MARINE MAMMAL SCIENCE, 23(3): 615–628 (July 2007)

DOI: 10.1111/j.1748-7692.2007.00121.x

PUPPING HABITAT USE IN THE MEDITERRANEAN MONK SEAL: A LONG-TERM STUDY

PANAGIOTIS DENDRINOS
ALEXANDROS A. KARAMANLIDIS
SPYROS KOTOMATAS
MOm/Hellenic Society for the Study and Protection of the Monk Seal,
18 Solomou Street, 106 82 Athens, Greece
E-mail: p.dendrinos@mom.gr

ANASTASIOS LEGAKIS
School of Sciences, Faculty of Biology,
National and Kapodistrian University of Athens, Panepistimioupolis,
Zografou 157 84 Athens, Greece

ELENI TOUNTA
MOm/Hellenic Society for the Study and Protection of the Monk Seal,
18 Solomou Street, 106 82 Athens, Greece

JASON MATTHIOPOULOS
NERC Sea Mammal Research Unit, Gatty Marine Lab,
University of St. Andrews,
St. Andrews, Fife KY16 8LB, Scotland
and Centre for Research into Ecological and Environmental Modelling,
The Observatory, University of St. Andrews,
St. Andrews, Fife KY16 9LZ, Scotland

ABSTRACT

The Mediterranean monk seal gives birth almost exclusively in coastal caves. Given its critical conservation status, the identification and protection of such sites is important for the survival of the species. From 1990 to 2004 we collected data on physical and environmental variables and monitored pupping events in thirty-four coastal caves in Greece. We modeled the probability of cave occupancy as a function of the properties of each cave. Model selection and model averaging enabled us to rank the variables that influenced use of potential pupping sites. Environmental variables related to cave seclusion, substrate, and degree of protection from wind and wave action were the most important among them. The relative importance and directions of these relationships confirm the long-standing assumption that Mediterranean monk seals require sheltered pupping sites, far from sources of human disturbance and thus are progressively limited to isolated parts of the country's coastline. We used cross-validation to examine the predictive ability of our analysis and quantified the sensitivity of our predictions to the degree of extrapolation. We conclude that, although more data are required, the model is capable of predicting occupancy for caves close to the middle of the environmental space examined in this study.

Key words: cave use, conservation, endangered species, generalized linear models, Greece, management, model averaging, *Monachus monachus*, Mediterranean monk seal, reproductive behavior.

With an estimated total population of fewer than 600 individuals (Johnson *et al*. 2006), the Mediterranean monk seal (*Monachus monachus*) is one of the world's most endangered marine mammals. Over the centuries, human disturbance and persecution have led to a marked reduction of the species original geographical range, while now increased habitat loss, and fragmentation and deterioration of suitable habitat threaten its survival and have prompted the World Conservation Union (IUCN) to describe it as "critically endangered" (Baillie *et al*. 2004). A recent historical review (Johnson and Lavigne 1999) has documented the various phases in this expulsion, from the initial occupation of open beaches, shoreline rocks, and spacious arching caves to the subsequent displacement, almost exclusively, to secluded coastal caves.

Female monk seals tend to be more selective in their choice of caves used for pupping than for resting (Karamanlidis *et al.* 2004*a*). Previously, observational work has indicated that this behavioral trait limits their choice to caves with a dry surface area and a long entrance corridor (Mursaloglu 1986, Karamanlidis *et al.* 2004*a*). Such a pupping habitat is considered as the bare minimum required by individual females for parturition and has been linked to various negative effects at the population level, such as the limitation of social interaction and low pup survival rates (Sergeant *et al*. 1978, Gazo *et al.* 2000).

Greece currently has the greatest concentrations of Mediterranean monk seals, located mainly over the Aegean and Ionian islands, and the coastlines of the continental central and southern part of the country (Adamantopoulou *et al.* 1999). Greece features an extensive coastline of approximately 15,000 km and roughly 4,000 islands, and the amount of potential habitat makes it the focus of conservation and management efforts for the species in the eastern Mediterranean. MOm/Hellenic Society for the Study and Protection of the Monk Seal is a national nongovernmental organization with lengthy experience in conducting research on the biology of the species and carrying out conservation initiatives within the country (Adamantopoulou *et al.* 2000). In 1990 MOm initiated its research program, aiming to advance the knowledge of the species' ecology, to identify and monitor the main populations, and thus, to ultimately promote the conservation of the species within Greece. As part of this program, this study aimed at identifying the specific terrestrial habitat and the physical and environmental factors that influence habitat choice and use by Mediterranean monk seals during pupping and thus contribute to the knowledge of the species' reproductive behavior.

Materials and Methods

Study Area

The study was carried out within the archipelago of the Northern Sporades, a complex of islands located in the Northwestern Aegean Sea, which previous research had identified as important to the survival of the Mediterranean monk seal (Schultze-Westrum 1977, Kouroutos *et al.* 1986). In order to protect the unique ecosystem of the area and promote the recovery of the species, the Hellenic State established the National Marine Park of Alonnisos, Northern Sporades (NMPANS) in 1992. The

NMPANS has an area of approximately 2,200 km^2 and is divided into three main zones with varying degrees of protection (Fig. 1). Access to the Core Zone of the NMPANS is strictly prohibited (scientific research and management of the island Piperi excluded), whereas human activities within Zone A are regulated. Access and most activities within Zone B of the park are permitted.

