Environment-driven changes in terrestrial habitat use and distribution of the Galapagos sea lion

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ABSTRACT: Understanding habitat use patterns of marine apex predators is of paramount importance for the effective design of conservation plans. Due to their amphibious life cycle, pinnipeds are one of the most vulnerable groups to habitat loss and degradation. Reducing knowledge gaps that still exist regarding temporal changes in tropical pinniped habitat use is therefore of particular importance for conservation efforts. We analyzed terrestrial habitat use phenology of a tropical otariid, the Galapagos sea lion *Zalophus wollebaeki*. Regular land-based censuses were carried out in Wreck Bay of San Cristóbal Island, Galapagos, between 2008 and 2012 to explore seasonal changes in sea lion abundance, distribution, and preferences among different habitat types. A daily cycle of haul-out patterns was observed. Animals aggregated on sandy beaches during the coldest periods of the day and were more abundant on rocky and artificial structures when air temperature was warmer. The use of artificial floating platforms as resting places by *Z. wollebaeki* was described for the first time and linked to environmental variability, suggesting that this may be a successful management tool for pinnipeds inhabiting low latitudes. Further, this species demonstrated seasonal distribution changes, aggregating in high densities during warm seasons and maintaining more even distributions during cold seasons. Sea surface temperature, air temperature, and the onset of the breeding season were the variables that most significantly influenced haul-out patterns of *Z. wollebaeki*, indicating that this species can adapt to changing environmental conditions by displaying a high degree of plasticity regarding its distribution and terrestrial microhabitat preferences.

KEY WORDS: *Zalophus wollebaeki* · Sea lion · Pinnipeds · Haul-out patterns · Galapagos · Habitat use · Environmental variability

INTRODUCTION

Marine ecosystems today are threatened by an increasing array of anthropogenic impacts that lead to multiple perturbations. Habitat destruction and degradation are among the most serious threats impacting coastal systems (Kappel 2005). Marine apex predators play an important role in these ecosystems. As top-down regulators of the food web, they have a key ecological function, the loss of which can result in cascading effects throughout ecosystems and on a global scale (Myers et al. 2007). The conservation of these species is therefore of paramount importance to preserve the integrity of marine

ecosystems (Yodzis 2001, Baum & Worm 2009). In recent decades, many studies have focused on understanding how apex predators respond to natural and anthropogenic perturbations (e.g. Hindell et al. 2003, Rosa & Seibel 2008).

Pinnipeds are top predators in coastal areas and depend on terrestrial habitats or ice for breeding, molting, and raising their young (Bartholomew 1970, Riedman 1989). Due to their amphibious life-cycle, pinnipeds are particularly vulnerable to terrestrial habitat loss and degradation. Numerous pinniped populations have declined over the last century, and some species have become Extinct (*Zalophus japonicus*, *Monachus tropicalis*) or Critically Endangered (e.g. *M. monachus*, *M. schauinslandi*). As a result, awareness and concern regarding the status and conservation of seals and sea lions throughout the world has grown steadily in recent years (Costa et al. 2006).

Habitat selection is a hierarchical process composed of several innate and learned behavioral decisions made by individuals regarding their habitat preferences at different environmental scales (Hutto 1985). Potential drivers for terrestrial habitat selection in pinnipeds generally include predation risk and availability of shelter zones, proximity to feeding grounds, and the presence of suitable breeding and resting sites (Sigler et al. 2004, González-Suárez & Gerber 2008, Womble et al. 2009). Nonetheless, various studies on temperate species have revealed that terrestrial habitat use patterns can vary depending on changing environmental parameters (Pauli & Terhume 1987, Jemison et al. 2001).

As endotherms, pinnipeds experience thermal stress if temperatures rise above certain critical limits and they must therefore maintain a constant internal temperature in both aquatic and terrestrial environments. Pinnipeds are adapted to the aquatic environment, having developed several morphological features to reduce heat loss when foraging in cold waters. Conversely, they are exposed to solar radiation and absorb heat directly through their skin when resting on land. The warming of the surrounding substrates reduces the heat gradient and minimizes heat loss, even adding heat gain through conduction (Campagna & Le Boeuf 1988, Norris et al. 2010). Thus, the thermoregulation response is especially challenging for pinnipeds due to the differences in thermal fluxes in both environments and also because their large body size limits the effectiveness of surface heat loss (Norris et al. 2010). Behavioral responses such as the thermoregulation mechanism are known to be important drivers of haul-out patterns in many temperate pinniped species (White & Odell 1971, Witthow et al. 1971, Odell 1974, Campagna & Le Boeuf 1988, Francis & Boness 1991, Twiss et al. 2002). However, little is known about temporal variations in haul-out behavior and thermoregulation of pinnipeds inhabiting low latitudes.

