Contributed Paper

Effects of Multiple Levels of Social Organization on Survival and Abundance

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Abstract: *Identifying how social organization shapes individual behavior, survival, and fecundity of animals that live in groups can inform conservation efforts and improve forecasts of population abundance, even when the mechanism responsible for group-level differences is unknown. We constructed a hierarchical Bayesian model to quantify the relative variability in survival rates among different levels of social organization (matrilines and pods) of an endangered population of killer whales (*Orcinus orca*). Individual killer whales often participate in group activities such as prey sharing and cooperative hunting. The estimated age-specific survival probabilities and survivorship curves differed considerably among pods and to a lesser extent among matrilines (within pods). Across all pods, males had lower life expectancy than females. Differences in survival between pods may be caused by a combination of factors that vary across the population's range, including reduced prey availability, contaminants in prey, and human activity. Our modeling approach could be applied to demographic rates for other species and for parameters other than survival, including reproduction, prey selection, movement, and detection probabilities.*

Keywords: hierarchical Bayesian, killer whale, model selection, population dynamics, random effects, social organization

Efectos de Niveles Múltiples de Organización Social sobre la Supervivencia y Abundancia

Resumen: *La identificación de la forma en que la organización social moldea el comportamiento, la supervivencia y fecundidad individual de animales que viven en grupos puede informar a los esfuerzos de conservación y mejorar los pronósticos de abundancia poblacional, aun cuando no se conozca el mecanismo responsable de las diferencias a nivel de grupo. Construimos un modelo Bayesiano jerárquico para cuantificar la variabilidad relativa en las tasas de supervivencia entre diferentes niveles de organización social (matrilíneas y agrupaciones) de una población en peligro de ballenas asesinas (*Orcinus orca*). Las ballenas individuales a menudo participan en actividades grupales como compartición de presas y cacería cooperativa. Las probabilidades estimadas de supervivencia por edades específicas y las curvas de supervivencia difirieron considerablemente entre grupos y en menor medida entre matrilíneas (dentro de los grupos). En todos los grupos, los machos tuvieron menor esperanza de vida que las hembras. Las diferencias en supervivencia entre grupos pudo deberse a una reducción en la disponibilidad de presas, contaminantes en las presas y actividad humana. Nuestro método de modelado podría ser aplicado a las tasas demográficas de otras especies y para parámetros distintos a la supervivencia, incluyendo reproducción, selección de presas, desplazamiento y probabilidades de detección.*

Palabras Clave: ballena asesina, Bayesiano jerárquico, dinámica poblacional, efectos aleatorios, organización social, selección de modelos

Introduction

Some species have a hierarchical social organization, such as family, extended family, social group, subpopulation, and population. Social organization affects individual behaviors, habitat use, diet, and ultimately individual survival and reproduction (Parrish & Edelstein-Keshet 1999; Krause & Ruxton 2002). Because demographic rates respond to social organization, the growth and probability of persistence of a population with hierarchical social organization is determined by group-level rather than average individual survival and reproduction (Brault & Caswell 1993; Courchamp et al. 1999; Purvis et al. 2000). Commonly used software packages for population viability analysis, such as ALEX (Possingham & Davies 1995) and VORTEX (Lacy 1993), can explicitly include demographic differences among groups. But to include such information, one needs to identify which levels of social grouping affect demographic rates and differences in those rates among social groups.

Discerning the extent to which group membership affects survival of an individual is often difficult because slight differences among groups may be masked by interactions among age, sex, year, or external covariates. Hierarchical Bayesian models provide a flexible solution for estimating these effects in the context of multiple levels of variability (Clark et al. 2005; Gelman & Hill 2006; Cressie et al. 2009). At each level of social organization, random effects may be used to model demographic parameters as being drawn from a larger probability distribution (Lindley & Smith 1972; Pinheiro & Bates 2000; Gelman et al. 2004). We used a time series of census data from an endangered population of killer whales (*Orcinus orca*) to demonstrate use of these hierarchical approaches to evaluate alternative hypotheses about the effect of group membership on survival and forecasts of population abundance, even when the mechanism responsible for group differences is unknown. Killer whales are a predatory marine mammal with a social organization that is complex and static over many years. A typical population interacts within three social groups: matriline (a mother and offspring), pod (several matrilines), and subpopulation (multiple pods). The size and composition of each group are in part related to prey specialization. For example, fish-eating, resident populations of killer whales have larger, more cohesive groups than transient populations that eat mammals (Bigg et al. 1990).