Data Collection

During the initial phase of the study in 1990, we circumnavigated the entire coastline of the study area with a small inflatable boat, at a distance of 40 m from the shoreline in order to locate all potential caves. Once a cave was located, we recorded its GPS position and its specific physical and environmental features (Table 1) and created a raw sketch of the cave morphology. During a subsequent visit, we collected the measurements that were required to create a scale map. These measurements provided estimates of the total beach area, main beach area, and wet area (Table 1). To minimize disturbance, we took all measurements during late spring and early summer when in-cave seal activity is low (Dendrinos *et al*. 1994). Taking into account that breeding females and their pups can change caves from the early stages of a pup's life (Dendrinos *et al*. 1999*a*), we defined pupping sites as the caves that were used by a mother–pup pair during the first month after birth. We determined date of birth

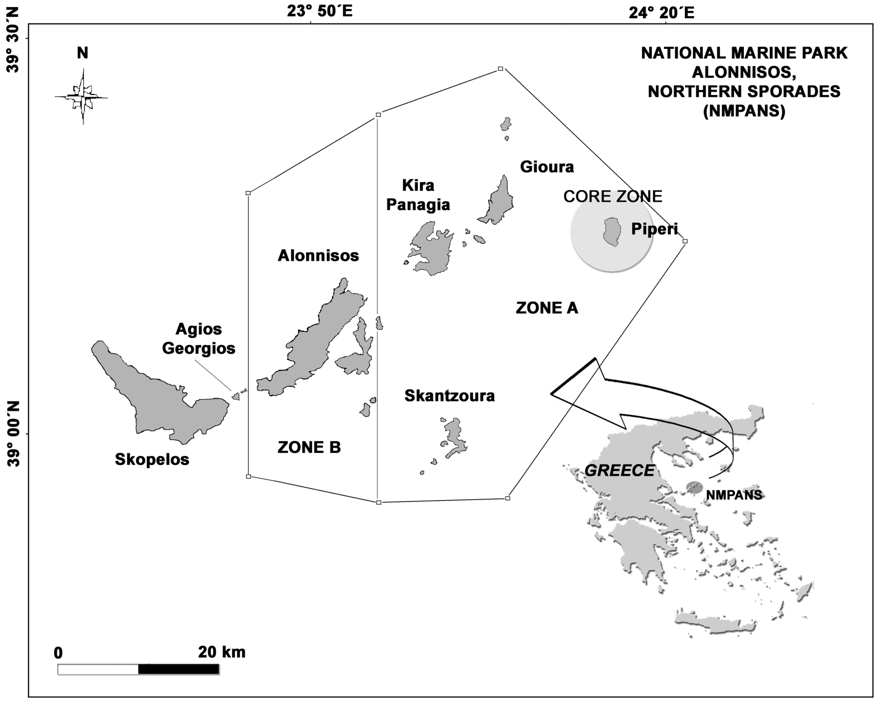


Figure 1. The National Marine Park of Alonnisos, Northern Sporades (NMPANS), indicating the location and size of the three main protection zones.

Table 1. Variables used to describe the potential Mediterranean monk seal pupping habitat in the Northern Sporades archipelago.

Variable	Description
Entrance direction	Direction of the main entrance in relation to North (in degrees)
Entrance width	Distance (m) at sea level between the two points defining an entrance
Entrance height	Vertical distance (m) between the middle of the entrance and the cave ceiling
Entrance depth	Vertical distance (m) between the middle of the entrance and the bottom of the sea
Wind susceptibility	Susceptibility (low, medium, high) of a cave, based on the direction of the cave entrance, to the prevailing winds during October
Number of entrances	Total number of entrances, both below and above water, leading into the interior of the cave
Number of beaches	Total number of dry surfaces bigger than 2 m^2 allowing a seal to come onto land
Corridor length	Direct distance at sea level (m) between the middle of the entrance and the middle of the main beach
Beach visibility	Ability to see the dry surface in the interior of the cave from a distance of 30 m outside the entrance of the cave (not visible, partially visible, visible)
Luminance	Amount of daylight (low, medium, high) at the main beach in the cave's interior
Total beach area	Size (m^2) of all dry surfaces within the cave
Main beach area	Size (m^2) of the main dry surface used by monk seals for resting or pupping
Main beach substrate	Type of substrate of the main beach (sand/pebbles, stones, boulders, rock platform)
Wet area	Area (m^2) of the water surface in the interior of the cave
Human activity	Intensity of the human activity (low, medium, high) within a 2-km radius from the cave's entrance

and age of the pup based on a field method developed in the study area (Dendrinos *et al*. 1999*b*).

During the entire study period, we monitored human activity within the NMPANS and used these observations to determine the intensity of human activity near the caves (Karamanlidis *et al*. 2004*b*).

