

Chapter 3

The Galapagos Sea Lion: Adaptation to Spatial and Temporal Diversity of Marine Resources Within the Archipelago

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Abstract Galapagos sea lions are the smallest sea lion species worldwide. The population consists of about 20,000 individuals, is endemic to the Galapagos Islands and has been separated for about 2.5 million years from the California sea lion. The equatorial environment differs from that of other pinnipeds by terrestrial heat and reduced marine productivity. Growth and development is strongly influenced by marine variability, particularly El Niño events, which also decrease juvenile and adult survival. Large males establish aquatic territories, but smaller non-territorial males also achieve reproductive success. Time at the colony proves the best predictor of reproductive success, which reflects the long drawn-out reproductive season often lasting 6 months. Females mature relatively late at about 5 years and reproduce often only every other year. Juveniles need exceptionally long to become nutritionally independent. The long period of lactation (2–5 years) often leads to competition between offspring born in different years. Adult females dive to great depths (max. 580 m) and mostly forage on shelf areas as well as along the shelf edge. Juveniles need many years to reach adult diving abilities. Increased human-sea lion contact in fast growing settlements and through boat traffic and fishery poses new and potentially highly dangerous threats to the population.

Introduction

Galapagos sea lions (*Zalophus wollebaeki*) are a particularly interesting pinniped species since they occur right on the equator, exposed to thermoregulatory problems ashore and lower marine productivity than more temperate or subpolar species. Nevertheless, their marine environment can be characterized as a local

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productivity hotspot in the equatorial Pacific. As described in more detail in Chaps. 1 and 2, the cold waters of the Humboldt Current and strong local upwelling of eastward flowing undercurrents around the western coast of the islands of Fernandina and Isabela generate the local productivity of the archipelago. Thus, sea surface temperature (SST) becomes an indicator of productivity as it reflects the intensity of influx of cold, productive waters.

The species has settled in the islands a long time ago. Genetic analyses suggest a separation from the populations of the California sea lion (*Zalophus californianus*) for 2.5 ± 0.5 million years. It is now considered a separate species, endemic to the Galapagos (Wolf et al. 2007a). Surprisingly, the sea lions living in the west of the archipelago (Fernandina and western Isabela) proved to be genetically and morphologically slightly but significantly differentiated from the population living in the centre and northeastern parts (Wolf et al. 2008).

The species breeds on all major islands, with highest density in the southern and central parts of the archipelago. Local densities are always low in comparison to California sea lions. Estimates of sea lion abundance vary considerably: An early census in 1978 resulted in a total count of about 8,000 sea lions representing an estimated 30,000–40,000 animals in total (Trillmich 1979; Trillmich, unpubl. data). Alava and Salazar (2006) estimated 18,000 animals, based on a census in 2001, a few years after the major El Niño of 1997/1998. It is not entirely clear why these estimates differ so widely since the census in 2001 also yielded a total of 7,942 counted sea lions and correction factors used for the 1978 and 2001 censuses seem very similar (Alava and Salazar 2006). Trying to err on the safe side, Aurióles and Trillmich (2008) mentioned an estimate of about 20,000 animals for the whole archipelago, following the more recent estimate. However, the evidence on which these estimates are based is very weak given that, for example, the count of San Cristobal was 334 individuals in 1978 (Trillmich and Trillmich, unpubl. data), 917 in 2001 (Alava and Salazar 2006) and 1,496 in 2013 (Diego Paez, Bulletin Parque Nacional Galapagos, 11 Jan 2013). These discrepancies more likely reflect variance in numbers of animals ashore during a given census due to tidal state, time of day and degree of coverage of a given area rather than realistic changes in local population size. Nevertheless, it is clear that during the strong El Niño events (like 1982/1983 and 1997/1998), when food availability for marine foragers is drastically reduced, numbers may substantially decline (perhaps by about a third). During these events pups of the year and adult territorial males were most affected (Trillmich and Limberger 1985; Trillmich and Dellinger 1991; Salazar and Bustamante 2003).

Perhaps in adaptation to or as a consequence of its relatively less productive marine environment, the species is the smallest of all sea lions with females weighing about 60 kg (max. 95 kg) at a length of 156 cm (max. 176 cm). Male weights are less well documented as we never caught any of the largest males (the largest caught was 158 kg, the longest had a standard length of 205 cm). Fully grown males when fattened up for the breeding season may weigh between 150 and 200 kg at a length between 170 and 210 cm.