The 30-year time series of data we used in our analyses was collected on the southern resident population of killer whales that occurs in the northeast Pacific Ocean. Thirty years is shorter than the lifespan of this species (50–60 years for females; Krahn et al. 2004). Individuals within the population spend their entire lives in closely related matrilines. A typical matriline consists of <20 animals spanning one to four generations (Wiles 2004). Multiple matrilines form pods, and matrilines remain within the same pod over generations.

The southern resident population of killer whales was listed as endangered under Canada's Species at Risk Act in 2004 and under the U.S. Endangered Species Act in 2005. A 2008 census of the population recorded 83 individuals. In summer the population inhabits portions of Puget Sound (Washington, U.S.A.) and the southern Strait of Georgia (British Columbia, Canada). Less is known about the population's distribution in winter, when detection is more difficult and search effort is reduced. In winter one pod appears to remain largely within Puget Sound, whereas the other pods are thought to leave Puget Sound and travel south along the coast into waters off Oregon and California (U.S.A.) (Krahn et al. 2004). Factors influencing survival may include declines in abundance of prey (particularly Chinook salmon, *Oncorhynchus tshawytscha*) and human activities such as operation of whale-watching vessels and release of pollutants into the ocean (Krahn et al. 2004). Although more than 30 years of detailed demographic data have been collected on this population, the factors driving its decline in abundance and potential demographic differences among matrilines, pods, and subpopulations remain largely unknown. We used hierarchical Bayesian modeling to test different hypotheses concerning the effect of different levels of social organization on survival of southern resident killer whales.

Methods

An intensive mark-resight study has been conducted on the southern resident population of killer whales since 1976. Every individual in the population has been photoidentified with techniques developed by the Center for Whale Research (after 1976, all individuals have been identified in the first year of life), and animals are resighted in subsequent years by scientists with the center and the governments of the United States and Canada (CWR 2008). Because every animal is observed every year, the effort is a complete population census. The population has three distinct pods, J, K, and L, and each pod consists of multiple matrilines. Because no immigration or emigration occurs (Krahn et al. 2004), the status of all individuals is assumed; animals not seen in a given year are considered dead. Among the pods there were 19 matrilines and 165 individuals.

Incorporating Social Organization into Demographic Models

We considered four models of population demography, each with different social organization: a model with no social organization; a model with variation in survival among matrilines (but not pods); a model with variation in survival among pods (but not matrilines); and a

model with variation in survival among both matrilines and pods.

Data from the annual census are binary (presence or absence). Simultaneously estimating probabilities of capture and survival from presence–absence data often requires capture–recapture models (Royle & Link 2002; Barry et al. 2003). Because we had annual data on all individuals in the population, we used a simpler logistic regression to model survival. This approach allows the binary response to be linked to covariates with generalized linear models (GLMs) that have a logit transform. Covariates can include both fixed and random effects. Because there appeared to be substantial differences in survival rates among years (Ford et al. 2010), we included year as a random effect in each candidate model. The model without social organization is

$$\text{logit } (\phi_{i,t}) = B_0 + B_1 a_{i,t} + B_2 a_{i,t}^2 + B_3 s_i$$
$$+ y_t; y_t \sim \text{normal}(0, \sigma_{\text{year}}), \quad (1)$$

where $\phi_{i,t}$ is the survival probability of animal i at time t. Following Krahn et al. (2004), B_1 and B_2 are coefficients that allow the effect of age (a) to be quadratic, and B_3 is a coefficient that allows survival to differ between sexes. The temporal deviate, y_t, allows average survival to vary among years. This model assumes that after age and sex are accounted for survival probability is equal for all individuals in a given year, regardless of matriline or pod. In this model, differences in survival probability are determined by differences in the number of deaths. Individual effects cannot be included because at the individual level the number of deaths is limited to one.

