Marine Mammal Science

MARINE MAMMAL SCIENCE, 31(4): 1521–1537 (October 2015)

DOI: 10.1111/mms.12241

Habitat use by southern right whales, *Eubalaena australis* (Desmoulins, 1822), in their main northernmost calving area in the western South Atlantic

ELISA SEYBOTH,[1] Universidade Federal do Rio Grande, Instituto de Oceanografia, Laboratório de Ecologia e Conservação da Megafauna Marinha, Rio Grande, Rio Grande do Sul, Brazil; **KARINA R. GROCH,** Projeto Baleia Franca, Centro Nacional de Conservação da Baleia Franca, Imbituba, Santa Catarina, Brazil; **EDUARDO R. SECCHI** and **LUCIANO DALLA ROSA,** Universidade Federal do Rio Grande, Instituto de Oceanografia, Laboratório de Ecologia e Conservação da Megafauna Marinha, Rio Grande, Rio Grande do Sul, Brazil.

ABSTRACT

The subtropical and temperate coastal waters of the western South Atlantic are an important calving ground for southern right whales, *Eubalaena australis*. From 2002 to 2008, data on right whale distribution and habitat characteristics were collected in 14 bays along the coastline of Santa Catarina State, Brazil. Generalized linear models with a negative binomial error distribution were used to determine which environmental (beach morphotype, bay mouth width, bay inclination angle, north-south and east-west wind components), and temporal (month and year) variables best explained the aggregation pattern of individuals. Our results suggested that both cow-calf pairs and adults unaccompanied by calves prefer bays with dissipative beaches, and that cow-calf pairs apparently avoid bays facing southeast during days of strong east-west winds. The number of sightings peaked in September and tended to increase over the study period. One particular embayment (Ribanceira beach) had considerably higher numbers of animals and may be considered a preferred spot in this calving ground. Our findings contribute to a better understanding of the species' habitat use and ecological requirements and should be taken into account if new management measures are implemented to further increase protection of southern right whales in the region.

Key words: distribution, environmental variables, generalized linear models, cetacean, habitat modeling, management, Brazil.

INTRODUCTION

Understanding the relationship between distribution and habitat is an important aspect of determining how to conserve wild populations. It can point to processes and factors influencing habitat use (Redfern *et al.* 2006) and in turn enable better assessment of the potential impacts of human activities on the animals and their habitat (Rowntree *et al.* 2001, Austin 2002).

[1]Corresponding author (e-mail: elisaseyboth@gmail.com).

Cetacean habitat use may be influenced by a variety of environmental (biotic and abiotic) and anthropogenic factors (Borcard *et al.* 1992, Jaquet 1996, Forcada 2002). Most studies, however, have focused on areas where food availability determines animal aggregation patterns (*e.g.,* Cañadas *et al*. 2002, Moore and Laidre 2008, Dalla Rosa *et al*. 2012, Sveegaard *et al*. 2012). In general, baleen whales migrate seasonally between feeding (summering) and breeding (wintering) grounds (Gaskin 1982). Habitat use in the wintering ground, where the animals mate, give birth and nurse their young (Cummings 1985), may be determined by environmental factors that favor calf survival (*e.g.,* Martins *et al*. 2001, Rowntree *et al*. 2001, Elwen and Best 2004*a*).

In their breeding area off South Africa, southern right whales (*Eubalaena australis*) show a preference for coastal areas, and yet favor certain bays or stretches of coastline over others (Best 2000). Gentle slopes, protection from wind and swell, seafloor type, and proximity to freshwater discharge influence their distribution along the coast (Elwen and Best 2004*b*). Freshwater discharge has the potential benefit of facilitating skin exfoliation or loss of external parasites (Elwen and Best 2004*b*). Over smaller spatial scales, sandy bottoms seem to be preferred over rocky bottoms, which could be related either to the sound dampening properties that this floor type provides or to lower risk of injury from rocky projections (Elwen and Best 2004*a*). In addition, cow-calf pairs seem to have a different distribution from adults unaccompanied by calves (*e.g.,* Payne 1986, Best 2000, Elwen and Best 2004*a*). Pregnant females tend to move to nearshore areas to give birth and stay for a postpartum period presumably because of the protection offered by these regions (Burnell and Bryden 1997). Ocean temperature influences prey availability and, therefore, may be one of the factors determining cetacean distribution in feeding areas (*e.g.,* Dalla Rosa *et al*. 2012). However, such a variable may also directly influence cetacean distribution in reproductive areas, as it might affect calf development (Gaskin 1982, Keller *et al*. 2006, Rasmussen *et al*. 2007).

Data on southern right whale distribution along the southern Brazil coast started to be gathered in 1981 (Palazzo and Flores 1998). Sighting data collected since then were useful to identify an area of primary use during the reproductive period (from July to November), which in the year 2000 was declared an environmental protection area (EPA) in Santa Catarina State (Federal Decree of 14 September 2000). The main purpose of the EPA was to give special protection to habitat crucial to the life cycle of the species. However, the factors influencing southern right whale distribution in this area are not known. Identifying the factors that drive habitat selection of adults unaccompanied by calves and cow-calf pairs can be relevant for establishing or refining conservation strategies. Habitat modeling can be a powerful tool for predicting cetacean distribution and understanding the ecological processes involved in habitat selection (Redfern *et al*. 2006).

The goal of this study was to investigate the relationship between southern right whale distribution and environmental and temporal variables and to identify preferred calving areas in southern Brazil. Whaling drastically reduced the population size and distribution to a restricted area along the Santa Catarina coast. As the population recovers from whaling, it is expected to expand and, possibly, reoccupy prewhaling grounds northward to Bahia state (Ellis 1969, Palazzo and Flores 1999). Such an expansion is likely to increase conflicts between southern right whales and human activities along the coast, emphasizing the importance of determining factors that drive habitat use for the species.

Methods

Study Area

The study area encompasses the central-southern sector of Santa Catarina State, southern Brazil (Fig. 1). This coastal region is an important calving ground for southern right whales and is characterized by the presence of many embayments. The surveyed area includes 14 bays located within the EPA.