Sexual size dimorphism is already evident at birth when males weigh about 6.7 kg and females 5.8 kg (Kraus et al. 2013). Mass at birth and initial growth rate during the first 60 days of life decline with increasing SST, and pup mortality increases indicating the close connection between marine conditions and early development (Kraus et al. 2013; Mueller et al. 2011). Birth mass and initial growth rate predict mass at 1 year of age. Thus a head start with a high birth mass benefits both early growth and survival to 1 year. Only about two thirds of all newborns survive to the age of 1 year and roughly 51 % to that of 2 years (Kraus et al. 2013). By 3 years of age, males weigh on average 40.5 kg and females 35.2 kg. However, as most juveniles are rarely seen at their natal colonies at this age, averages of the whole cohort are likely higher. Females begin to mature shortly thereafter. Males start becoming reproductively active at an age of 5. They continue to grow for a long period before reaching final size.

Development to Independence

The development to independent foraging starts late and is exceptionally slow compared to other pinniped species, likely a consequence of the slow growth and development of physiological diving abilities found in this species (Mueller et al. 2011; Trillmich et al. 2008). Juvenile Galapagos sea lions depend on average for the first 2 years of life on maternal input, while slowly shifting from complete reliance on maternal milk to independent foraging. Galapagos sea lion pups are terrestrial at birth and start swimming in shallow open water at around 2–3 months. Substantial diving activity starts at approximately 12 months of age, when juveniles dive on average to depths of 30 m and for 2.5 min (Jeglinski et al. 2012). Successful independent foraging supplementing continuing milk consumption seems to take place even later, on average at around 18 months. Diving performance increases with age and body mass, but 2-year-old juveniles still dive to only approximately 75 % of the average diving depths of adult females (Jeglinski et al. 2012).

Development to independence varies considerably. Annual variation in marine productivity seems to cause differences between cohorts. During mild El Niño conditions, when food availability decreases, the onset of independent foraging was shifted beyond the age of 18 months (Jeglinski et al. 2012). Further, onset of diving and independent foraging varies between colonies, possibly as a consequence of local differences in marine productivity (Jeglinski et al. 2012, 2013; Jeglinski 2013; Piedrahita and Trillmich, pers. obs.). Considerable variation exists between the developmental pace of individuals: Some juveniles were observed suckling from their mothers up to an age of 7 years (unpubl. data).

Mating System and Its Implications for Social Structure

The following descriptions of social structure and behaviour rest largely on our long-term study on the islet of Caamaño. Given the variance in habitats and marine conditions within the archipelago, whether this information is valid for the whole archipelago still needs to be determined.

Galapagos sea lions display the otariid polygynous mating system. Adult males try to monopolize access to females. Due to thermoregulatory constraints, males (as well as females) need direct access to water. Accordingly, the largest and most competitive males defend semiaquatic territories along beaches where females haul out to nurse the young (Trillmich and Trillmich 1984; Wolf et al. 2005). Females come into oestrus approximately 4 weeks after parturition (Heath 1989). The long reproductive season (September–January) and the predominance of aquatic mating make it impossible for males to monopolize access to receptive females. In contrast to other otariid species, they display and appear to depend on being chosen by a female, rather than copulating with each female that comes into oestrus on their territory. Accordingly, reproductive success of Galapagos sea lions within a given season is not highly skewed towards territorial males (Pörschmann et al. 2010). Indeed, non-territorial males sire more than 50 % of the annual number of pups where paternity could be assigned (Pörschmann et al. 2010).

The duration of attendance at the breeding colony best predicts male reproductive success (Pörschmann et al. 2010). Accordingly, large male body size might be selected for to allow extended fasting rather than to increase fighting abilities. The small colony sizes and low density within Galapagos sea lion colonies further suggest comparatively low pay-offs for territoriality. However, males establish territories in areas with highest female densities, thus increasing their chance to encounter receptive females. Further, returning to territories where they previously gained matings increases territorial males' lifetime reproductive success (Meise et al. 2013). For non-territorial males, the probability to encounter oestrus females and mate successfully correlates positively with the size of their home range within a given season and thus with their ability to sneak into foreign territories (Wolf et al. 2005; Meise et al. 2013).