To model differences in survival probabilities among matrilines, we constructed a hierarchical version of the model with random effects in matrilines (Gelman & Hill 2006):

$$\text{logit } (\phi_{i,t}) = B_0 + B_1 a_{i,t} + B_2 a_{i,t}^2 + B_3 s_i$$
$$+ g_i + y_t; y_t \sim \text{normal}(0, \sigma_{\text{year}}), \quad (2)$$

where g_i is the difference of the matriline of animal i from the population mean (B_0). We modeled these matriline differences as normally distributed, which yielded the binomial-normal model (Royle & Link 2002), in which $g_i \sim \text{normal}(0, \sigma_g)$, and σ_g controls variation among matrilines. We assumed that the difference from mean survival probability (a function of sex and age) of all individuals in a matriline was equal, and we held these differences constant over time. To model differences in survival probability among pods, we replaced the matriline differences (g_i) with pod differences (p_j) : $p_j \sim \text{normal}(0, \sigma_p)$.

In the full model with variation among both matrilines and pods, we assumed the matriline differences were normally distributed around the pod mean rather than the population mean, so the matriline effect was distributed $g_i \sim \text{normal}(p_j, \sigma_g)$. The pod effect had a mean of zero because the deviation of each pod was distributed around

the population mean (B_0):$p_j \sim \text{normal}(0, \sigma_p)$. The full model had seven parameters: three sources of variability ($\sigma_{\text{year}}, \sigma_p, \sigma_g$) and four fixed-effect coefficients (age, age^2, sex, and population intercept B_0).

Constructing an Informative Prior

A northern population of resident killer whales also occurs along the west coast of the United States and Canada. The habitat of the northern population is adjacent to that of the southern population; however, the populations are genetically distinct (Krahn et al. 2004). We did not include data from the northern population in the same model as the southern resident data because the northern population is not censused annually and its social organization is thought to differ from the southern population (Ford et al. 2000). Nevertheless, survey data from the northern population is informative with respect to differences in survival between ages and sexes, and we used these data to construct an informative prior for our analyses of the southern population.

We fit the logistic regression model without pod or matriline differences (Eq. 1) to data from surveys of the northern population conducted from 1976 to 2007 (Ford et al. 2000; Ellis et al. 2007). All model coefficients were assigned broad normal (0, 10) priors. We used MCMCpack library in *R* to estimate posterior distributions of the parameters: $B_0 \sim \text{normal}(4.11, \sigma = 0.25)$; $B_1 \sim \text{normal}(0.045, \sigma = 0.02)$; $B_2 \sim \text{normal}(-11.79E - 04, \sigma = 3.0E - 04)$; $B_3 \sim \text{normal}(-0.40, \sigma = 0.25)$. We used these posteriors as prior distributions in the analyses of the data from the southern population. Following Gelman (2006), we used uniform (0, 10) priors on standard deviations of random effects for social groupings and temporal deviations.

Model Selection

Each of the hierarchical models represented a different hypothesis about the effect of social organization on survival. We used two Bayesian model-selection techniques to evaluate whether the data supported the different hypotheses. First, we used the deviance information criterion (DIC) (Spiegelhalter et al. 2002). The DIC is convenient to use (available in BUGS software; Lunn et al. 2000) and its effective number of parameters approximate the complexity of hierarchical models (Spiegelhalter et al. 2002). Second, we estimated the posterior model probabilities by treating each level of variation as a mixture of fixed and random effects (mixture random effect model) (Xia et al. 2005). We included each level of variability with indicator functions: $G_1 = 1$ if group level variation was included and $G_1 = 0$ otherwise. For example, when we applied the mixture random effect to pod differences, pod effects became a mixture of the mean with and without random effects: $p_{\text{mix},j} = G_1 p_j + (1 - G_1)B_0$. Output from this approach is similar to reversible jump Markov

Table 1. Deviance information criterion (DIC) weights and posterior probabilities for four different models used to evaluate whether social organization affects survival of killer whales.*

Model	$\hat{\sigma}_p$	$\hat{\sigma}_g$	DIC	DIC weight	Posterior P[M|Y]
1	0.72 (0.24)	0.25 (0.18)	757.7	0.45	0.26
2	0.71 (0.26)	–	758.4	0.31	0.37
3	–	0.28 (0.19)	761.2	0.08	0.15
4	–	–	759.7	0.16	0.22

Parameter medians and standard errors for the estimated variance parameters are in parentheses. The parameter $\hat{\sigma}_p$ controls variation in survival among pods; the parameter $\hat{\sigma}_g$ controls variation in survival among matrilines. The DIC weights and model complexity (p_D) are calculated for each model and then used to calculate the normalized DIC model weights (Spiegelhalter et al. 2002). The posterior probability, P[M|Y], is computed by treating each source of variability as a mixture of fixed and random effects with indicator functions.

chain Monte Carlo (Green 1995) in that the posterior probability of each model is explicitly estimated. Although the second approach is slightly more complicated than the first, model uncertainty in the second approach is represented as probabilities.