Among pinnipeds, tropical otariids are particularly dependent on terrestrial habitat, as they have extended lactation periods of up to 3 yr due to food scarcity (Elorriaga-Verplancken 2009, Villegas-Amtmann et al. 2009). Two endemic species of otariids, the Galapagos sea lion (GSL) *Zalophus wolle-baeki* and the Galapagos fur seal *Arctocephalus galapagoensis*, live under such conditions in the Galapagos Archipelago. Morphological, physiological, and behavioral adaptations have allowed them to survive in this environment, where they face a periodic lack of feeding resources (Villegas-Amtmann et al. 2009, Jeglinski et al. 2012, Páez-Rosas et al. 2012).

The GSL is found around all major islands of the Galapagos, with the larger colonies located in the South and East of the archipelago. The species was listed as Endangered in the Red List of Threatened Species by the International Union for Conservation of Nature (IUCN) due to a large population reduction of approximately 50% over the past 30 yr (Aurioles & Trillmich 2008). Among the major threats are introduction of new diseases through human and animal contact (i.e. cats, dogs, rats), bycatch and entanglement, marine pollution, and habitat loss and degradation. The negative consequences of anthropogenic disturbances may be amplified by acting synergistically with El Niño-Southern Oscillation (ENSO) events that occur periodically in the Galapagos, leading to a lack of feeding resources in the marine environment (Trillmich & Limberger 1985, Salazar 2003, Palacios 2004, Alava & Salazar 2006, Alava et al. 2011, Brock et al. 2013, Hanna & Cardillo 2013).

Today, the GSL is protected within the Galapagos Marine Reserve and is the focus of conservation efforts of many local and international organizations. One of these projects aimed to provide undisturbed resting sites and to reduce anthropogenic disturbances by installing 3 floating platforms in Wreck Bay (WB) on San Cristóbal Island, where the presence of invasive species and the recent habitat degradation represent major threats to the sea lion population. This is an innovative wildlife management tool that could bring potential benefits for the conservation of this Endangered species. However, knowledge is still lacking about the temporal dynamics of habitat use patterns in tropical pinnipeds, which makes it difficult to evaluate and

improve these kinds of management and conservation actions.

In the present study, we aim to reduce existing knowledge gaps by investigating the patterns and phenology of terrestrial habitat use and movements of GSL in WB at different temporal scales. Specifically, we aim to explore changes in abundance, distribution, and terrestrial microhabitat preferences at a seasonal and daily scale and test whether the observed changes are driven by the high environmental variability of the Galapagos Islands.

MATERIALS AND METHODS

Study area

The study was conducted in WB on San Cristóbal Island (0° 54′ 8.1″ S, 89° 36′ 44.1″ W), a long-established breeding and resting site for GSL. Five beaches are found in WB: Zona Naval (ZN), Los Marinos (LM), Playa de Oro (PO), Playa Mann (PM), and Carola (CA) (Fig. 1). The main beaches are separated by rocky areas. Two artificial wooden floating platforms (25 m^2) and numerous small boats in WB serve as resting places for the sea lions (boats and platforms are henceforth referred to as 'artificial structures').

Data collection

From 2008 to 2012, a total of 455 land-based surveys were conducted, in which the total number of animals, age class, and sex were recorded according to the classification by Wolf et al. (2005). Between May and August 2011, we complemented these data with a total of 486 regular censuses (n = 54) in each of the 9 study sites (5 sandy beaches, 3 rocky areas, and artificial structures) twice per day to account for daily variation: at sunrise (06:00 h) to observe the nocturnal behavior of the species with a minimum degree of disturbance, and 1 h after midday (13:00 h) to observe behavior during periods of maximum air temperature. In total, 941 censuses were included in the analysis. For each survey, we recorded air temperature, tide level, and weather conditions. Weather conditions were defined using a 3-level scale (1 = sunny with no clouds; 2 = sky partially covered; 3 = sky completely covered). Sea surface temperature (SST) was obtained from the National Oceanic and Atmospheric Administration website (www.noaa.gov).