In order to evaluate the effect of wave and wind action on cave usage, we estimated the susceptibility of each cave entrance above a Beaufort scale of four during the month of October. The month of October was chosen because evidence suggested that this is the time of highest usage of the terrestrial habitat by mother–pup pairs (Dendrinos *et al*. 1994, 1999*a*). We excluded from our analysis values below a Beaufort scale of four because field observations indicated that they are not strong enough to wash seals out of caves. The station on the neighboring island of Skyros provided meteorological data.

From 1991 to 2004 we monitored all caves identified during the initial phase of the study in 1990 using the standard methodology of Mediterranean monk seal monitoring projects in the eastern Mediterranean (Panou *et al*. 1993, Gucu *et al.* 2004). We visited all caves repeatedly in order to minimize the risk of pseudo-absences in the data. Coastal caves are continuously subjected to wind and wave action and sometimes undergo severe structural changes. As a result, data for some caves do not span the entire study period. Specifically, cave PIP1 underwent serious changes in 1997 and was therefore treated in the analysis as two morphologically different caves (PIP1a ceased to exist in 1996 and PIP1b appeared in 1997). Similarly, SKO2 appears as SKO2a from 1991 to 2003 and is replaced by SKO2b in 2004, and cave SKO12 was formed in 2002.

Statistical Analysis

The response variable for this analysis was the proportion ($\hat{p}_i = n_i/N_i$) of years (n_i) in which the *i*th cave was used for breeding, over the total number of years (N_i) it was being monitored. We regressed this against the set of variables measured in the study using a binomial generalized linear model with a logit link function. In implementing this model in the package R, we used the total number of years available for each cave as a weight, hence accounting for variations in the duration of observation effort between different caves.

We carried out the following preparations of the variables before modeling: The circular variable "entrance direction" was sine- and cosine-transformed to reflect the fact that values close to 0° and 360° represent similar orientations. The variables "Beach Visibility," "Luminance," and "Human Activity" were qualitative indices and therefore entered the model as ordinal factors.

Because this was an exploratory analysis, we examined the entire space of 32,768 models comprising all possible additive combinations of our fifteen variables. Such "data dredging" may result in overfitted models (Burnham and Anderson 2002), particularly in the presence of multicollinearity. To address this, we first calculated the Variance Inflation Factors (VIFs) for the saturated model (Fox 1997). We used Generalized VIFs to account for the presence of ordinal factors in our set of explanatory variables. Some of the terms had Generalized VIF values many orders of magnitude above the acceptable threshold of 4 (Fox 2002). This indicated that multicollinearity was certainly a problem with the saturated model and potentially a problem with simpler models. We therefore decided to calculate the Generalized VIFs for the entire set of 32,768 models and exclude all those that had explanatory terms with Generalized VIF values above 4.

We then calculated the Akaike weight (Burnham and Anderson 2002) of every model still remaining in the set. We constructed a confidence set of models by selecting the subset that comprised 99% of the Akaike weights and renormalized the weights in the confidence set (Burnham and Anderson 2002). We obtained model parameters, parameter confidence intervals, and predictions, by model averaging, using these renormalized weights. We used the Akaike weights across all the models in the confidence set to generate estimates of relative importance for all the environmental variables in our data set (Burnham and Anderson 2002). This approach is increasingly finding application in ecology (*e.g.*, Brook *et al.* 2006) because it offers gains in model robustness.

We used percentage of deviance explained and the count of caves bracketed by the prediction CIs to monitor the model's goodness of fit to the data and obtained the model-averaged prediction CIs by simulation, as follows: For each cave, we simulated 10,000 realizations of the proportion $\hat{p}_i = n_i/N_i$, each time, generating n_i from the binomial distribution $B(N_i, p_{ij})$ where p_{ij} is the probability of occupancy predicted for the *i*th cave by the *j*th model in the confidence set. We determined the frequency with which each of the models was used, stochastically, from a multinomial distribution with 10,000 trials and probability vector $P = \{w_j\}$ comprising the normalized Akaike weights. Confidence intervals of 95% were then obtained as the 2.5 and 97.5 percentiles of that data set.

We carried out four diagnostics on the dominant model (*i.e.*, the one with the highest AIC weight) in the confidence set. First, we checked if use of the probit link function would improve the fit. Second, we used Component + Residual plots (Fox 1997) to investigate the need for a nonlinear (*e.g.*, Generalized Additive) model. We implemented a quasi-binomial error structure to check if the data were affected by overdispersion (Fox 2002). Finally, we investigated whether interactions between our explanatory variables would offer considerable improvements to goodness of fit.

We examined the predictive ability of our analytic approach by means of 1-point cross-validation. Specifically, we repeated the entire fitting, model selection, and model averaging procedure thirty-four times, each time with a cave omitted from the data. We were particularly interested in the precision and accuracy of the predictions, the robustness of our ranking of the environmental variables, and the sensitivity of our results on the degree of extrapolation. We investigated the latter by examining prediction accuracy and precision as a function of how extreme the properties of a cave were in relation to the observed ranges. To do this, we first obtained percentiles from frequency histograms of caves along each of the ten most important environmental variables. We then constructed ten subsets of the data set containing caves in the central 100%, 95%, 90%, . . ., 55%, 50% of the environmental space defined by these ten variables. The data set containing 100% of the environmental space also contained all thirty-four caves. It was postulated that if the model's predictions were sensitive to extrapolation they should become more accurate and precise as the outer percentiles were gradually removed. We inferred relative accuracy from the average residuals of the predictions from the observations and relative precision from the average CI width over all predictions.