Projections of Population Size

We used the posterior parameter estimates from the best model to project the population size of the southern resident population of killer whales. To project abundance over the next 10 years, we used the posterior distributions of the annual deviations estimated from the last 10 years because environmental conditions or prey availability may be correlated among years (Ford et al. 2010). This approach assumes that future conditions will be similar to past conditions. Each of 5000 projections was initialized from the 2008 age and sex structure of the southern population. To allow for population growth, we used previously published estimates of age-specific fecundity rates and reproductive senescence (Ward et al. 2009). Although the animals born in our 10-year simulations would not reach sexual maturity, on the basis of existing data (CWR 2008), we assumed 55% of the animals born would be male.

Results

Both model-selection criteria (DIC and posterior model probabilities) supported the inclusion of pod effects. The highest posterior probability excluded matriline effects (Table 1), whereas DIC assigned the most weight to the model with both matriline and pod effects. In the multilevel model with random effects in both the matrilines and pods, the difference between pods was estimated to be greater than the difference between matrilines (Table 1). Thus, even when effects at the matriline level were included, they had less influence on survival than effects at the pod level. Hereafter, we focus on results from the model with pod effects only; however, the results were similar to the model with both matriline and pod effects.

The influence of the prior from the northern population on the estimated survival curves appeared to be relatively minor (Fig. 1). On the basis of analyses of the CWR resight data, the southern population had a substantially lower survival probability than the northern population. Additionally, survival estimates differed substantially across the three pods of the southern population. Females in J and K had a median life expectancy of over 30 years, whereas females in the L pod had a median life expectancy of slightly over 20 years (Fig. 1). Survival curves among all models differed between sexes; as expected males had lower survival rates (Fig. 1; Promislow
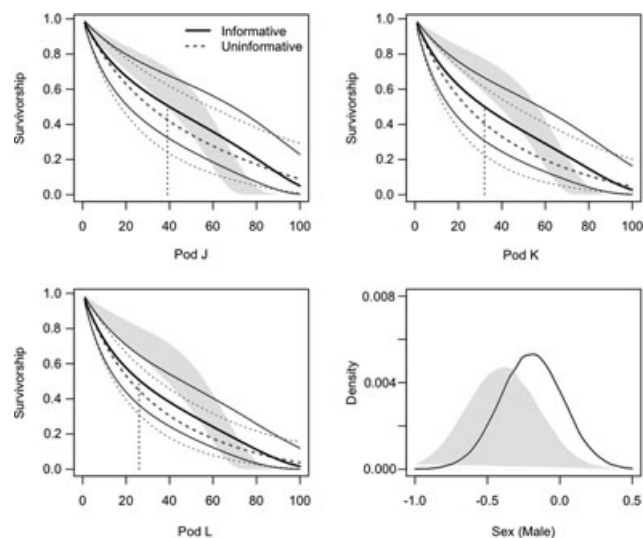