Data Collection

Right whales were observed from elevated points on shore along the study area between 2002 and 2008, during the reproductive season (July to November). Observers, generally one on each bay, used 12 × 50 binoculars to scan the area from observation sites positioned between 20 and 90 m above sea level, to enable a broad view of the bay. Each observer was responsible for monitoring a bay for a period of up to a month, and then a rotation was performed so that each bay was surveyed by different observers within and between seasons. The searching protocol was to scan the entire area for 10 min followed by a 5 min resting interval. On some occasions, a 50 min focal animal sampling (Altmann 1974) was performed to record animal behavior, followed by a 10 min resting interval, and the continuation of the scans. In such case, at least one 10 min scan was conducted to search for new groups that could have entered the bay during the focal sampling. Whales were tracked in order to avoid multiple counting. On a few occasions, however, it was not possible to be certain about group location. In such cases, the same group may have been resampled within a sampling period and the data mistakenly attributed to separate groups.

Sampling was divided into half-day shifts of monitoring effort. For each shift, information on environmental conditions (cloud cover, visibility, wind direction, and Beaufort sea state) and sightings (number of groups and individuals and group composition) was recorded on standardized worksheets. The positions of the individuals were plotted on nautical charts. Groups were classified as cow-calf pairs, adults unaccompanied by calves (lone adults or groups of multiple adults without a calf), or undetermined (when the observer was unable to determine the composition). Solitary subadults were treated as unaccompanied adults because of the subjectivity involved in determining this class in the absence of a size reference.

Observation effort was halted when environmental conditions deteriorated due to low visibility (<5–6 km), precipitation, or sea state >4 on the Beaufort scale. Sampling periods shorter than 1 h were not included in the data set. The influence of weather conditions (sea state and visibility) on whale's detectability was analyzed by a Kruskal-Wallis test. Considering the results from this test, the 1 h minimum observation time and the broad views of the bays, we assume that all whales present in the bays were detected.

Environmental variables considered as potentially relevant to the distribution of the whales were also recorded, including sea surface temperature (SST), bay morphotype, east-west (E-W) and north-south (N-S) wind components, bay mouth width, and bay orientation angle (Table 1). These last three variables allowed us to assess physiographic features that may protect whales in the bay from wind and swell. Bay mouth width and bay orientation angle were measured using georeferencing tools. Bay mouth width was considered as the length of a line connecting one end of the bay to the other (Fig. 2). Bay orientation angle was assessed using a line perpendicular to

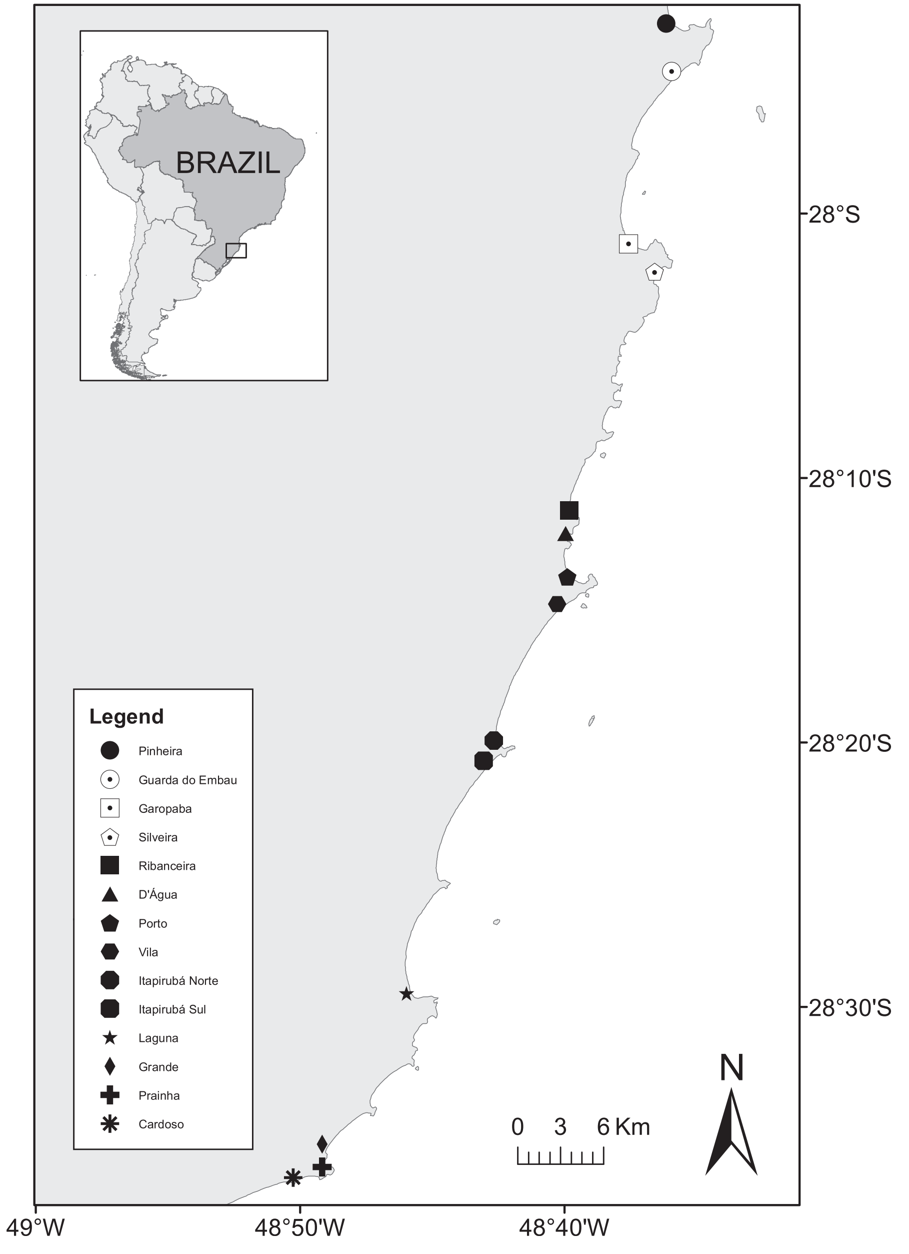

Figure 1. Study area in Santa Catarina State, Brazil. The monitored area is included in the Environmental Protection Area (EPA da Baleia Franca) created specifically to protect the southern right whale, *Eubalaena australis*. Symbols indicate the monitored bays and their colors refer to beach morphotype (black ones are used for dissipative beaches and white ones for intermediate beaches).