Results

During the monitoring period (1991–2004) we included thirty-four suitable monk seal caves, located at the islands of Agios Georgios ($n = 1$), Skopelos ($n = 13$), Alonnisos ($n = 1$), Kira Panagia ($n = 4$), Skantzoura ($n = 1$), Gioura ($n = 4$), and Piperi ($n = 10$) in the monitoring scheme. Information on the measurements carried out within these caves is provided in Table 2. We carried out a total of 3,522 visits to these caves and recorded 104 pupping events in 14 of them. The caves were occupied, on average, for 25% of the total number of years in the data. However, the distribution of occupancy was skewed, with 10% of the caves contributing 50% of the pupping events.

We obtained thirty-four values for the response variable at a sample size of 437 (caves × years). Following the rejection of strongly collinear models and the calculation of Akaike weights, the 99% confidence set contained fifty-one models. We used all fifty-one for model-averaged inference and prediction. We report on the composition of the first five models that took up more than 85% of the re-normalized Akaike weights (Table 3). Within the confidence set of models, ten environmental variables had weights exceeding 0.3 and the direction of the relationship between these and the response variable remained consistent across models (Table 4).

The dominant model explained about 70% of the deviance in the data and the model-averaged prediction CIs bracketed thirty-two of thirty-four caves (Fig. 2a). Use

Table 2. Descriptive statistics of the measurements carried out in the caves ($n = 34$).

	Minimum	Maximum	Mean	SD
Entrance direction (°)	22	350	167.52	103.40
Entrance width (m)	1.5	28	7.70	5.42
Entrance height (m)	0.1	18	5.15	4.77
Entrance depth (m)	0.1	6	2.04	1.41
Number of entrances	1	3	1.41	0.60
Number of beaches	1	3	1.26	0.56
Corridor length (m)	0	58	15.61	12.97
Beach visibility[a]	0	100	42.64	46.27
Luminance[b]	0	100	58.82	39.83
Total beach area (m^2)	3	748	82.05	131.99
Main beach area (m^2)	1	748	71.41	128.86
Main beach substrate[c]	12.5	100	23.16	22.64
Wet area (m^2)	0	800	141.85	144.27

[a]Ordinal variable: not visible (0), partially visible (50), visible (100).
[b]Ordinal variable: low (0), medium (50), high (100).
[c]Ordinal variable: sand/pebbles (12.5), stones (37.5), boulders (67.5), rock platform (100).

of the probit link made little difference to the quality of fit, and the Component + Residual plots gave no indication of nonlinearity. Implementing the dominant model in the confidence set with a quasi-binomial error structure estimated $\phi = 3$, giving evidence for overdispersion. We investigated the possibility that this was caused by zero inflation by implementing a hurdle approach, first modeling the probability that a cave was used at all during its observation period and then modeling the

Table 3. The five first models in the confidence set. Collectively, these take up more than 85% of the renormalized Akaike weights.

Model term	Model 1	Model 2	Model 3	Model 4	Model 5
Intercept	■	■	■	■	■
Beach visibility	■	■	■	■	■
Corridor length		■			
Entrance depth	■	■	■	■	■
Entrance direction					
Entrance height					
Entrance width		■			
Human activity	■		■	■	■
Luminance	■	■	■	■	■
Main beach area					
Main beach substrate	■		■	■	■
Number of beaches	■	■	■		
Number of entrances		■	■		■
Total beach area		■			
Wet area					
Wind susceptibility		■			
Akaike weight	0.243	0.240	0.230	0.100	0.056

Table 4. Relative importance of environmental variables. The rank of each variable was obtained as the sum of Akaike weights over all the models in the confidence set. The direction of each variable's relationship with the response variable was obtained from the most dominant models (Table 3).

	Variable	Ranking	Relationship
1	Luminance	1.000	+
2	Beach visibility	1.000	−
3	Entrance depth	0.939	+
4	Number of beaches	0.767	−
5	Main beach substrate	0.735	−
6	Human activity	0.624	−
7	Number of entrances	0.552	+
8	Corridor length	0.376	+
9	Entrance width	0.354	−
10	Wind susceptibility	0.303	−
11	Total beach area	0.266	––
12	Entrance direction	0.054	––
13	Main beach area	0.049	––
14	Wet area	0.001	––
15	Entrance height	0.000	––

proportion of use, conditional on occupancy. The combined model was neither more accurate nor more precise. We therefore reverted to the simpler, one-step approach. We also decided to omit interaction terms completely because they either led to high collinearity or overfitting (as confirmed by the decline in prediction precision in cross-validation).