Intrasexual competition among males leads to sexual segregation in the colonies, especially during the reproductive season. Females and their offspring gather along the water's edge where they aggregate in so-called communities. Communities, which exist independent of established territory boundaries, can be best explained by similar space use of group members (Wolf et al. 2007b). Females of the same community show a higher degree of relatedness than individuals from different communities (Wolf and Trillmich 2008) because of a high number of full or half siblings and mother-offspring pairs (even after weaning) within communities.

Males leave their natal areas after they are weaned and gather in inland habitats, which offer shade during the day (Wolf et al. 2005; Meise et al. 2013). Aggregations of close kin are therefore less likely among adult males. Still, the limited availability of shady spots for thermoregulation forces males to rest in close

proximity of each other. Clear spatial preferences and high overlap of males' home ranges within the colony provide a chance for long-lasting social relationships among males (Meise et al. 2013).

Female Maturation and Reproduction: Maternal Care and Sibling Competition

Galapagos sea lions reproduce annually as do other otariids, but the breeding season is unusually long, extending over a period of more than 5 months. On Caamaño, it may start in early September, with a peak of birth in early November (Mueller et al. 2011). As the onset of the breeding season varies slightly among colonies on different islands, females in various reproductive stages can be found throughout the year (Villegas-Amtmann et al. 2009).

Adult females initiate their reproductive life at an age of 5–6 years. Despite the annual reproductive cycle, individual females reproduce every 2–3 years. This low reproductive rate, compared to other otariid species, links to the variable productivity of the environment: Increased SST during the first 3 months after mating decreases female pupping probability (Mueller 2011). Also, given the long dependency periods of juvenile Galapagos sea lions, an annual reproduction would necessitate the simultaneous support of an older offspring, a newborn pup and self-maintenance, high costs that females rarely seem able to pay (Trillmich and Wolf 2008; Mueller et al. 2011). Infrequently (around 20 %), Galapagos sea lion females give birth to a pup while still suckling a dependent older offspring (Trillmich and Wolf 2008). This situation leads to sibling competition upon the newborn pup's birth and results in the death of the newborn pup when the older offspring is still around for suckling. Rarely, adult females manage to successfully support both the older offspring and the newborn, leading to the formation of a so-called trio (Trillmich and Wolf 2008).

Non-nursing, pregnant females return ashore 1–2 days prior to parturition (Trillmich 1986). Immediately after birth, females behave highly aggressive and defend the area around the newborn, calling frequently to it. The female stays on land with the newborn pup during a 4–7 days perinatal period. This period helps to establish an exclusive, mutual bond between mother and offspring (Trillmich 1981). Galapagos sea lion females, as income breeders, then resume a foraging cycle strategy, during which they continuously cycle between foraging trips at sea that last between 5 h and 4 days, in general increasing with offspring age (Trillmich 1986; Villegas-Amtmann et al. 2008; Jeglinski et al. 2012) and suckling bouts on land. Galapagos sea lion females lactate year-round. If a dependent offspring dies, lactation will end, but otherwise females will be essentially nursing all their reproductive lives as long as the pup or juvenile offspring survives.

Use of the Marine Environment

Galapagos sea lions are nonmigratory. Rarely, vagrants are recorded from the Mexican, Colombian and mainland Ecuadorian coast (e.g. Ceballos et al. 2010; Denkinger, pers. comm.).

Information on spatial movements and diving behaviour is available for adult females with dependent offspring and juveniles up to 2 years. Despite their small body size, compared to other sea lion species, Galapagos sea lions are exceptionally deep divers: 12-month-old juveniles already dive to a maximum depth of 367 m, and the deepest dive recorded for an adult female was 584 m (Jeglinski et al. 2012, 2013). However, adult females regularly dive to depths between 92 and 178 m for 3.3–4.7 min (Villegas-Amtmann et al. 2008; Villegas-Amtmann and Costa 2010; Jeglinski et al. 2012). Sea lions mix benthic and pelagic diving and forage both at day and at night, but there is considerable variation in foraging patterns within the species. Juvenile sea lions dive predominantly at night and to shallow depths, a likely consequence of their small body size (Jeglinski et al. 2012, 2013). The diving behaviour of adult females, especially diving depth and duration and activity period, differs between individuals (Villegas-Amtmann et al. 2008; Villegas-Amtmann and Costa 2010). To date it is not clear if these behavioural patterns are consistent throughout life or change with age, reproductive status or ecological conditions.