Data analysis

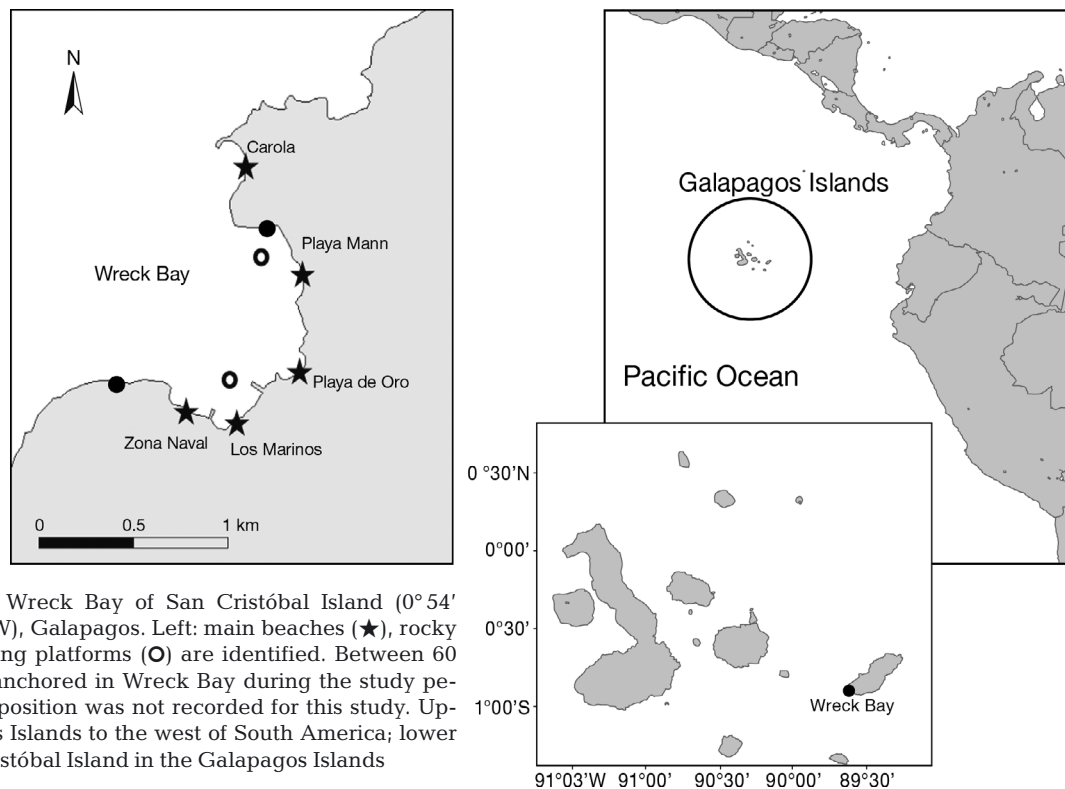To determine the factors that influence changes in sea lion distribution and habitat preferences, we ap-

Fig. 1. Study area: Wreck Bay of San Cristóbal Island (0° 54′ 8.1″ S, 89° 36′ 44.1″ W), Galapagos. Left: main beaches (★), rocky areas (●), and floating platforms (O) are identified. Between 60 and 80 boats were anchored in Wreck Bay during the study period but their exact position was not recorded for this study. Upper right: Galapagos Islands to the west of South America; lower right: San Cristóbal Island in the Galapagos Islands

plied generalized linear models (GLMs) at 2 different temporal scales: seasonal and diurnal. GLMs allow for a wide range of non-normal error distributions, and have the ability to work with some nonlinear functions (McCullagh & Nelder 1989). They were therefore the most appropriate for use in the present study. Due to an over-dispersion of the data (deviance/df > 2), the models were adjusted with a negative binomial distribution, which included an extra parameter describing dispersion. As this parameter approaches 0, over-dispersion decreases and the negative binomial distribution approaches a Poisson distribution.

The most suitable model was selected using an information-theoretic approach (Burnham & Anderson 2002). This approach requires the development of a set of plausible candidate models based on *a priori* predictions. In the present study, all recorded variables were hypothesized *a priori* to affect sea lion occupancy of a given site, and all potential models resulting from linear combinations of uncorrelated variables were considered. The limit for keeping a variable in the final model was set at p < 0.05. To aid model selection, we used Akaike's information criterion corrected for small sample sizes (AIC$_c$), the difference in AIC$_c$ between each model and the model with the lowest AIC$_c$ (ΔAIC$_c$), and AIC$_c$ weight (w_i). The model with the lowest AIC$_c$ and those with ΔAIC$_c \leq 2$ were considered to be supported. AIC$_c$ was calculated using the following equations:

$$AIC = -2L + 2k \tag{1}$$

$$AIC_c = AIC + 2k\,(k + 1) / (n - k - 1) \tag{2}$$

where L is the log-likelihood, k is the number of parameters in the model, and n is the number of observations. Furthermore, the amount of variance that the models explained (D^2) was calculated using the equation:

$$D^2 = [(ND - RD)/ND] \times 100 \tag{3}$$

where ND is the null deviance of the data and RD is the residual deviance.

To determine whether abundance changes resulted from internal movements between WB sites, Spearman correlations were conducted for observed abundances on the 5 main haul-out sites during the study period (2008 to 2012). All analyses were conducted using the software language R (R Development Core Team 2008).

RESULTS

Changes in terrestrial microhabitat preferences

GSL terrestrial habitat preferences altered throughout the day. An average of 448 ± 13 (SE) animals were counted at sunrise (06:00 h), with 91% observed on sandy beaches, 5% on artificial structures, and the remaining 4% in rocky areas. In contrast, we counted an average of 390 ± 8 (SE) animals 1 h after midday (13:00 h), of which 60% were observed on sandy beaches, 21% on artificial structures, and 19% in rocky areas (Fig. 2).