Table 1. Covariates included in analyses, with their respective type and data included in the models.

Covariate	Type	Data
Year	Continuous	2002–2008
Month	Continuous	July to November
Morphotype	Categorical	Dissipative and Intermediate
Bay mouth width	Continuous	0.70–12.35 km ($\bar{x}$ = 4.40)
N-S wind component	Continuous	–4–4
E-W wind component	Continuous	–4–4
Bay inclination angle	Continuous	55°–150° ($\bar{x}$ = 102.85°)
SST	Continuous	15.37°C–22.30°C ($\bar{x}$ = 19.10°C)

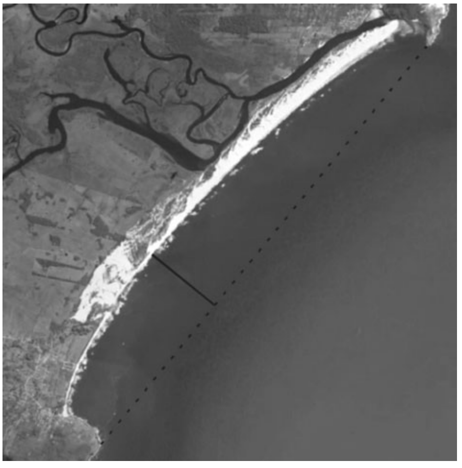

Figure 2. Scheme of the measures for the covariates bay mouth width (dashed line) and bay inclination angle (solid line).

a line across the bay mouth (Fig. 2). Wind components were determined based on the prevailing wind speed and direction during each half-day shift. In quadrants of a compass, the wind direction and speed gave the angle and the length of the vector, respectively. The N-S and E-W components were obtained by trigonometry. Beach morphotype was defined based on a classification system (Silveira *et al.* 2011) that considers beaches as dissipative, intermediate, or reflective (Fig. 3). In general, a dissipative beach has a gentle slope and its wave energy is attenuated by the breaking process along a wide surf zone. Reflective beaches, on the other hand, have a very narrow surf zone, where the wave energy is generally low and the presence of beach cusps is common. Beach cusps are regular longitudinal series of horns and embayments, resulting in an undulating shoreline (Garnier *et al.* 2010). In reflective beaches, the wave energy can be trapped by refraction. Intermediate beaches have narrow surf zones and generally exhibit a sequence of sand or gravel bars, which are submerged embankments built in the breaker zone due to the action of breaking waves and edge-currents (Bharatdwaj 2009). In our study area only dissipative and intermediate types occur (Silveira *et al.* 2011).

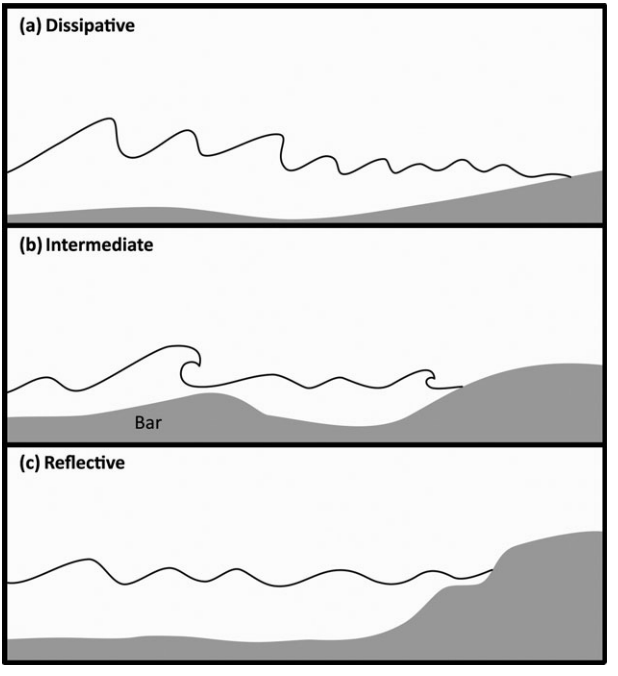

Figure 3. Scheme of the main bay morphotypes: (a) dissipative, (b) intermediate, and (c) reflective. The types in the study region are just dissipative and intermediate.

Monthly SST data with a 4 km resolution were obtained from the MODIS-Aqua satellite (available at http://oceancolor.gsfc.nasa.gov/cms/). Monthly means were used because of the high number of missing daily or weekly values resulting from cloud cover. In addition, given the relatively small size of the study area, satellite SST data did not differ markedly between the bays.

Data Analysis

Count data were modeled using Generalized Linear Models (GLMs) (McCullagh and Nelder 1997) under R software (R Development Core Team 2010) version 2.13.1. Poisson and negative binomial distributions were used to fit models to the data (Zuur *et al*. 2007). The response variable was the number of right whale cow-calf pairs or unaccompanied adults sighted per half-day shift, and the explanatory variables included temporal (month and year) and environmental ones. Of all variables tested, only beach morphotype was included in the models as categorical (Table 1); all others were numerical, and used in their standardized form ($x - \bar{x}/SD[x]$). Quadratic terms for month and year were added in the models to account for nonlinear patterns in relation to the response variable.

Differences in habitat use between cow-calf pairs and adults unaccompanied by calves were examined by fitting separate models for each whale group category. Model selection was based on AIC (Akaike Information Criterion) using a backward stepwise approach (Zuur *et al*. 2009). Model validation followed graphical assessment of standardized residuals of the models that better explained the species distribution (Zuur *et al*. 2009).

Results

Sightings

A total of 10,978 individuals were sighted during 6,196 half-day shifts of monitoring from 2002 to 2008. Half-day shifts lasted from 1 to 6 h ($\bar{x} = 2$ h). In most cases, no whale was sighted, but on one occasion 35 whales were sighted in a shift; a mean of 0.7 cow-calf pairs and 0.3 adults unaccompanied by calves were sighted per half-day shift. As high numbers of whales were rarely observed, possible recounts of the same individuals are unlikely to have led to an inflation of the number of sightings in the bays. In all years, the number of cow-calf pairs was greater than the number of adults unaccompanied by calves. There was no significant influence of sea state ($\chi^2 = 6.64$, df = 4, $P = 0.16$) or visibility conditions ($\chi^2 = 4.40$, df = 4, $P = 0.35$) on the number of sightings.