Galapagos sea lions feed predominantly on small benthic and pelagic fish from approximately 12–33 different species and, in some colonies, on cephalopods; a few fish species from the families Engraulidae, Carangidae, Serranidae and Myctophidae dominate the diet (Dellinger and Trillmich 1999; Salazar and Bustamante 2003; Páez-Rosas and Aurióles-Gamboa 2010). There are distinct dietary differences between sea lions in the centre of the archipelago that feed on a large variety of different fish species and western sea lions that mainly feed on sardines (*Sardinops sagax*) (Dellinger and Trillmich 1999), suggesting ecological differences in line with the genetic differentiation found in the species (Wolf et al. 2008). In the western archipelago, Galapagos sea lions are sympatric to the Galapagos fur seal (*Arctocephalus galapagoensis*), but both species exploit very different foraging niches (Dellinger and Trillmich 1999; Jeglinski et al. 2013; Páez-Rosas and Aurióles-Gamboa 2010).

Sea lions forage on the shelf platform of the archipelago and, in the western archipelago, along its edge. Adult females with a dependent offspring travel maximum distances between 50 and 97 km away from their colony, while juveniles cover maximum distances of less than 15 km (Jeglinski et al. 2013; Villegas-Amtmann et al. 2008; Villegas-Amtmann and Costa 2010). These foraging sojourns are short in comparison to other sea lions. Both age groups haul out on numerous sites apart from their home colony, including other sea lion colonies (Jeglinski 2013; Villegas-Amtmann et al. 2008; Villegas-Amtmann and Costa 2010).

Threats to the Species

The life history and population dynamics of Galapagos sea lions are strongly influenced by pronounced climatic variability, and the species has developed adaptations, e.g. highly plastic maternal strategies, providing some resilience against the deleterious effect of environmental unpredictability. Still, an increase in the frequency of El Niño, as has been predicted by some as an effect of anthropogenically induced climate change (Trenberth and Hoar 1997; but see Cobb et al. 2013), could reduce the population below sustainable levels.

The Galapagos Islands have undergone drastic change in the last four decades. The previously uninhabited, remote archipelago is today well connected to the Ecuadorean mainland, permanently inhabited by about 30,000 persons, and receives 180,000 visiting tourists per year (Trillmich 1992; Grenier 2012). The drastic increase of human use of terrestrial and marine resources has the strong potential to influence the Galapagos sea lion population negatively. Possible effects include an increased frequency of disturbance at foraging, breeding and haul out sites, an increased potential for boat strikes, direct physical damage from fishing gear, negative interactions with fishermen and an increased possibility for severe damage to the marine ecosystem by ship accidents as clearly demonstrated by the Jessica oil spill in 2001 (Salazar 2003). Some of the largest sea lion colonies are close to or even within human settlements (Caamaño close to Puerto Ayora and Puerto Baquerizo Moreno on San Cristobal). In the latter colony, pups and juveniles had significantly higher levels of immune activity compared to animals from an uninhabited colony, possibly as a consequence of a higher presence of harmful pathogens or pollution from sewage and chemicals (Brock et al. 2013). Especially the direct contact between sea lions and domestic dogs, rats and cats on inhabited islands poses a direct threat to the population, opening a potential for infectious disease transmission, such as canine distemper virus (Alava and Salazar 2006; Auriolles-Gamboa and Trillmich 2008). Given the high connectivity between colonies in the central archipelago (Wolf et al. 2008; Villegas-Amtmann et al. 2008; Jeglinski 2013), diseases would likely spread from these hotspots throughout the range of the population with a high potential to endanger the whole population.

Likely, the synergy between the drastic consequences of climatic variation and recent, anthropogenically induced and increasingly influential effects poses the largest threat with the potential to critically endanger the small population of Galapagos sea lions.