Figure 1. Posterior probabilities of survival to age x (Lx, survivorship) for three pods (J, K, L) in the southern resident population of killer whales. The mode of the survivorship at age x (thick line) and 95% CI (thin lines) are shown for females with (solid line) and without (dashed line) an informative prior. The shaded region represents the informative prior constructed from the adjacent northern resident population of killer whales. For each pod, 50% survival is marked with a dotted vertical line. The prior (shaded) and posterior of the male effect are shown in the bottom right graph.
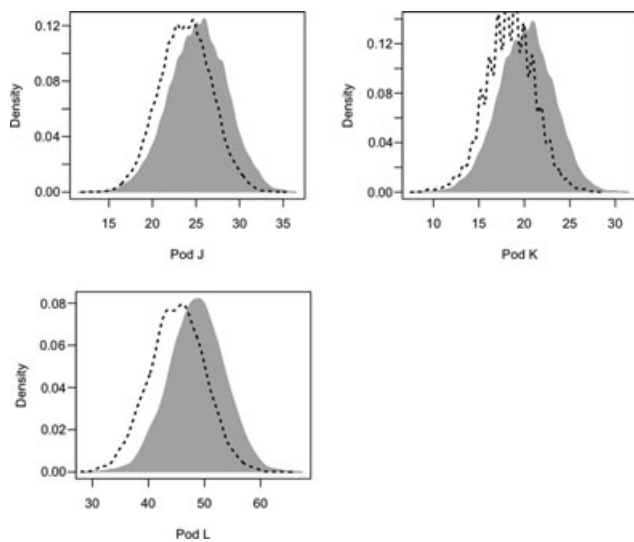
Figure 2. Projected population sizes of southern resident killer whales in 10 years on the basis of the results of the model of killer whale survival with highest posterior probability given the data (one level of social organization and pod-specific survival rates) (shaded area, posterior distribution when social organization is not accounted for; dashed line, posterior distribution with social organization included; 5000 MCMC iterations).

1992). The posterior of the sex-level differences was essentially the same as the prior (Fig. 1), which indicated the effect of gender on survival probability was similar between the northern and southern populations.

Using the model with pod-level effects only, we projected the size of the southern population over 10 years and compared those estimates to those generated by a model without pod effects (Fig. 2). Although 10 years is short relative to the lifespan of killer whales, the model with pod effects produced a slightly less variable estimate of the population size after 10 years ($\sigma_{N_{2018}} = 6.95$, 7.20, respectively) and a smaller population size after 10 years (94.5% of the size projected by the model without pod effects; $\overline{x}_{N_{2018}} = 89.08$, 94.27, respectively).

Discussion

Our analyses of census data on the southern, resident population of killer whales suggest that pod membership has a greater effect on survival among individuals than does matriline membership. The variation in survival among pods translates into large differences in life expectancy; of the three pods, pod L had the lowest median life expectancy. Although the mechanism for pod-level differences in survival is unknown, we suspect prey availability, which may differ among pods, may play a

role. The pods have different spatial distributions within Puget Sound in summer (Hauser et al. 2007) and occupy the outer coast of the United States to differing degrees during winter (Krahn et al. 2004). Ford and Ellis (2006) found a correlation between an index of annual abundance of Chinook salmon and temporal differences in survival of the entire southern population. Thus, the different spatial distributions of the pods may be associated with differential access to prey. Nevertheless, the lack of fine-resolution spatial data on prey availability for each pod limits one's ability to test the hypothesis that prey availability affects survival.

Additionally, potential regional differences in contaminant concentrations or composition in the prey consumed by killer whale pods could lead to differences in survival among pods. Pod L (and occasionally pod K) migrate long distances in winter, in some years as far as central California (Krahn et al. 2004). Concentrations of contaminants in salmon from California and Puget Sound or British Columbia may differ. If the concentrations are sufficiently high to affect the health of whales, one might expect the southern resident population to have lower survival than the northern resident population. First, these two whale populations are exposed to different levels of human activity (Krahn et al. 2004). The southern population spends more time near urban areas in Puget Sound, where vessels frequently encounter whales. Research on ambient noise (Holt et al. 2009) and vessel–whale interactions (Noren et al. 2009) suggests that vessels may alter whale behavior, including foraging, and vocalization patterns. Second, concentrations of contaminants in prey consumed by the two populations may differ. The quantity of organic pollutants is several times higher in salmon from Puget Sound than in salmon from more northern waters consumed by the northern resident population (Cullon et al. 2009). Third, the southern population may have higher levels of inbreeding, potentially because of intrapod mating (M. Ford, personal communication). The southern population is smaller than the northern population and went through a population bottleneck in 1950s and 1960s when it was the target of a live-capture fishery. Results of previous research show that these two populations have different fecundity rates; females in the southern population are less productive (Ward et al. 2009). Our findings suggest that, regardless of the mechanism, lower survival is contributing to the relatively low population growth of the southern population over time.

Although we applied the Bayesian hierarchical framework to analyses of structure in the survival of individuals in a population, these techniques are not limited to applications involving social organization or binary data. These methods have been applied to problems with nested variation in a range of disciplines (Gelman & Hill 2006) and may be applied to virtually any ecological data that are clustered on one or more levels.

Acknowledgments

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