During the study period, adults unaccompanied by calves left the calving ground before cow-calf pairs. The number of unaccompanied adults declined in October and only two were seen in the study area in November. The number of sightings of cow-calf groups also started to decline in October, but a considerable number of individuals were still present in the bays in November (Table 2). Ribanceira Bay had the highest number of individuals compared to the other bays (Table 3), a pattern that remained throughout the reproductive season.

Model Selection

Data exploration indicated that the explanatory variables month and SST were highly correlated ($r > 0.7$). Therefore, as the latter was based on monthly means, it was not included in the models to avoid issues of collinearity.

The negative binomial distribution fitted better than the Poisson, based on AIC (not presented). Models built with this distribution, and the respective AIC, are shown in Table 4. The selected models in each whale class suggest that there are some similarities of the variables that influence the occurrence and distribution of cow-calf pairs and adults unaccompanied by calves, especially if we considered competing models for unaccompanied adults based on very small AIC differences (see Burnham and Anderson 2002) from the best model (Table 4).

Table 2. Number of southern right whale cow-calf pairs, adults unaccompanied by calves and from undetermined class sighted per month during the breeding season, from 2002 to 2008.

Whale class	July	August	September	October	November
Cow-calf	67	970	1,759	1,250	290
Adults unaccompanied by calves	208	994	819	58	2
Undetermined	30	69	123	3	0

Table 3. Monitored bays and the related environmental characteristics, total effort and average number of sightings considering data from 2002 to 2008.

Bay	Morphotype	Mouth width (km)	Inclination angle (°)	Effort (half-day shifts)	Mean number (per half-day shift) (±SD)
Cardoso	Dissipative	1.63	155	317	1.03 (±2.42)
Prainha	Dissipative	2.26	50	77	1.41 (±2.23)
Praia Grande	Dissipative	4.48	117	110	0.89 (±2.12)
Laguna	Dissipative	8.04	100	583	0.82 (±1.71)
Itapirubá Sul	Dissipative	10.19	112	771	1.01 (±2.00)
Itapirubá Norte	Dissipative	12.35	108	772	1.63 (±2.94)
Vila	Dissipative	0.62	134	816	1.14 (±2.23)
Porto	Dissipative	1.65	60	313	0.43 (±1.14)
D'Água	Dissipative	0.7	120	302	2.50 (±3.10)
Ribanceira	Dissipative	4.5	108	736	6.73 (±8.49)
Silveira	Intermediate	1.5	127	393	0.62 (±1.62)
Garopaba	Intermediate	5.96	60	523	1.30 (±2.49)
Guarda do Embaú	Intermediate	7.08	115	172	0.44 (±1.25)
Pinheira	Dissipative	2.26	93	365	0.40 (±1.52)

Parameter Estimates

Parameter estimates of the selected models for cow-calf pairs and unaccompanied adults are listed in Tables 5 and 6, respectively. The intercept provides an estimate of the log-density (*i.e.*, expected number of whales per half-day shift) for a dissipative beach type when all numeric variables are set equal to zero; that is, at their mean (used in standardization) for each whale class. For cow-calf pairs and for adults unaccompanied by calves, models indicate that there were fewer right whale sightings at intermediate than dissipative beaches and that the number of whales sighted increased over time (Fig. 4). Our models also show that during the reproductive season, whale numbers increase until they reach a peak in September, and then start to decrease (Fig. 5).

Some variables were selected only in the model for cow-calf pairs. The north-south wind component alone, with a negative coefficient value, indicates that fewer cow-calf pair sightings occurred when this wind component was strong. The interaction term of bay angle with the east-west wind component, with its constitutive terms and estimated coefficients, indicate that larger bay angles had a negative influence on whale numbers, which increased with stronger east-west winds. That is, lower numbers of cow-calf pairs were observed at bays facing south/southeast when wind was blowing east-west. Bay angle in the selected model for adults unaccompanied by calves resulted in a positive coefficient, but caution is necessary in interpreting this variable as the effect is small and nonsignificant.

Discussion

Right whale distribution was nonuniform among different bays in the Santa Catarina calving area during the study period, as shown by the different numbers of individuals observed at these sites. Elwen and Best (2004*a*) reported a similar pattern

Table 4. Models generated for cow-calf pairs and for adults unaccompanied by calves in the stepwise backwards model selection with their respective AIC. The selected model in each whale class is in bold. ".q" indicates quadratic terms for some explanatory variables and "*" refers to interactions between explanatory variables. morphotype = beach morphotype; bayangle = bay orientation angle; mouth = bay mouth width; east_west = east-west wind component; north_south = north-south wind component.

Class	Model	AIC	ΔAIC
Cow-calf pairs	year + year.q + month.q + month + morphotype + bayangle * mouth + bayangle * north_south + bayangle * east_west + mouth * north_south + mouth * east_west	11,892	7
	year + year.q + month.q + month + morphotype + bayangle * mouth + bayangle * east_west + mouth * north_south + mouth * east_west	11,890	5
	year + year.q + month.q + month + morphotype + bayangle * mouth + bayangle * east_west + mouth * north_south	11,888	3
	year + year.q + month.q + month + morphotype + bayangle * mouth + bayangle * east_west + north_south	11,887	2
	year + year.q + month.q + month + morphotype + mouth + bayangle * east_west + north_south	11,887	2
	year + year.q + month.q + month + morphotype + bayangle * east_west + north_south	**11,885**	0
	year + year.q + month.q + month + morphotype + bayangle * east_west	11,890	5
	year + year.q + month.q + month + morphotype + bayangle + east_west	11,892	7
	year + year.q + month.q + month + morphotype + bayangle	11,897	12
	year + year.q + month.q + month + morphotype	11,903	18
	year + year.q + morphotype	12,235	350
	year + year.q	12,268	383
Adults unaccompanied by calves	year + year.q + month.q + month + morphotype + bayangle * mouth + bayangle * north_south + bayangle * east_west + mouth * north_south + mouth * east_west	7,410.1	10.3
	year + year.q + month.q + month + morphotype + bayangle * mouth + bayangle * north_south + mouth * north_south + mouth * east_west	7,408.1	8.3
	year + year.q + month.q + month + morphotype + bayangle * mouth + bayangle * north_south + mouth * east_west	7,406.4	6.6
	year + year.q + month.q + month + morphotype + bayangle * mouth + north_south + mouth * east_west	7,404.6	4.8