Implications for Conservation and Management

The continuously increasing interface between humans and wildlife on the islands makes management steps to control and reduce the negative effects on the endangered Galapagos sea lion vital. A direct regulatory measure in the form of strict

enforcement of regulations for the management of domestic dogs and dog vaccination programmes (Wolf et al. 2007b; Levy et al. 2008) could significantly diminish the potential for disease transmission. Further, management measures should aim to reduce direct anthropogenic impact (pollution, ship traffic, numbers of tourists visiting the islands) to minimize synergistic effects with the negative impact of inevitable climate change. Here, detailed information on spatial movements and distribution of Galapagos sea lion foraging areas (Villegas-Amtmann et al. 2011; Jeglinski 2013; Jeglinski et al. 2013) can be used as basis for refined zonation and regulation of traffic within the Galapagos Marine Reserve. Given the sparse data on population size and development and associated methodological uncertainties, the recent establishment of a population monitoring scheme by the Galapagos National Park is an excellent first step to provide a firm basis on which to base further management decisions.

References

- Alava JJ, Salazar S (2006) Status and conservation of otariids in Ecuador and the Galápagos Islands. In: Trites AW, Atkinson SK, DeMaster DP, Fritz LW, Gelatt TS, Rea LD, Wynne KM (eds) Sea lions of the world Alaska Sea Grant College Program, University of Alaska, Fairbanks, pp 495–520
- Aurioles D, Trillmich F (2008) *Zalophus wollebaeki*. IUCN 2008. IUCN Red List of Threatened Species. <http://www.iucnredlist.org>
- Brock P, Hall A, Goodman SJ, Cruz M, Acevedo-Whitehouse K (2013) Applying the tools of ecological immunology to conservation: a test case in the Galapagos sea lion. *Anim Conserv* 16:19–31
- Ceballos G, Pompa S, Espinoza E, García A (2010) Extralimital distribution of Galapagos (*Zalophus wollebaeki*) and Northern (*Eumetopias jubatus*) sea lions in Mexico. *Aquat Mamm* 36:188–194
- Cobb KM, Westphal N, Sayani HR, Watson JT, Di Lorenzo E, Cheng H, Edwards RL, Charles CD (2013) Highly variable El Niño–Southern Oscillation throughout the holocene. *Science* 339:67–70
- Dellinger T, Trillmich F (1999) Fish prey of the sympatric Galápagos fur seals and sea lions: seasonal variation and niche separation. *Can J Zool* 77:1204–1216
- Grenier C (2012) Nature and the world. A geohistory of Galapagos. In: Wolff M, Gardner M (eds) The role of science for conservation. Routledge, London, pp 256–274
- Heath CB (1989) The behavioral ecology of the California sea lion, *Zalophus californianus*. PhD thesis, University of California, Santa Cruz, CA
- Jeglinski JWE (2013) Ecological differentiation in the Galapagos Sea: the role of foraging ontogeny and competition. PhD thesis, Department of Behavioural Biology, University of Bielefeld
- Jeglinski JWE, Robinson PW, Werner C, Costa DP, Trillmich F (2012) Age, body mass and environmental variation shape the foraging ontogeny of Galapagos sea lions. *Mar Ecol Progr Ser* 453:279–296
- Jeglinski JWE, Goetz KT, Werner C, Costa DP, Trillmich F (2013) Same size – same niche? Foraging niche separation between sympatric juvenile Galapagos sea lions and adult Galapagos fur seals. *J Anim Ecol*. doi:10.1111/1365-2656.12019

