Any acceptable management strategy should have a low probability of undesirable outcomes; in addition, a good strategy should have a high probability of desirable outcomes. Table 2 shows the probabilities of desirable and undesirable outcomes for eight management strategies under three assumptions about mobbing response.

Given that we do not know the actual mobbing response, how does Table 2 suggest we should respond to the mobbing problem? Inaction (Strategy 1) has a high probability of undesirable outcomes and a low probability of desirable outcomes, unless we assume a very weak mobbing response (slope = 0.10). Because we do not know whether the mobbing response is weak or strong, this could be an argument for delaying a decision—the problem might correct itself. In fact, the results from the delay scenario (Strategy 8) suggest that waiting six years before deciding whether or not to intervene is always better than no action for all outcomes. However, the male removal strategies (2 through 6) look even better. Introducing yearling females (Strategy 7) is not highly effective.

Thus, these results support a management strategy of immediately removing males. It might not be necessary to intervene, but it is an effective insurance policy because it is likely to significantly reduce the number of mobbing fatalities, and, depending on the true nature of the mobbing response, it could improve the situation in other ways. The cost of our ignorance is that we may

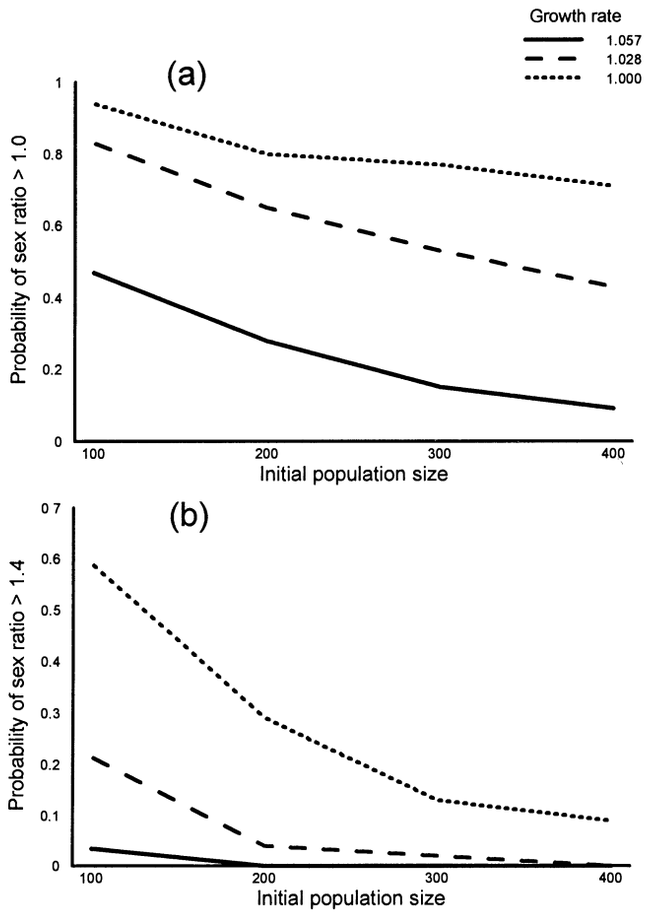

Figure 3. Effects of the initial population size and average population growth rate on the probability that the adult sex ratio will, at some time during 25 years, exceed 1.0 (a) and 1.4 (b) in a population without mobbing.

intervene when, with perfect knowledge, it would have been apparent that the intervention was unnecessary.

We have already shown that our conclusions regarding management strategies are relatively insensitive to varying assumptions regarding the mobbing response. Our demographic parameter values are another source of uncertainty. It is unlikely that the average growth rate in the absence of mobbing will be greater than 1.06. A reduction in the average growth rate to 1.03 represents a significant change in parameter estimates. A replicate set of experiments at this lower growth rate strengthened the case for immediate management intervention and the removal of males.

A third source of uncertainty is whether or not the population will respond immediately to management intervention, as the model assumes. A suite of experiments with a delayed response (using the device of mobbing memory) produced results that were different in detail from the previous results (for example, there was higher mobbing mortality and a need for more frequent intervention), but the arguments developed from the previous results were still valid and the conclusions unchanged.

The assumptions and parameters used in a modeling exercise can always be questioned. We have illustrated, however, how the model can be used to address such questions as they arise, and how it can be used to evaluate additional management strategies and to recalculate probabilities as new data become available.

Conclusions

We began this modeling exercise to identify factors likely to facilitate the development of male-biased adult sex ratios in monk seal populations and to determine the extent to which uncertainty about the mobbing response precludes an evaluation of the probable success of alternative management options.