Under 1-point cross-validation the procedures chosen for fitting (binomial GLM with logit link), model selection (Generalized VIF and 95% confidence set), and model averaging (Akaike weights with simulated CIs) gave predictions that bracketed the observations for 26 of 34 caves (Fig. 2b). There were marked reductions in both accuracy and precision in going from fitting (Fig. 2a) to prediction (Fig. 2b), although the relative importance of environmental variables (Table 4) was robust to cross-validation. We found no evidence that the loss of accuracy in predictions was the result of extrapolation (Fig. 3a), but there was a clear trend of increasing precision within the central 60% of environmental space (Fig. 3b). To offer some guidance for the practical use of the model for prediction, we provide a description of the more precisely predicted volume of environmental space in Table 5.

Discussion

We have presented the results of what is currently the longest in duration and most extensive field study on cave use by Mediterranean monk seals. These data have enabled us to identify the physical and environmental determinants that influence cave use for pupping and to construct a model of the pupping habits of this critically endangered species.

The ranking and direction of the relationships between cave use and cave characteristics was our most robust finding. Based on the Akaike weights (Table 4) and in order of decreasing importance, luminance, beach visibility, entrance depth, number of beaches, main beach substrate, human activity, number of entrances, corridor

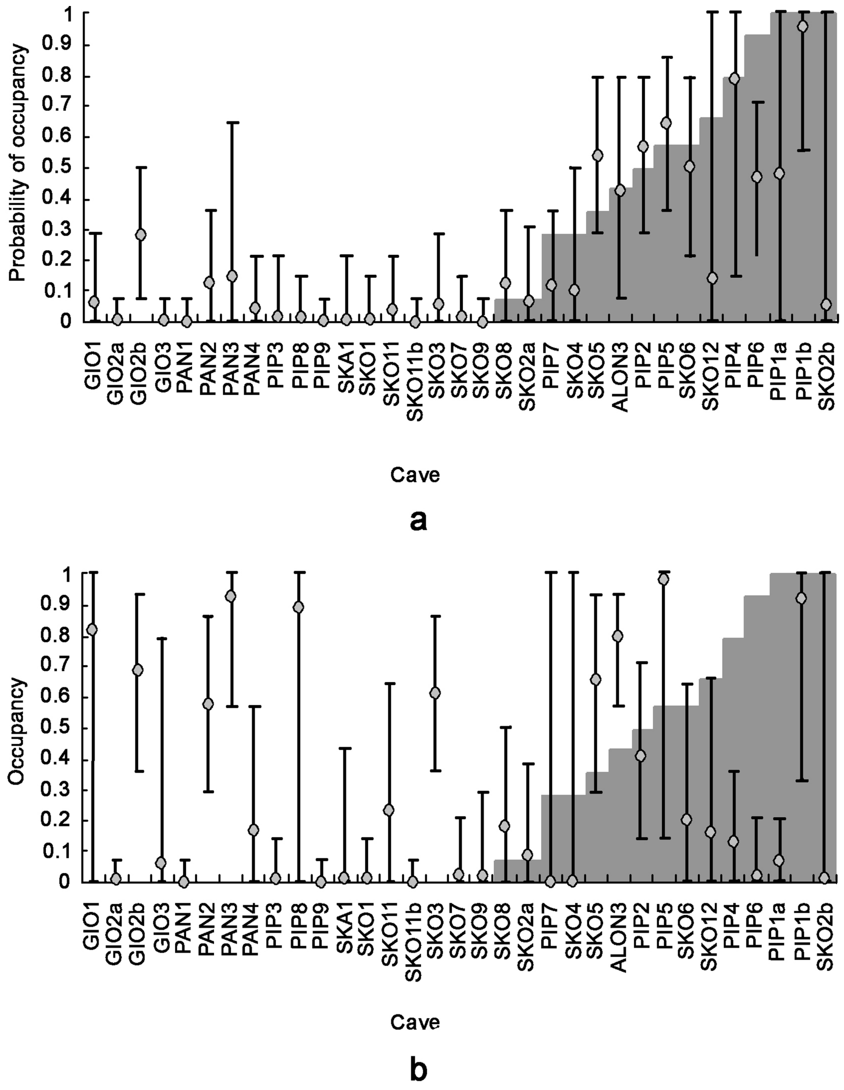
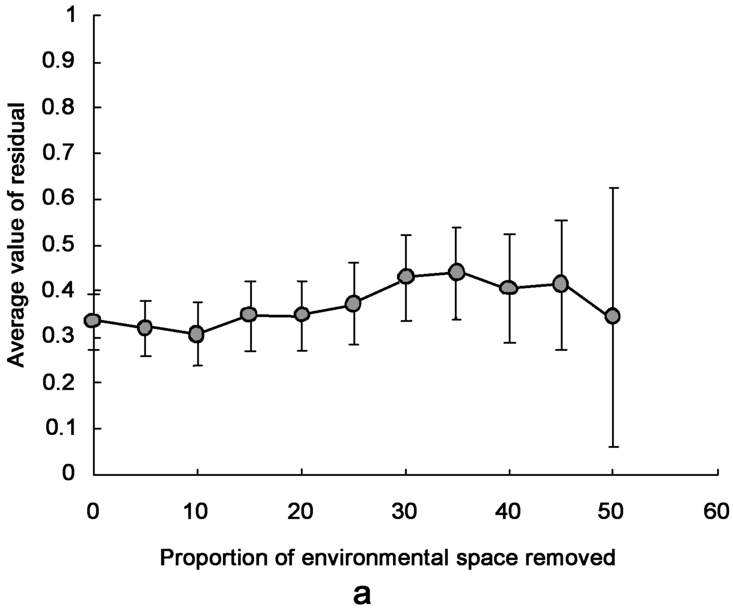