(Continued)

Table 4. *(Continued)*

Class	Model	AIC	ΔAIC
	year + year.q + month.q + month + morphotype + bayangle * mouth + mouth * east_west	7,402.6	2.8
	year + year.q + month.q + month + morphotype + bayangle * mouth + east_west	7,401.3	1.5
	year + year.q + month.q + month + morphotype + bayangle * mouth	7,400.6	0.8
	year + year.q + month.q + month + morphotype + bayangle + mouth	7,400.7	0.9
	year + year.q + month.q + month + morphotype + bayangle	**7,399.8**	0
	year + year.q + month.q + month + morphotype	7,400	0.2
	year + year.q + month.q + month	7,422.8	23
	month.q + month	7,457.8	58

Table 5. Estimates and *P*-values of coefficients for selected GLM fitted to right whale cow-calf pairs. ".q" indicates quadratic terms for some explanatory variables and "*" refers to interactions between explanatory variables. morphotype = beach morphotype; bayangle = bay orientation angle; mouth = bay mouth width; east_west = east-west wind component and north_south = north-south wind component.

Parameter	Estimate	*P*
intercept	−0.09254	0.10994
year	0.50607	$<2 \times 10^{-16}$
year.q	0.1985	7.99×10^{-9}
month.q	−0.67305	$<2 \times 10^{-6}$
month	0.04329	0.22218
morphotype (intermediate)	−0.82048	$<2 \times 10^{-16}$
bayangle	−0.09448	0.00432
north_south	−0.0429	0.01402
east_west	−0.01673	0.51222
bayangle:east_west	−0.05643	0.00725

Table 6. Estimates and *P*–values of coefficients for selected GLM fitted to right whale adults unaccompanied by calves sightings. ".q" indicates quadratic terms for some explanatory variables. morphotype = beach morphotype and bayangle = bay orientation angle.

Parameter	Estimate	*P*
intercept	−130,265	$<2 \times 10^{-16}$
year	0.17772	4.43×10^{-6}
year.q	0.2361	4.79×10^{-8}
month.q	−0.92731	$<2 \times 10^{-16}$
month	−169,879	$<2 \times 10^{-16}$
morphotype (intermediate)	−0.51201	6.96×10^{-6}
bayangle	0.06305	0.126

in South Africa, where animals were considered to have a discontinuous but predictable distribution. Moreover, other studies have shown that in calving areas some coastal regions seem to be preferred by southern right whales (Best 2000).

It is worth emphasizing, however, that the greater number of cow-calf pairs (n = 4,336) sighted during the study period, compared to the total number of adults unaccompanied by calves (n = 2,081), demonstrates the importance of this area as a calving site. Although a birthing event has not been observed in Santa Catarina, sightings of small calves, sometimes with fetal folds, are evidence that births occur in this area. The inversion of the ratio of cow-calf pairs to adults unaccompanied by calves between August and September represents further evidence (Table 2). In fact, some of the groups classified as unaccompanied adults in the beginning of the season were likely to be pregnant females. Witnessing a right whale birth is rare (Foley *et al.* 2011), and there is no observation of such an event for southern right whales. For North Atlantic right whales (*Eubalaena glacialis*), some evidence of births has been recorded but only after many years of systematic aerial surveys (Zani *et al.* 2008, Patrician *et al.* 2009, Foley *et al.* 2011). Moreover, the conspicuous increase in the ratio of cow-calf pairs to adults unaccompanied by calves from September to October (Table 2) suggests that unaccompanied adults leave the area earlier than cow-calf pairs.

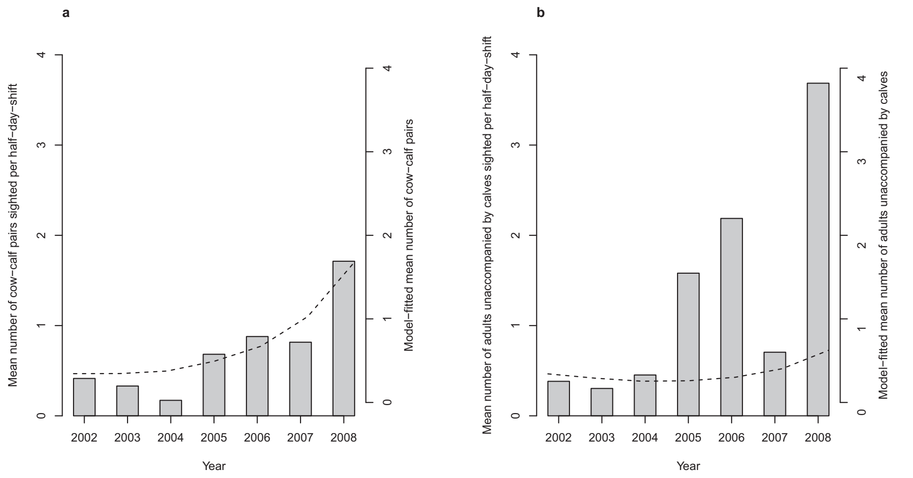

Figure 4. Mean number of southern right whale cow-calf pairs (a) and adults unaccompanied by calves (b) sighted per half-day shift along the coast of Santa Catarina state between 2002 and 2008 (bars), and the corresponding model-fitted values (dashed lines).