We conclude that a male-biased sex ratio, and hence a mobbing problem, is far more likely to occur in a small population (100–200 individuals) rather than a large (400) population of monk seals. Many Hawaiian monk seal populations are small: population estimates for Laysan and Lisianksi from 1983 to 1988 were generally between 200 and 400, and estimates for many of the other populations were less than 100 (Gilmartin et al. 1995). Unbalanced sex ratios are also more likely to occur in slower-growing populations than in faster-growing populations. Thus, unbalanced sex ratios are likely to remain a problem until we achieve demographically healthy—large or rapidly increasing—monk seal populations.

The results of the with-mobbing version of the model demonstrate how, despite the lack of data on the mobbing response, we could make strong inferences about the probable effectiveness of various management strategies. They also suggest that it would likely be very difficult and time-consuming (see Fig. 1) to measure the mobbing response in the field. For endangered populations, the risk of inaction while waiting for better data may often be greater than the risk of management action based on imperfect information (Maguire 1991; Taylor & Gerrodette 1993). The monk seal case—along with many others (Starfield & Bleloch 1991)—illustrates that modeling often can provide considerable help in these situations.

Acknowledgments

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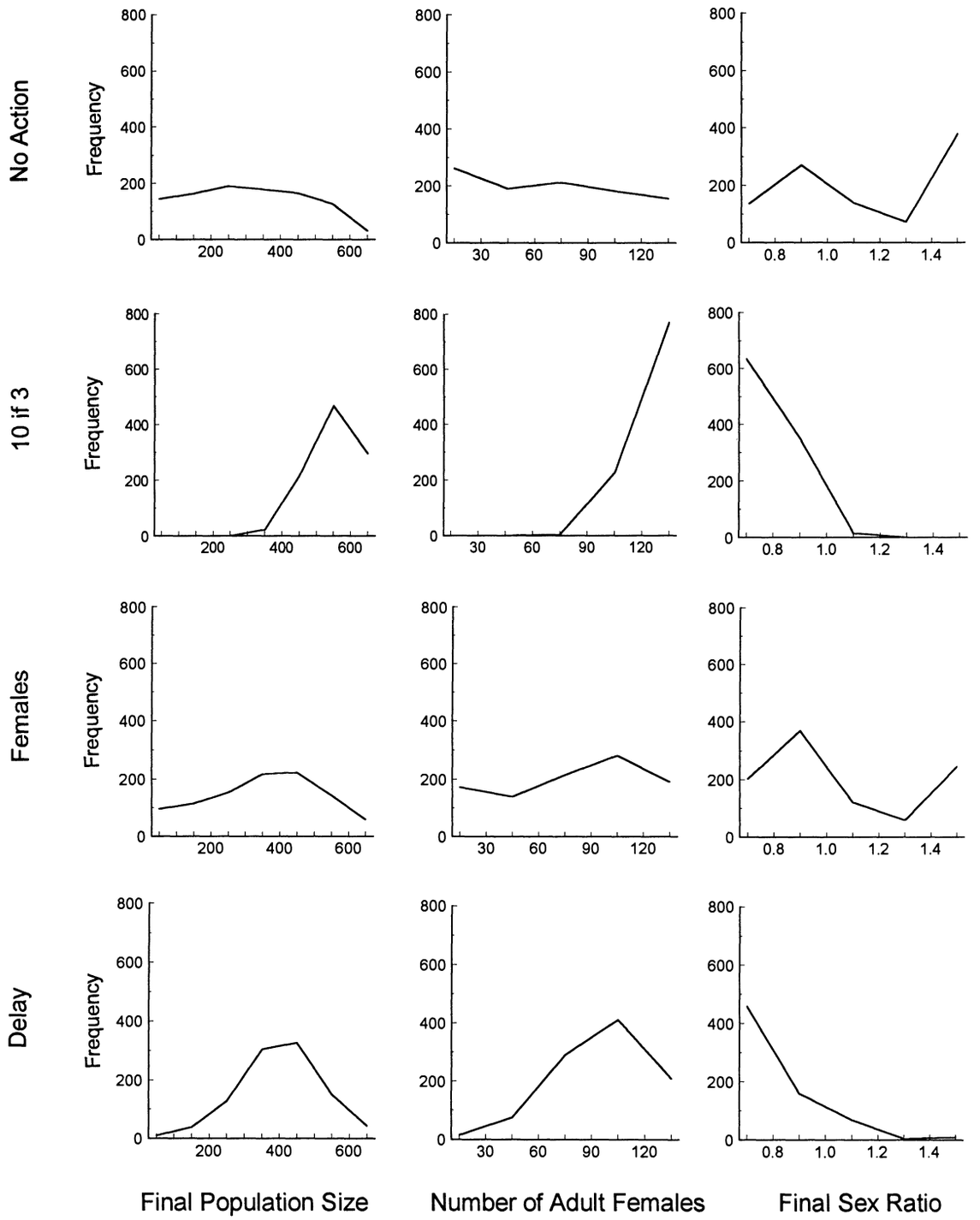

Figure 4. Distributions of final population size, number of adult females, and sex ratios generated by 1000 replicates of the with-mobbing version of the model under various management stratagies. (10 if 3 = remove 10 males each year in which mobbing deaths total more than 3; females = add 10 one-year-old females each year in which adult sex ratio is greater than 1.2; delay = no action for 6 years then remove 10 males each year in which mobbing deaths total more than 6).