To analyze the influence of environmental drivers of GSL habitat preferences, we applied a set of GLMs for 3 microhabitat types present in WB (sandy beaches, rocky areas, and artificial structures). Air temperature, time of day, weather conditions, and tide level demonstrated significant effects on the abundance of animals. As time of day and air temperature revealed high correlation (Kendall's tau = 0.7; p < 0.001), we only included air temperature in the final models.

Air temperature was present in the best fitted models for the 3 analyzed habitat types (Table 1). On sandy beaches, abundance decreased with increases in air temperature, whereas on rocky areas and artificial structures, the observed pattern was the opposite, with abundance increasing along with air temperature (Fig. 3). Tide level indicated a significant but weaker effect on sea lion abundance on sandy beaches and rocky areas, with slight increases on sandy beaches and a simultaneous decrease on rocky areas at high tide. The use of artificial structures as resting habitat was also influenced by weather con-

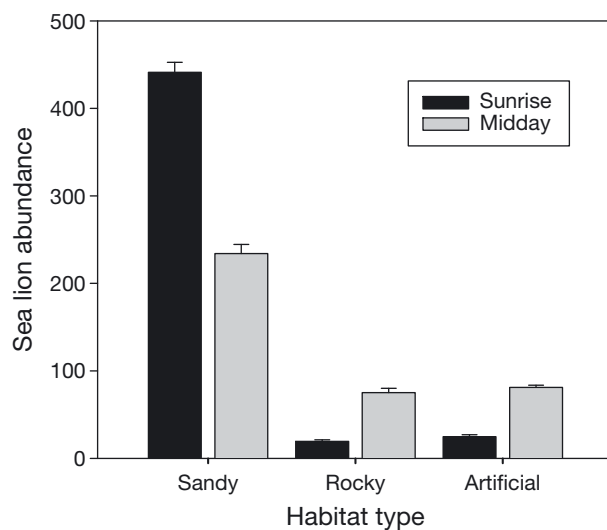
Fig. 2. *Zalophus wollebaeki*. Mean ± SE of animals counted in the 3 habitat types in Wreck Bay, Galapagos: sandy beaches (n = 54), rocky areas (n = 54), and artificial structures (n = 50). Censuses were conducted regularly at sunrise (06:00 h) and 1 h after midday (13:00 h) from May to August 2011

Table 1. Model selection and criteria utilized in the analysis of changes in habitat preferences and influencing factors in each habitat type. Supported models ($\Delta AIC_c \leq 2$) are marked in **bold**. Temperature: air temperature; k: number of parameters in the model; % Var: % variance explained by the model; AIC_c: Akaike's information criterion corrected for small sample sizes; ΔAIC_c: difference in AIC_c between each model and the model with the lowest AIC_c

Site	Model	k	% Var	AIC_c	ΔAIC_c
Sandy areas (n = 54)	**Temperature**	**2**	**69.27**	**610.1**	**0**
	Temperature + Tide	**4**	**70.68**	**611.8**	**1.6**
	Temperature + Weather	4	70.33	612.4	2.3
	Temperature + Weather + Tide	6	72.26	613.9	3.8
	Temperature + Weather + Tide + Date	7	73.59	614	3.9
	Temperature × Weather	6	71.09	616.2	6
Rocky areas (n = 54)	**Temperature + Tide**	**4**	**76.38**	**446.2**	**0**
	Temperature × Tide	6	77.49	448.8	2.7
	Temperature + Weather + Tide + Date	7	77.62	451.2	5.1
	Temperature + Weather + Tide	6	76.39	451.3	5.2
	Temperature	2	71.26	451.8	5.6
	Temperature + Weather	4	71.42	456.2	10.1
Artificial structures (n = 50)	**Temperature**	**2**	**90.82**	**362.9**	**0**
	Temperature + Weather	**4**	**91.42**	**364.5**	**1.6**
	Temperature × Tide	6	92.04	366	3.1
	Temperature + Tide	4	90.88	367.3	4.4
	Temperature + Tide + Weather	6	91.6	368.6	5.8
	Temperature × Weather	6	91.56	369	6.1
	Temperature + Weather + Tide + Date	7	91.78	370.4	7.1

ditions, as more animals were observed on sunny days compared to cloudy days. The strong effect of air temperature on GSL habitat preferences was supported by a strong correlation between animal abundance and habitat type: negative on sandy beaches ($R^2 = 0.71$; $p < 0.01$), and positive on rocky areas ($R^2 = 0.65$; $p < 0.01$) and artificial structures ($R^2 = 0.89$; $p < 0.01$) (Fig. 3).