Figure 2. Overview of the performance of the model. Point and interval estimates from the model are shown as gray circles and error bars. The observed proportions of occupancy for each cave are shown as gray bars. The caves along the x-axis have been sorted in increasing order of observed occupancy. Goodness of fit of the model to the data is shown in (a) and the predictions for individual caves, following cross-validation, are shown in (b).

length, entrance width, and wind susceptibility are the main determinants of suitable pupping habitat for the species.

Five of the ten variables identified (*i.e.*, entrance depth, number of beaches, number of entrances, corridor length, and entrance width) are related to the morphology of the cave. This finding is in agreement with previous, descriptive studies from Turkey,



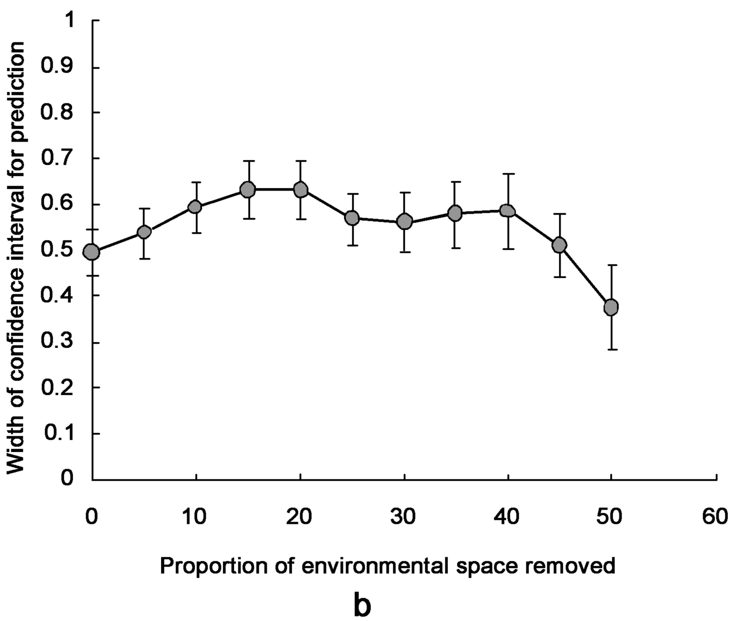


Figure 3. Sensitivity of predictions under extrapolation. The abscissa represents gradual removal from cross-validation of the caves outermost in the environmental space defined by ranges of the ten most dominant environmental variables in Table 3. The ordinate in (a) gives the average residual of predictions from observations for those caves in the remaining core of environmental space. Low values imply relatively high accuracy. The ordinate in (b) gives the average width of prediction CIs for those caves in the interior of the remaining environmental space. Low values imply relatively high precision.

Table 5. Conditions under which the present model and data set can predict proportion of cave occupancy with higher precision. Sensitivity of model predictions to extrapolation drops sharply within the central 60% of environmental space (Fig. 3b). This region is defined by the variable ranges (minimum to maximum) shown below.

Variable	Minimum value	Maximum value
Luminance[a]	0	100
Beach visibility[b]	0	100
Entrance depth (m)	0.5	3.0
Number of beaches	1	2
Main beach substrate[c]	12.5	37.5
Human activity	1	3
Number of entrances	1	2
Corridor length (m)	6.0	20.0
Entrance width (m)	4.1	12.1
Wind susceptibility	1	9

[a]Ordinal variable: low (0), medium (50), high (100).
[b]Ordinal variable: not visible (0), partially visible (50), visible (100).
[c]Ordinal variable: sand/pebbles (12.5), stones (37.5), boulders (67.5), rock platform (100).

Madeira, and Mauritania (Mursaloglu 1986; Gonzalez *et al.* 1997, 2002; Karamanlidis 2004*a*). However, the more extensive data set and quantitative approach followed by the present work allows us to draw the following, specific biological inferences.

The requirement for luminance serves the biological and behavioral needs of a mammal that, not long ago in evolutionary terms, used to breed on open beaches (Johnson and Lavigne 1999). In contrast, the requirement for low visibility of the beach in the interior of the cave probably aims to minimize the risk of interactions with humans. Caves with multiple narrow and deep entrances increase security further by providing a choice of escape routes, while limiting human accessibility to the interior of the cave. Long entrance corridors contribute to concealment but also act as wave breakers, offering additional protection for lactating pups. The preference for a soft substrate inside the caves seems to serve the biological and behavioral requirements of the species during parturition and is in accordance with observations from Mauritania, where females prior to parturition dug hollows in the sand, which they actively defended against approaching seals (Layna *et al.* 1999).