Table 2. Probabilities of desirable and undesirable outcomes in Hawaiian monk seals for eight management strategies under three assumptions about the mobbing response.[a]

	Linear Model (slope = 0.20)[b] Management Strategy								*Linear Model (slope = 0.10)[b] Management Strategy*			
Outcomes	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*1*	*2*	*3*	*4*
	No Action	*Remove Males*					*Add Females*	*Delay*	*No Action*	*Remove Males*		
Undesirable												
Total population <100	0.61	0.00	0.00	0.00	0.00	0.00	0.55	0.19	0.00	0.00	0.00	0.00
Sex ratio > =1.4	0.76	0.00	0.00	0.00	0.00	0.00	0.70	0.16	0.05	0.00	0.00	0.00
Mobbing Deaths > = 100	0.90	0.00	0.00	0.01	0.03	0.01	0.89	0.66	0.14	0.00	0.00	0.00
Intervene >3 times	——	0.06	0.19	0.15	0.20	0.87	0.99	0.40	——	0.01	0.02	0.01
Desirable												
Total population > = 400	0.10	0.95	0.95	0.84	0.78	0.83	0.12	0.21	0.77	0.99	0.99	0.92
Sex ratio <1.0	0.18	0.97	0.99	0.97	0.99	0.97	0.21	0.78	0.76	0.96	0.98	0.92
Mobbing Deaths <40	0.01	0.88	0.96	0.55	0.44	0.54	0.01	0.01	0.34	0.99	0.99	0.67
Intervene <2 times	——	0.10	0.02	0.11	0.02	0.00	0.00	0.17	——	0.29	0.27	0.76

	Linear Model (slope = 0.10)[b] Management Strategy				*Fuzzy Model[c] Management Strategy*							
Outcomes	*5*	*6*	*7*	*8*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
	Remove Males		*Add Females*	*Delay*	*No Action*	*Remove Males*					*Add Females*	*Delay*
Undesirable												
Total population <100	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.08	0.03
Sex ratio > = 1,4	0.00	0.00	0.02	0.00	0.49	0.00	0.00	0.00	0.00	0.00	0.36	0.02
Mobbing Deaths > = 100	0.00	0.00	0.09	0.01	0.98	0.42	0.01	0.05	0.25	0.31	0.96	0.58
Intervene >3 times	0.03	0.31	0.95	0.00	——	0.46	0.70	0.61	0.58	0.98	1.00	0.60
Desirable												
Total population > = 400	0.96	0.97	0.87	0.83	0.03	0.40	0.75	0.64	0.44	0.40	0.05	0.21
Sex ratio <1.0	0.98	0.97	0.84	0.89	0.11	0.91	0.99	0.99	0.99	0.98	0.16	0.96
Mobbing Deaths <40	0.83	0.91	0.37	0.38	0.00	0.08	0.38	0.17	0.08	0.05	0.00	0.01
Intervene <2 times	0.31	0.13	0.00	0.84	——	0.01	0.00	0.01	0.00	0.00	0.00	0.05

[a] *The population would grow at an average rate of 1.06 in the absence of mobbing.*
[b] *Linear model assumes that mobbing deaths are a linear function of the adult sex ratio.*
[c] *Fuzzy model simulates a trend of increased mobbing, with higher sex ratios accompanied by a large variance in the incidence of mobbing.*

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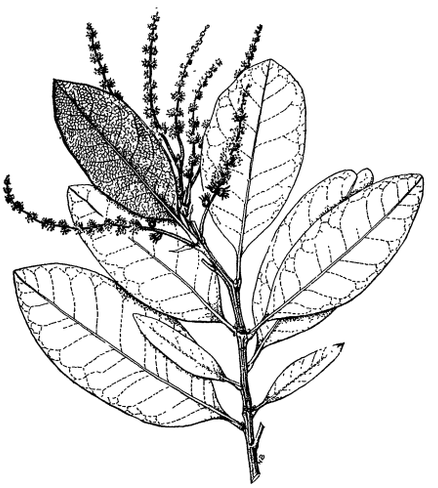
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