Seasonal changes in distribution

GSL revealed terrestrial distribution changes between seasons. While the total number of individuals in WB did not demonstrate significant seasonal differences, a high degree of seasonality in the number of animals per haul-out site within the bay occurred. During warm seasons, LM beach maintained a high abundance of animals, while at the remaining beaches, abundance was low; during cold seasons, animals distributed more evenly between haul-out sites (Figs. 4 & 5). The seasonal reduction in sea lion numbers observed at LM was approximately 50%, while numbers increased by 74% at PM, by 49% at CA, and by 37% in ZN (Fig. 5). No seasonal patterns were observed at PO, the smallest haul-out site, where mainly adult males were found (Fig. A1 in the Appendix). The variables that best explained the observed fluctuations and distribution changes were:

season, time of day, and year. Season had a significant influence and was present in the best fitted models for the 4 primary haul-out sites analyzed (CA, PM, ZN, and LM), confirming its influence on sea lion colony dynamics (Table 2). Further, in terms of temporal changes in abundance, the 4 main beaches (CA, PM, ZN, and LM) appeared to be highly correlated (Table 3).

DISCUSSION

We investigated temporal dynamics of terrestrial habitat use of GSL in WB of San Cristóbal Island and observed seasonal and daily changes in their haul-out behavior and microhabitat preferences related to environmental variability.

Changes in terrestrial microhabitat preferences

GSL terrestrial microhabitat preferences change throughout the daily cycle and are linked to air temperature and weather conditions. A fine-scale temporal analysis revealed a clear daily pattern in their terrestrial haul-out behavior; most animals rest on sandy beaches at sunrise when air temperatures are low, and change to artificial structures and rocky areas at midday when temperatures are higher.
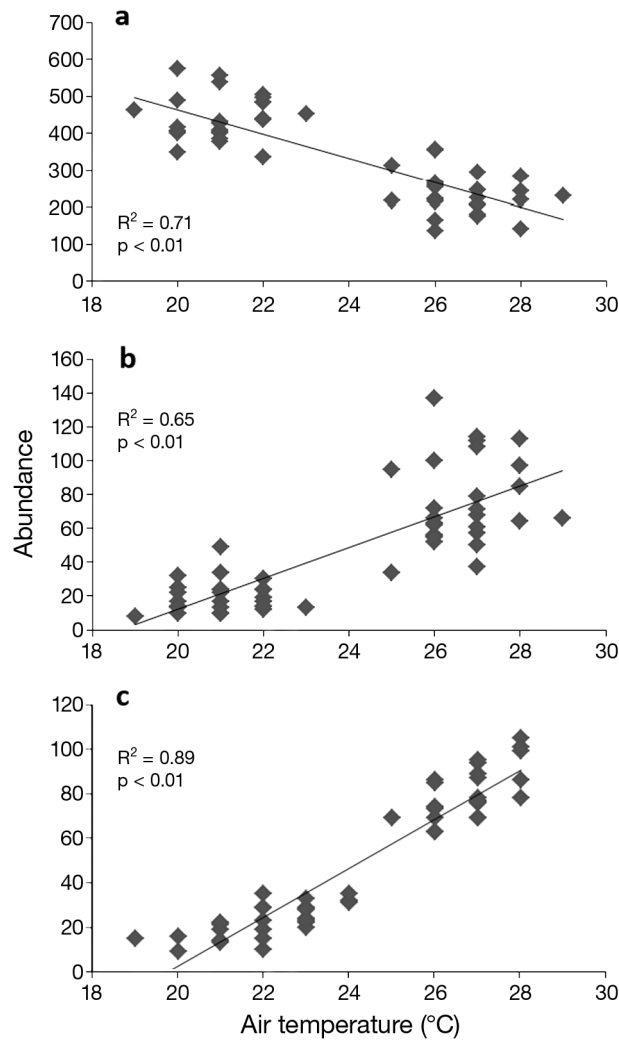
Fig. 3. *Zalophus wollebaeki*. Relationship between observed number of animals and air temperature in the 3 analyzed habitat types: (a) sandy areas (n = 54), (b) rocky areas (n = 54), and (c) artificial structures (n = 50)

Fig. 4. *Zalophus wollebaeki*. Temporal changes in terrestrial distribution of Galapagos sea lions during the year. Monthly mean ± SE of animals counted in 5 main haul-out sites in Wreck Bay, Galapagos, during the study period (2008 to 2012)

Fig. 5. *Zalophus wollebaeki*. Mean ± SE of animals counted in 5 main haul-out sites in Wreck Bay, Galapagos, during the study period (2008 to 2012), in the cold season (July to November) and the warm season (January to May). See Table 2 for site abbreviations