All the above characteristics seem to take precedence over the animals' preference for areas with low human activity. Due to the scarcity of available pupping habitat however, monk seals may use morphologically suitable caves that are in proximity to humans and up to an unknown threshold level of disturbance. Once this threshold is exceeded, these pupping sites may be abandoned, actually limiting suitable pupping sites even further.

Weather-related variables, such as wind susceptibility and entrance direction, did not feature prominently in the models of the confidence set. This may be due to the fact that lactating females reduce the risk of pups being lost during storms by changing shelters after birth. In contrast to previous reports, mothers and newborn pups have been observed to travel distances of up to 2 km, as early as 10 d postpartum, in order to reach a more weather-protected cave (Dendrinos *et al*. 1999*a*). In Mauritania, females were observed to seek out the farthest end of caves in order to protect themselves and potentially their pups against wave action during parturition (Layna *et al.* 1999).

We conclude that pupping monk seals select caves where they cannot be seen, but that are not completely dark, have multiple escape routes, are not easily accessible to humans, have a low risk of pup washout, and the benefit of beaches with soft substrate. These requirements about the interior of the caves seem to be more important than conditions of weather and human activity prevailing at its exterior.

In terms of its overall performance, arguably, the model gives a good fit (Fig. 2a) but predicts poorly (Fig. 2b) under cross-validation, especially for certain caves. We are satisfied that this is not due to model misspecification because our investigation did not give evidence of nonlinearities in residuals, the need for interaction terms, or a more suitable link function. We also excluded the possibility of overfitting due to multicollinearity and the need for a hurdle modeling approach to account for overdispersion.

This leaves the possibility that the poorly predicted caves were atypical in the values of either the response or the explanatory variables. The first explanation implies high variability in occupancy between caves and the second, that the model is predicting occupancy by extrapolation for these caves. High variability in use between similar caves might imply a fundamentally unpredictable element in the behavior of different monk seal mothers. This possibility can only be investigated by collecting individual-specific histories about cave use (*e.g.*, by using tagging or pelage patterns). Alternatively, it might imply that despite our attempt to measure every conceivable aspect of each cave (no matter how correlated with other aspects), we have omitted some important environmental covariate of cave usage. Both of these possibilities will need further research.

The possibility that low-quality predictions were due to extrapolation was tackled in this paper. Our evidence (Fig. 3b) suggests that predictions within the central 60% of environmental space (as described in Table 5) would be relatively more precise. As well as serving as a caveat for the use of this model for extrapolation, this finding underlines the need for spot-sampling of caves in additional areas so as to increase the diversity of conditions provided to the model. Given that the analysis presented here can deal with variable sampling effort, past and newly collected data should be pooled to provide a more robust model.

The monitoring program of the Northern Sporades monk seal population has allowed us to reveal more detail on the use of caves as pupping sites by the species. We have shown that there is useful information about occupancy to be extracted from habitat data for this species. This information will be valuable for predicting usage outside our study region but not outside the ranges of environmental conditions covered by our observations. The overall statistical methodology is relevant to any species with well-defined breeding sites whose occupancy can be censused in the field. Considering that the availability of suitable pupping sites within the species' geographical range is limited, further development of the approach presented here and collection of the additional data outlined above would provide a useful tool for the identification of critical pupping sites and contribute toward the design of more effective measures for the conservation of the Mediterranean monk seal.

Acknowledgments

We would like to express our gratitude toward T. Anagnostou, A. Alexiou, A. Kottas, N. Lambadariou, and K. Paneris for their assistance in the field, the people of Steni Vala, Alonnisos for their hospitality and the Hellenic Ministry of Rural Development and Food for its support.

We are grateful to Jason Baker, Corey Bradshaw, Geert Aarts, and an anonymous referee for their constructive comments. This project was partially funded by the International Fund for Animal Welfare, the European Commission, D.G. XI, Contract No. 6610(90)9165 and 4-3010(92) 7829, the Hellenic Ministry for the Environment, Physical Planning and Public Works, and the Prefecture of Magnisia. Jason Matthiopoulos was supported by a UK-NERC core grant to SMRU.

LITERATURE CITED

ADAMANTOPOULOU, S., E. ANDROUKAKI AND S. KOTOMATAS. 1999. The distribution of the Mediterranean monk seal based on an information network. Contributions to the Zoogeography and Ecology of the Eastern Mediterranean Region 1:399–404.

ADAMANTOPOULOU, S., K. ANAGNOSTOPOULOU, P. DENDRINOS, S. KOTOMATAS, N. LABADARIOU, V. PIPINIS, G. STROUFLIOTIS, E. TOUNTA AND V. ZAVRAS. 2000. Conserving critical habitats for the Mediterranean monk seal in Greece through the creation of a network of protected areas. Page 33 *in* Proceedings of the 14th Annual Conference, European Cetacean Society, Cork, Ireland.

BAILLIE, J. E. M., C. HILTON-TAYLOR AND S. N. STUART. 2004. 2004 IUCN red list of threatened species. A global species assessment. IUCN, Gland, Switzerland.