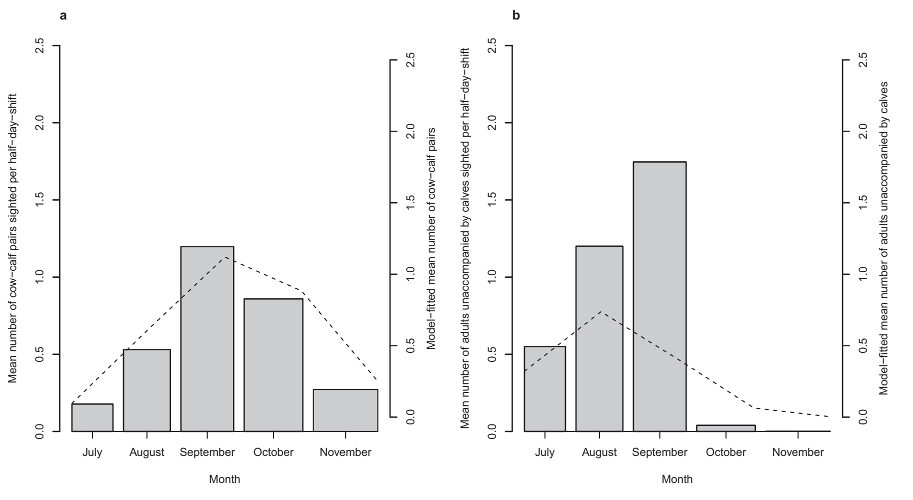

Figure 5. Mean number of southern right whale cow-calf pairs (a) and adults unaccompanied by calves (b) sighted per half-day shift during the breeding season along the coast of Santa Catarina state (bars), and the corresponding model-fitted values (dashed lines).

The preference for specific bays by individuals during the study period might indicate a change in the distribution pattern of this population. In early years (from 1986 to 2003) Laguna Bay stood out due to its high number of animals (Groch 2000, 2005). Our research shows that, of the 14 bays studied, Ribanceira, Praia D'Água, Itapirubá Norte, and Itapirubá Sul were the preferred bays from 2002 to 2008. Changes might be related to factors such as individual preference, social cohesion, or habitat disturbance (Rowntree *et al.* 2001). Alternatively, they could be a result of the increasing number of animals using Santa Catarina as a calving ground, since the population increased at a rate of 12% from 1987 to 2010 (IWC 2012).

Many studies have shown differences in distribution between southern right whale cow-calf pairs and adults unaccompanied by calves (*e.g.*, Payne 1986, Best 2000, Rowntree *et al*. 2001, Elwen and Best 2004*a*). In general, cow-calf pairs are found in shallower waters and in locations that offer higher protection from unfavorable sea conditions. Both adults unaccompanied by calves and cow-calf pairs seem to prefer sandy instead of rocky beaches. In our study, the higher concentration of whales in some bays, regardless of the class, suggests that similar environmental or behavioral conditions might influence the distribution of all classes, at least at larger spatial scales. The presence of cow-calf pairs may attract unaccompanied adults waiting for the opportunity to mate with the cow or with other females in the area, especially considering that mating behavior has been observed on some occasions. In addition, some females may arrive at the breeding ground accompanied by their subadult offspring, abandoning it afterwards, as it has been documented at Península Valdés (Thomas and Taber 1984). Nevertheless, our models do support some differences between unaccompanied adults and cow-calf pairs.

The temporal variables year and month presented opposite signals for the quadratic terms. The positive signal for year indicates that the relationship between these variables could be represented by a curve with a concave pattern. In fact, the total number of sightings for both cow-calf pairs and adults unaccompanied by calves decreased from 2002 to 2003. In 2004, sightings started to increase, reaching a maximum in 2007 and 2008, the last years included in our analyses. The general increase in sighting numbers in the latter years agrees with the population recovery observed in this calving area (Groch *et al*. 2005). The negative signal in the quadratic term for month was expected, as it is known that in the initial months of monitoring individuals were just starting to arrive in this calving area, until a peak was reached in September. During the last months of the reproductive season, individuals started their migration back to the feeding areas.

Regarding beach morphotype, individuals preferred dissipative rather than intermediate beaches, probably because of the gentler slope of dissipative beaches, which may be particularly favorable to cow-calf pairs. The shallow depths close to shore at dissipative beaches may help avoid male mating attempts and offer fewer directions from which either predators or conspecifics can approach (Elwen and Best 2004*a*). Because the exact position of the observed individuals was not recorded in our study, it is not possible to investigate differences between the spatial distribution of adults unaccompanied by calves and cow-calf pairs inside the bays. Groch (2000) reported that southern right whales were seen in the area more frequently within the 5 m isobath than the 10 and 20 m isobaths, behind the breaking waves. This is similar to the distribution pattern of right whale mothers with calves observed off Argentina (Payne 1986) and South Africa (Best 2000).

In the best model for cow-calf pairs, the east-west wind component, bay orientation angle and their interaction term suggest that whales may avoid bays facing southeast during strong winds from the east-west component. The north-south wind component also had a negative effect on cow-calf numbers, further emphasizing the influence of variables related to protection against wind and swell. For unaccompanied adults, such effects seem less important based on the best model, although competing models also included these variables. Additional studies to investigate whale movements using satellite telemetry would help to understand whale behavior and confirm whether they tend to stay away from bays during rough weather conditions.

Some variables that are thought to influence right whale distribution in other reproductive areas could not be included in our models because of study area characteristics. This is the case, for instance, for seafloor type and proximity to freshwater discharge. The dominance of sedimentary floors in the study area (Santos 2008) and the difficulties in defining important freshwater runoff due to flow variability prevented us from assessing the relevance of these variables in determining whale preference among bays. Furthermore, kelp gull (*Larus dominicanus*) harassment may influence right whale behavior and distribution at Península Valdés, Argentina (Rowntree *et al*. 1998, Sironi *et al*. 2009). This kind of event is considered relatively rare in our study area, with only two attacks observed in the region (Groch 2001).

Behavioral and cultural factors may also influence cetacean distribution; therefore, their inclusion would be required for a complete understanding of habitat use (Hastie *et al*. 2004). Behavioral influences on habitat use may include foraging, sexual (mating and courtship), or social contexts guiding species distribution (Tyack 2002). Cultural aspects, such as philopatry, are transmitted through maternal fidelity to a specific location within the reproductive area (Clapham *et al*. 2008). Although right whales seem to have philopatric plasticity (*e.g*., Rowntree *et al*. 2001), it could still contribute towards the use of preferential areas. Site fidelity of southern right whales from Península Valdés to feeding grounds seems to last for several generations (Valenzuela *et al.* 2009) and, added to the species' natal philopatry (*e.g.*, Best 2000), such factors could restrict the animals' ability to use alternative reproductive and feeding grounds other than those learned from their mothers. Although information on site fidelity of the population breeding off Brazil is limited, 10% of the individuals registered in the Brazilian Right Whale Catalogue until 2003 have been resighted in the reproductive area (Groch *et al*. 2005).