Among all analyzed environmental parameters, air temperature was the most influencing variable in all 3 habitat types. The high correlation between air temperature and observed abundances supports the hypothesis that climatic forces are an important driver of GSL haul-out preferences. Sandy beaches were more intensively used during the coolest periods, while rocky areas revealed higher abundances at warmer times of day (Fig. 2). Within WB, sandy beaches are generally protected from the cold winds, a feature that would provide a suitable resting place during the cooler times of day. The gregarious behavior of this species on flat substrates allows for increased direct contact between individuals, and it may help animals to reduce heat loss,
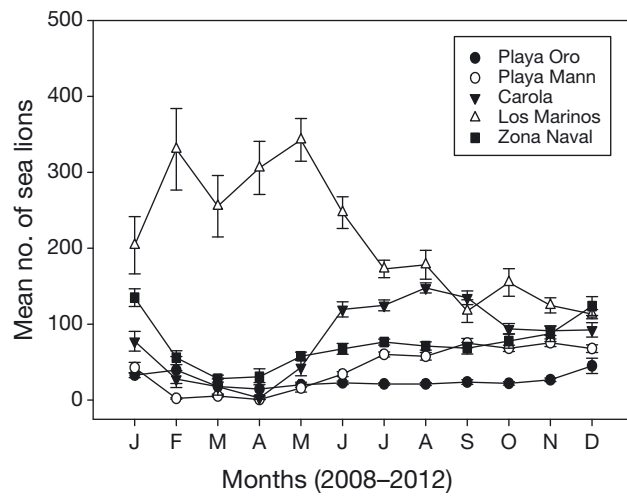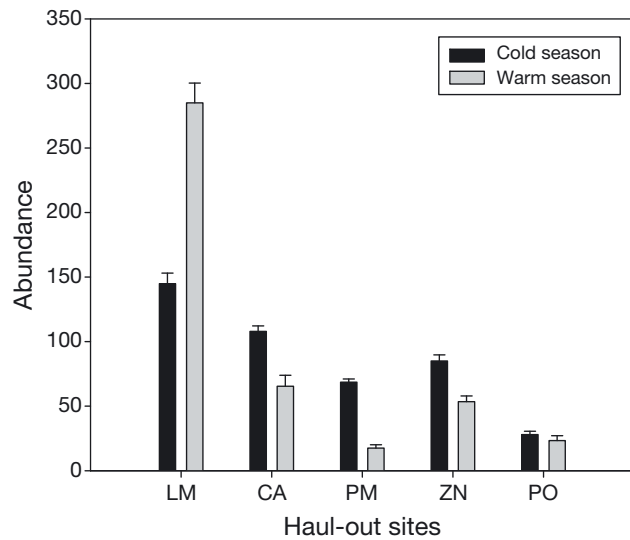
as suggested for the New Zealand sea lion *Phocarctos hookeri*, which enacts behavioral changes during cooler times of day to avoid overcooling (Beentjes 2006). On the other hand, as observed for the GSL's congener, the California sea lion *Zalophus californianus*, rocky areas may play a key role in thermoregulation processes during periods of high temperatures, as they provide direct access to water and their complex structure increases shaded

Table 2. Model selection and criteria utilized in the analysis of seasonal changes in abundance and distribution for each site studied. Supported models ($\Delta AIC_c \leq 2$) are marked in **bold**. See Table 1 for abbreviations. CA: Carola; PM: Playa Mann; PO: Playa de Oro; LM: Los Marinos; ZN: Zona Naval

Site	Model	k	% Var	AIC_c	ΔAIC_c
LM (n = 216)	**Year + Season + Time**	**7**	**57.7**	**2370.4**	**0**
	Year × Season + Time	**9**	**59.6**	**2374.1**	**3.6**
	Season × Time	12	60.7	2375.2	4.7
	Year + Season × Time	13	61	2375.8	5.4
	Season + Time	6	57.8	2377.5	7.1
CA (n = 209)	**Season × Time**	**12**	**32.1**	**2225.5**	**0**
	Year + Season × Time	**13**	**32.5**	**2226.2**	**0.7**
	Year × Season + Time	15	32.7	2232.8	7.2
PM (n = 203)	**Year + Season + Time**	**9**	**67.3**	**1745.9**	**0**
	Year + Season + Time + Date	12	58.9	1784	38.2
ZN (n = 141)	**Year + Season + Time**	**9**	**32.7**	**1356.1**	**0**
	Season + Time	6	28.6	1358.1	2.1
	Year + Season + Time + Date	8	29.5	1360.7	4.6
PO (n = 177)	**Year × Season + Time**	**17**	**36.9**	**1380.6**	**0**
	Year + Month + Date + Tide + Time	11	24.7	1386.6	6
	Year + Season + Date + Tide + Time	12	22.6	1386.7	6.1

area availability, thereby reducing direct solar radiation (Thompson et al. 1987, González-Suárez & Gerber 2008). This behavioral thermoregulatory mechanism, described for the first time in a tropical pinniped in the present paper, the GSL, is shared by other temperate pinnipeds. Southern sea lions *Otaria flavescens*, Juan Fernandez fur seals *Arctocephalus philippii*, and grey seals also use behavioral thermoregulatory mechanisms, demonstrating movements towards shorelines and into the ocean in summers, when temperatures are high (Campagna & Le Boeuf 1988, Francis & Boness 1991, Twiss et al. 2002). Our results are in agreement with Wolf et al. (2005), who suggested that GSL habitat preferences are linked to thermoregulatory requirements.