BROOK, B. W., L.W. TRAILL AND C. J. A. BRADSHAW. 2006. Minimum viable population size and global extinction risk are unrelated. Ecology Letters 9:375–382.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd edition. Springer-Verlag, New York.

DENDRINOS, P., E. TOUNTA, S. KOTOMATAS AND A. KOTTAS. 1994. Recent data on the Mediterranean monk seal population of the Northern Sporades. Bios (Macedonia/Greece) 2:11–16.

DENDRINOS, P., S. KOTOMATAS AND E. TOUNTA. 1999*a*. Monk seal pup production in the National Marine Park of Alonissos-N. Sporades. Contributions to the Zoogeography and Ecology of the Eastern Mediterranean Region 1:413–419.

DENDRINOS, P., E. TOUNTA AND S. KOTOMATAS. 1999*b*. A field method for age estimation of Mediterranean monk seal (*Monachus monachus*) pups. Page 48 *in* Proceedings of the 13th Biennial Conference on the Biology of Marine Mammals, Maui, Hawaii.

FOX, J. 1997. Applied regression analysis, linear models and related methods. Sage, Thousand Oaks, CA.

FOX, J. 2002. An R and S-plus companion to applied regression. Sage, Thousand Oaks, CA.

GAZO, M., F. APARICIO, M.A. CEDENILLA, J. F. LAYNA AND L. M. GONZALEZ. 2000. Pup survival in the Mediterranean monk seal (*Monachus monachus*) colony at Cabo Blanco Peninsula (Western Sahara-Mauritania). Marine Mammal Science 16:158–168.

GONZALEZ, L. M., A. AGUILAR, L. F. LOPEZ JURADO AND E. GRAU. 1997. Status and distribution of the Mediterranean monk seal *Monachus monachus* on the Cabo Blanco Peninsula (Western Sahara Mauritania) in 1993–1994. Biological Conservation 80:225–233.

GONZALEZ, L. M., M.A. CEDENILLA, P. F. LARRINOA, J. F. LAYNA AND F. APARICIO. 2002. Changes in the breeding variables of the Mediterranean monk seal (*Monachus monachus*) colony of Cabo Blanco Peninsula after a mass mortality episode. Mammalia 6:173–182.

GUCU, A. C., G. GUCU AND H. OREK. 2004. Habitat use and preliminary demographic evaluation of the critically endangered Mediterranean monk seal (*Monachus monachus*) in the Cilician Basin (Eastern Mediterranean). Biological Conservation 16:417–431.

JOHNSON, W. M., AND D. M. LAVIGNE. 1999. Monk seals in antiquity. The Mediterranean monk seal (*Monachus monachus*) in ancient history and literature. The Netherlands Commission for International Nature Protection, Leiden, Mededelingen 35:1–101.

JOHNSON, W. M., A.A. KARAMANLIDIS., P. DENDRINOS, P. F. DE LARRINOA, M. GAZO, L.M. GONZALEZ, H. GÜÇLÜSOY, R. PIRES AND M. SCHNELLMANN. 2006. Monk seal fact files. Biology, behaviour, status and conservation of the Mediterranean monk seal, *Monachus monachus*. The Monachus Guardian. http://www.monachus-guardian.org.htm (accessed 20 September 2006).

KARAMANLIDIS, A. A., R. PIRES, N. C. SILVA AND H. C. NEVES. 2004*a*. The availability of resting and pupping habitat for the critically endangered Mediterranean monk seal *Monachus monachus* in the archipelago of Madeira. Oryx 38:180–185.

KARAMANLIDIS, A. A., P. DENDRINOS, E. TOUNTA AND S. KOTOMATAS. 2004*b*. Monitoring human activity in an area dedicated to the protection of the endangered Mediterranean monk seal. Coastal Management 32:293–306.

KOUROUTOS, V., D. PAPAPANAYOTOU AND P. KOKKINIA. 1986. Observations on the behaviour of the monk seal, *Monachus monachus*, in the N. Sporades, Greece. Biologia Gallo-Hellenica 12:249.

LAYNA, J. E., M.A. CEDENILLA, F. APARICIO AND L. M. GONZALEZ. 1999. Observations of parturition in the Mediterranean monk seal (*Monachus monachus*). Marine Mammal Science 15:879–882.

MURSALOGLU, B. 1986. Pup-mother-environment relations in the Mediterranean monk seal, *Monachus monachus* (Hermann, 1979), on Turkish coasts. Communications of the Faculty of Science of the University of Ankara, Series C 4:1–8.

PANOU, A., J. JACOBS AND D. PANOS. 1993. The endangered Mediterranean monk seal *Monachus monachus* in the Ionian Sea, Greece. Biological Conservation 64:129–140.

SCHULTZE-WESTRUM, T. 1977. Mönchsrobben im Nord-Sporaden Gebiet. Oryx 13:421.

SERGEANT, D., J. BOULVA, F. BERKES AND K. RONALD. 1978. Recent status of *Monachus monachus*, the Mediterranean monk seal. Biological Conservation 14:259–287.

Received: 27 March 2006
Accepted: 5 February 2007