The growth of this population and its expected habitat expansion will likely increase interactions with human activities. Industrial developments are a cause of concern. The ongoing expansion of Imbituba Harbor, in particular, is likely to affect right whale distribution because of the increase in vessel traffic and noise in the area. Such environmental disturbances are known to have influenced bottlenose dolphin populations in other areas (*e.g.,* Wells and Scott 1997, Nowacek *et al*. 2001) and southern right whales in the Península Valdés calving area (Rowntree *et al*. 2001). Cetacean habitat use should be investigated prior to industrial development, so that changes can be detected and appropriate mitigation measures implemented (Macleod *et al*. 2003).

Overall, our findings on whale distribution highlight the preference for specific bays within the area of largest concentration of the species in Brazilian waters. We also show that some temporal and environmental variables influence the habitat used by both adults unaccompanied by calves and cow-calf pairs. Such information can be useful to environmental managers aiming to provide higher protection to the most critical bays for the conservation of this southern right whale population. It may also help identify relevant areas in a scenario of population expansion, assuming that the same ecological requirements will determine habitat selection in newly occupied areas.

The continued monitoring of the species in the southern Brazil calving area is necessary to provide further information about the environmental and behavioral factors that determine habitat use patterns, and to detect potential changes in whale distribution due to industrial and naval development in an area that represents critical habitat for this population.

Acknowledgments

We are grateful to all observers from Projeto Baleia Franca involved in data collection. We also thank Paul Kinas and Artur Andriolo for their valuable comments and suggestions to the earlier versions of this manuscript. Funding from PETROBRAS Brazilian Oil Company to Projeto Baleia Franca was vital for data collection. Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided a scholarship to ES and a fellowship to ERS (PQ 307846/2014-8). KRG was supported by Comissão de Aperfeiçoamento de Pessoal (CAPES–Ministry of Education) and CNPq with a Ph.D. scholarship from 2001 to 2005. This is a contribution of the Research Group "Ecologia e Conservação da Megafauna Marinha–EcoMega/CNPq."

Literature Cited

Altmann, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49:27–267.

Austin, M. P. 2002. Spatial prediction of species distribution: An interface between ecological theory and statistical modeling. Ecological Modelling 157:101–118.

Best, P. B. 2000. Coastal distribution, movements and site fidelity of right whales *Eubalaena australis* off South Africa, 1969–1998. South African Journal of Marine Science 22:43–55.

Bharatdwaj, K. 2009. Physical geography: A landscape appreciation. Discovery Publishing House, New Delhi, India.

Borcard, D., P. Legendre and P. Dapreau. 1992. Partialling out the spatial component of ecological variation. Ecology 73:1045–1055.

Burnell, S. R., and M. Bryden. 1997. Coastal residence periods and reproductive timing in southern right whales, *Eubalaena australis*. Journal of Zoology 241:613–621.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer, New York, NY.

Cañadas, A., R. Sagarminaga and S. García-Tiscar. 2002. Cetacean distribution related to depth and slope in the Mediterranean waters off southern Spain. Deep-sea Research Part I 49:2053–2073.

Clapham, P. J., A. Aguilar and L. Hatch. 2008. Determining spatial and temporal scales for management: Lessons from whaling. Marine Mammal Science 24:183–201.

Cummings, W. C. 1985. Right whales, *Eubalaena glacialis* (Müller, 1776) and Eubalaena australis (Desmoulins, 1822). Pages 275–304 *in* S. H. Ridgway and S. R. Harrison, eds. Handbook of marine mammals. Volume 3. The sirenians and baleen whales. Academic Press, London, U.K.

Dalla Rosa, L., J. K. B. Ford and A. W. Trites. 2012. Distribution and relative abundance of humpback whales in relation to environmental variables in coastal British Columbia and adjacent waters. Continental Shelf Research 36:89–104.

Ellis, M. 1969. A baleia no Brasil Colonial [The whale in colonial Brazil]. Melhoramentos, São Paulo, Brazil.

Elwen, S. H., and P. B. Best. 2004*a*. Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa I: Broad scale patterns. Marine Mammal Science 20:567–582.

Elwen, S. H., and P. B. Best. 2004*b*. Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa II: Within bay distribution. Marine Mammal Science 20:583–601.

Foley, H. J., R. C. Holt, R. E. Hardee, *et al*. 2011. Observations of a western North Atlantic right whale (*Eubalaena glacialis*) birth offshore of the protected southeast U.S. critical habitat. Marine Mammal Science 27:E234–E240.

Forcada, J. 2002. Distribution. Pages 327–333 *in* W. F. Perrin, B. Würsig and J. G. M. Thewissen, eds. Encyclopedia of marine mammals. Academic Press, London, U.K.

Garnier, R., M. Ortega-Sánchez, M. A. Losada, A. Falqués and N. Dodd. 2010. Beach cusps and inner surf zone processes: Growth or destruction? A case study of Traflagar Beach (Cádiz, Spain). Scientia Marina 74:539–553.

Gaskin, D. E. 1982. The ecology of whales and dolphins. Heinemann, London, U.K..

Groch, K. R. 2000. Ocupação preferencial de áreas de concentração pela baleia franca austral, *Eubalaena australis* (Desmoulins, 1822) (Cetacea, Mysticeti), no litoral sul do Brasil [Preferred occupation of concentration areas for the southern right whale, *Eubalaena australis* (Desmoulins, 1822) (Cetacea, Mysticeti), on the southern coast of Brazil]. M.Sc. thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. 58 pp.

Groch, K. R. 2001. Cases of harassment by kelp gulls (*Larus dominicanus*) on right whales (*Eubalaena australis*) in southern Brazil. Biotemas 14:147–156.

Groch, K. R. 2005. Biologia populacional e ecologia comportamental da baleia franca austral, *Eubalaena australis* (Desmoulins, 1822) (Cetacea, Mysticeti), no litoral sul do Brasil [Population biology and behavioral ecology of the southern right whale *Eubalaena australis* (Desmoulins, 1822) (Cetacea, Mysticeti), on the southern coast of Brazil]. Ph.D. thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. 168 pp.