Table 3. Matrix of Spearman rank correlation coefficients among sea lion abundances at the various sites of Wreck Bay (WB), Galapagos, during the study period (2008 to 2012). Relationships with total abundance in WB and sea surface temperature (SST) were also included. See Table 2 for site abbreviations. *Significant relationships at $p < 0.05$

	CA	PM	PO	LM	ZN	Total WB
CA						
PM	0.73*					
PO	0.09	−0.02				
LM	−0.51*	−0.74*	0.16			
ZN	0.36	0.52*	0.10	−0.52*		
Total WB	0.42*	0.51*	0.48*	−0.53*	0.21	
SST	−0.46*	−0.67*	−0.07*	0.33*	−0.37*	0.21

While pinnipeds using wooden floating platforms have been observed previously (e.g. the California sea lion *Zalophus californianus* in San Francisco Bay), the present study described and analyzed quantitatively this behavior for the first time. The high correlation with air temperature and weather suggests that those structures provide advantages to GSL for thermoregulation processes (Fig. 2). Artificial structures may represent a suitable resting place during periods of high temperature to optimize GSL's thermoregulatory requirements, as these provide rapid access to the water and shaded areas similar to the observed features of rocky areas. This behavioral adaptive capability would therefore indicate that GSL display a high degree of plasticity regarding habitat preferences, possibly allowing them to use new substrates as an extension of their own natural habitat. Given the observed capability of sea lions to use artificial structures as a resting place and the observed adaptations of this population in a human-modified environment, it is likely that similar patterns will occur in other pinniped populations after construction of marine structures (e.g. oil rigs). Thus, an assessment of pinnipeds' habitat preferences prior to any construction that could provide new substrates for these animals should be required in order to understand potential impacts on wild populations and to be able to minimize them.

The results presented here have important implications for the management of this species, as they highlight the importance of enforcing preservation of suitable habitat for thermoregulation requirements. Further, this study reveals that artificial

floating structures can be a relatively simple and cheap management tool useful at the local scale for providing a suitable substrate for rest during warm and energetically costly moments. This finding might be of interest in light of current global warming. Climatic models predict an increase of temperature between 2 and 3°C by the year 2100 in the Galapagos Islands area (IPCC 2007), and this increment may enhance GSL thermal stress during the warmest periods of the year.

Seasonal changes in distribution

GSL demonstrated seasonal changes in distribution linked to environmental variables. During warm seasons, sea lions aggregated in high densities on one of the beaches, while very few individuals were observed on the other beaches in WB. In contrast, during cold seasons, sea lions changed their haul-out patterns, showing a more even distribution across all the main beaches of WB. The observed changes between haul-out sites were highly correlated, suggesting that fluctuations in abundances among sites were caused by movements within WB and were not due to migrations or movements between different colonies from outside of WB (Table 2).

While several authors have described seasonal changes in habitat use and distribution in pinnipeds inhabiting temperate areas (Krieber & Barrette 1984, Montgomery et al. 2007), the present study represents the first time that a seasonal pattern of distribution change has been observed in a low-latitude pinniped. In higher latitudes, seasonal movements are often driven by proximity to feeding grounds (Jonker & Bester 1998); this determinant is unlikely to explain our results, as the movements undertaken by GSL in WB are shorter than 1 km, while this species moves average distances of 42 km for feeding (Villegas-Amtmann et al. 2009). Among other factors, molting periods and annual breeding cycles have been reported to influence seasonal changes in the distribution of pinnipeds (Rosas et al. 1994, Carlens et al. 2006, Leeney et al. 2010). GSL do not experience an annual molting period; however, the seasonal influence of the breeding cycle likely affects the species' habitat preferences, as the observed movements and distribution changes throughout the present study are in accordance with breeding activities. Although previous studies reported long-term site fidelity for this species (Wolf & Trillmich 2007, Meise et al. 2013), we observed seasonal variations throughout the year that result in 2 distinct situations: (1) an aggregation period in 1 haul-out site during non-breeding seasons, aligned with the warm seasons, and (2) a more evenly distributed abundance of animals during breeding seasons, aligned with the cold seasons. The breeding period of this species is very extended (Villegas-Amtmann et al. 2009), and the correlation between seasonal abundance changes and the onset of the breeding season suggest that special habitat requirements during this energetically costly period may be a potential driver of the observed movements. Further, in the present study, the small beach of PO, which primarily holds adult males not taking part in the breeding groups of WB (Fig. A1 in the Appendix), did not demonstrate seasonal changes in its number of animals, also supporting the hypothesis of breeding activity as a driver of seasonal movements. Although the present study itself does not allow us to determine the potential advantages that movements would represent for this species, it is likely that females are displaying small-scale distribution changes to reduce the high density of animals during the breeding period, thereby increasing the availability of shoreline habitat that provides rapid access to the sea and favors the mother–pup meeting after each feeding sojourn (Trillmich 1986). Further, the greater availability of rocky areas provided by these new places might be an important feature for females when choosing the most suitable habitat for pupping and raising their young. Rocky areas are essential for sea lion pups in providing shaded areas and small swimming pools that are suitable for acquiring swimming skills (Limberger et al. 1986, González-Suárez & Gerber 2008). Pinnipeds inhabiting lower latitudes often demonstrate special habitat requirements to avoid thermal stress, and this may lead to changes in habitat use preferences and mating systems, in which males often patrol resting sites that have direct access to the water, which are valued by females (Campagna & Le Boeuf 1988). In other pinniped species, males defending territories with direct access to water often hold greater numbers of females and have increased copulatory success compared to males patrolling waterless areas (Campagna & Le Boeuf 1988, Francis & Boness 1991).