Groch, K. R., J. T. Palazzo Jr., P. A. C. Flores, F. R. Adler and M. E. Fabian. 2005. Recent rapid increases in the right whale (*Eubalaena australis*) population off southern Brazil. Latin American Journal of Aquatic Mammals 4:41–47.

Hastie, G. D., B. Wilson, L. J. Wilson, K. M. Parsons and P. M. Thompson. 2004. Functional mechanisms underlying cetacean distribution patterns: Hotspots for bottlenose dolphins are linked to foraging. Marine Biology 144:397–403.

IWC (International Whaling Commission). 2012. Report of the workshop on the assessment of southern right whales. SC/64/Rep5. 34 pp.

Jaquet, N. 1996. How spatial and temporal scales influence understanding of sperm whale distribution: A review. Mammal Review 26:51–665.

Keller, C. A., L. I. Ward-Geiger, W. B. Brooks, C. K. Slay, C. R. Taylor and B. J. Zoodsma. 2006. North Atlantic right whale distribution in relation to sea-surface temperature in the southeastern United States calving grounds. Marine Mammal Science 22:426–445.

Macleod, K., M. P. Simmonds and E. Murray. 2003. Summer distribution and relative abundance of cetacean populations off north-west Scotland. Journal of the Marine Biological Association of the United Kingdom 83:1187–1192.

Martins, C. C. A., M. E. Morete, M. H. E. Coitinho, A. Freitas, E. R. Secchi and P. G. Kinas. 2001. Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground. Memoirs of the Queensland Museum 47:563–570.

McCullagh, P., and J. A. Nelder. 1997. Generalized linear models. Chapman & Hall/CRC, Boca Raton, FL.

Moore, S. E., and K. L. Laidre. 2008. Trends in sea ice cover within habitats used by bowhead whales in the western Arctic. Ecological Applications 16:932–944.

Nowacek, S. M., R. S. Wells and A. R. Solow. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Marine Mammal Science 17:673–688.

Palazzo, J. T., Jr., and P. A. C. Flores. 1998. Right whales *Eubalaena australis* in southern Brazil: A summary of current knowledge and research needs. Paper submitted to the IWC Scientific Committee SC/M98/RW14.

Palazzo, J. T., Jr., and P. A. C. Flores. 1999. Plano de ação para a conservação da baleia franca, *Eubalaena australis*, no estado de Santa Catarina [Action plan for the conservation of the right whale, *Eubalaena australis*, in the state of Santa Catarina]. Projeto Baleia Franca–IWC/Brasil, Imbituba, Brazil. 59 pp.

Patrician, M. R., I. S. Biedron, H. C. Esch, *et al.* 2009. Evidence of a North Atlantic right whale calf (*Eubalaena glacialis*) born in northeastern U.S. waters. Marine Mammal Science 25:462–477.

Payne, R. 1986. Long term behavioral studies of the southern right whale (*Eubalaena australis*). Report of the International Whaling Commission (Special Issue 10):161–167.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasmussen, K., D. Palacios, J. Calambokidis, *et al*. 2007. Southern Hemisphere humpback whales wintering off Central America: Insights from water temperature into the longest mammalian migration. Biology Letters 3:302–305.

Redfern, J. V., M. C. Ferguson, E. A. Becker, *et al*. 2006. Techniques for cetacean-habitat modeling. Marine Ecology Progress Series 310:271–295.

Rowntree, V. J., P. McGuiness, K. Marshall, R. Payne, M. Sironi and J. Seger. 1998. Increased harassment of right whales (*Eubalaena australis*) by kelp gulls (*Larus dominicanus*) at Península Valdés, Argentina. Marine Mammal Science 14:99–115.

Rowntree, V. J., R. S. Payne and D. M. Schell. 2001. Changing patterns of habitat use by southern right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina, and their long-range movements. Journal of Cetacean Research and Management (Special Issue 2):133–143.

Santos, D. P. D. 2008. Cartas de sensibilidade ambiental para a porção norte da Bacia de Pelotas, estado de Santa Catarina, Brasil [Maps of environmental sensitivity for the northern portion of the Pelotas Basin, state of Santa Catarina, Brazil]. M.Sc. thesis, Universidade Federal do Rio Grande, Rio Grande, Brazil. 131 pp.

Silveira, L. F., A. H. F. Klein and M. G. Tessler. 2011. Morphodinamical classification of beaches from Santa Catarina State and north coast of São Paulo using remote sensing. Brazilian Journal of Aquatic Science and Technology 15(2):13–28.

Sironi, M., V. J. Rowntree, C. T. Snowdon, L. Valenzuela and C. Marón. 2009. Kelp gulls (*Larus dominicanus*) feeding on southern right whales (*Eubalaena australis*) at Península Valdés, Argentina: Updated estimates and conservation implications. Paper SC/61/BRG19 presented to the International Whaling Commission Scientific Committee. 12 pp.

Sveegaard, S., J. Nabe-Nielsen, K. Staehr, T. F. Jensen, K. N. Mouritsen and J. Teilmann. 2012. Spatial interactions between marine predators and their prey: Herring abundance as a driver for the distributions of mackerel and harbor porpoise. Marine Ecology Progress Series 468:245–253.

Thomas, P. O., and S. M. Taber. 1984. Mother-infant interaction and behavioral development in the southern right whales, *Eubalaena australis*. Behavior 88:42–80.

Tyack, P. L. 2002. Behavior, overview. Pages 101–108 *in* W. F. Perrin, B. Würsig and J. G. M. Thewissen, eds. Encyclopedia of marine mammals. Academic Press, London, U.K.

Valenzuela, L. O., M. Sironi, V. J. Rowntree and J. Seger. 2009. Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). Molecular Ecology 18:782–791.

Wells, R. S., and M. D. Scott. 1997. Seasonal incidence of boat strikes on bottlenose dolphins near Sarasota, Florida. Marine Mammal Science 13:475–480.

Zani, M. A., K. D. Taylor and S. D. Kraus. 2008. Observation of a right whale (*Eubalaena glacialis*) birth in the coastal waters of the southeast United States. Aquatic Mammals 34:21–24.

Zuur, A. F., E. N. Ieno and G. M. Smith. 2007. Analysing ecological data. Springer, New York, NY.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.

Received: 11 December 2013
Accepted: 22 April 2015