The present results suggest that during the energetically demanding breeding seasons, GSL show special habitat requirements that may drive seasonal movements to rookeries with direct access to water and greater rocky area availability to facilitate their behavioral thermoregulatory mechanisms and improve breeding success.

CONCLUSIONS

This study has demonstrated that terrestrial habitat use patterns in a tropical pinniped, the GSL, show temporal variations that are strongly influenced by environmental variability on a diurnal and seasonal scale. The correlation between the observed changes in microhabitat use and the environmental variables of air temperature and weather conditions suggest that the GSL shows different preferences as a behavioral adaptation to enhance the effectiveness of its thermoregulatory mechanisms. A novel seasonal pattern of distribution change for tropical pinnipeds is also described and may be associated with specific habitat requirements during the breeding season and linked to thermoregulatory mechanisms. Further, we described and analyzed for the first time the use of artificial floating substrates by GSL as an extension of their own terrestrial habitat, and linked this haul-out behavior to environmental parameters. This is an example of a successful management tool that can provide suitable habitat and enhance the effectiveness of thermoregulatory processes that may have potential applications for other pinnipeds.
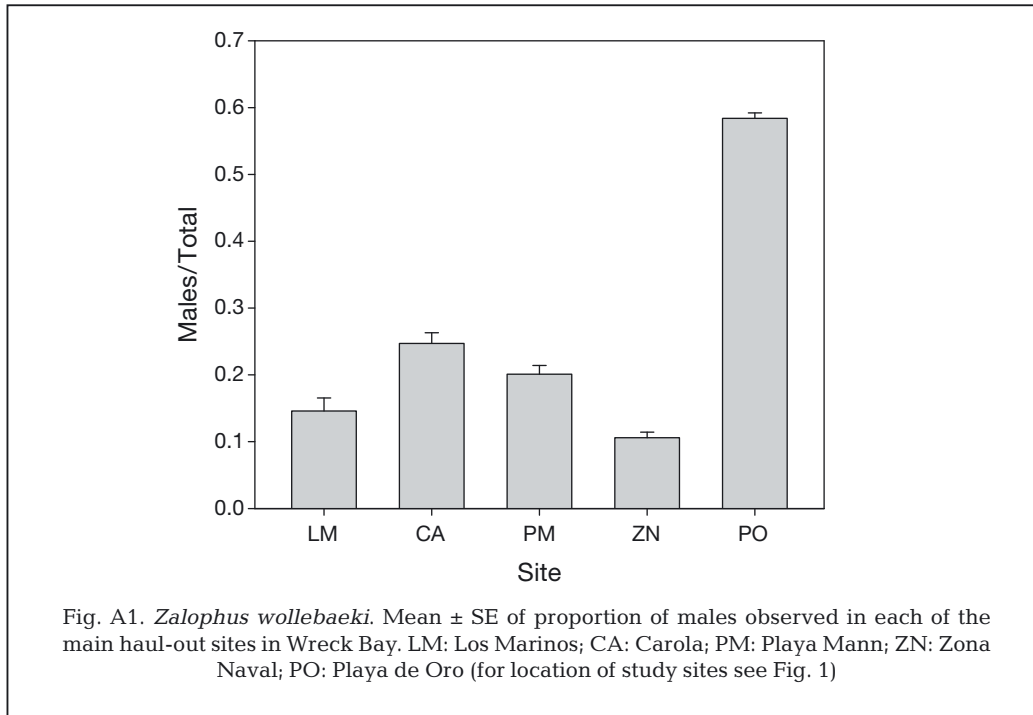
Finally, this study highlights the importance of including temporal dynamics in the conservation planning for this tropical pinniped. Because having a suitable haul-out site can be paramount for GSL's physiological requirements and breeding success, enforcing management actions towards habitat preservation that take into account thermoregulatory requirements and breeding activities will help to ensure the long-term survival of this Endangered species.

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Appendix. Sex ratio of Galapagos sea lions found at the study sites in Wreck Bay, Galapagos

Fig. A1. *Zalophus wollebaeki.* Mean ± SE of proportion of males observed in each of the main haul-out sites in Wreck Bay. LM: Los Marinos; CA: Carola; PM: Playa Mann; ZN: Zona Naval; PO: Playa de Oro (for location of study sites see Fig. 1)