- Kraus C, Mueller B, Meise K, Piedrahita P, Pörschmann U, Trillmich F (2013) Mama's boy: sex differences in juvenile survival in a highly dimorphic large mammal, the Galapagos sea lion. *Oecologia* 171:893–903
- Levy JK, Crawford PC, Lappin MR, Dubovi EJ, Levy MG, Alleman R, Tucker SJ, Clifford EL (2008) Infectious diseases of dogs and cats on Isabela Island, Galapagos. *J Vet Intern Med* 22:60–65
- Meise K, Krüger O, Piedrahita P, Trillmich F (2013) Site fidelity in male Galápagos sea lions: a lifetime perspective. *Behav Ecol Sociobiol*. doi:[10.1007/s00265-013-1526-5](https://doi.org/10.1007/s00265-013-1526-5)
- Mueller B (2011) Life under uncertainty, life history and reproductive strategies in Galapagos sea lions: from individual decisions to population dynamics. PhD thesis, Department of Behavioural Biology, University of Bielefeld
- Mueller B, Pörschmann U, Wolf JBW, Trillmich F (2011) Growth under uncertainty: the influence of marine variability on early development of Galapagos sea lions. *Mar Mamm Sci* 27:350–365
- Páez-Rosas D, Auriolos-Gamboa D (2010) Alimentary niche partitioning in the Galapagos sea lion, *Zalophus wollebaeki*. *Mar Biol* 157:2769–2781
- Pörschmann U, Trillmich F, Mueller B, Wolf JBW (2010) Male reproductive success and its behavioural correlates in a polygynous mammal, the Galapagos sea lion (*Zalophus wollebaeki*). *Mol Ecol* 19:2574–2586
- Salazar S (2003) Impacts of the Jessica oil spill on sea lion (*Zalophus wollebaeki*) populations. *Mar Pollut Bull* 47:313–318
- Salazar S, Bustamante RH (2003) Effects of the 1997–98 El Niño on population size and diet of the Galapagos sea lion (*Zalophus wollebaeki*). *Noticias de Galapagos* 62:40–45
- Trenberth KE, Hoar TJ (1997) El Niño and climate change. *Geophys Res Lett* 24:3057–3060
- Trillmich F (1979) Galápagos sea lions and fur seals. *Noticias de Galápagos* 29:8–14
- Trillmich F (1981) Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. *Behaviour* 78:21–42
- Trillmich F (1986) Attendance behavior of Galapagos sea lions. In: Gentry R, Kooyman G (eds) *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton, NJ, pp 196–208
- Trillmich F (1992) Conservation problems on Galápagos: the showcase of evolution in danger. *Naturwissenschaften* 79:1–6
- Trillmich F, Dellinger T (1991) The effects of EN on Galápagos pinnipeds. In: Trillmich F, Ono KA (eds) *Pinnipeds and El Niño: responses to environmental stress*. Springer Verlag, Heidelberg, pp 66–74
- Trillmich F, Limberger D (1985) Drastic effects of El Niño on Galápagos pinnipeds. *Oecologia* 67:19–22
- Trillmich F, Trillmich KGK (1984) The mating system of pinnipeds and marine iguanas: convergent evolution of polygyny. *Biol J Linn Soc* 21:209–216
- Trillmich F, Wolf J (2008) Parent–offspring and sibling conflict in Galapagos fur seals and sea lions. *Behav Ecol Sociobiol* 62:362–375
- Trillmich F, Rea L, Castellini M, Wolf JBW (2008) Age-related changes in hematocrit in the Galápagos sea lion (*Zalophus wollebaeki*) and the Weddell seal (*Leptonychotes weddelli*). *Mar Mamm Sci* 24:303–314
- Villegas-Amtmann S, Costa DP (2010) Oxygen stores plasticity linked to foraging behaviour and pregnancy in a diving predator, the Galapagos sea lion. *Funct Ecol* 24:785–795
- Villegas-Amtmann S, Costa D, Tremblay Y, Salazar S, Auriolos-Gamboa D (2008) Multiple foraging strategies in a marine apex predator, the Galapagos sea lion *Zalophus wollebaeki*. *Mar Ecol Progr Ser* 363:299–309
- Villegas-Amtmann S, Atkinson S, Costa DP (2009) Low synchrony in the breeding cycle of Galapagos sea lions revealed by seasonal progesterone concentrations. *J Mammal* 90:1232–1237

- Villegas-Amtmann S, Simmons SE, Kuhn CE, Huckstadt LA, Costa DP (2011) Latitudinal range influences the seasonal variation in the foraging behavior of marine top predators. *PLoS One* 6: e23166
- Wolf JBW, Trillmich F (2008) Kin in space: social viscosity in a spatially and genetically substructured network. *Proc R Soc Lond B* 275:2063–2069
- Wolf JBW, Kauermann G, Trillmich F (2005) Males in the shade: habitat use and sexual segregation in the Galapagos sea lion (*Zalophus californianus wollebaeki*). *Behav Ecol Sociobiol* 59:293–302
- Wolf JBW, Tautz D, Trillmich F (2007a) Galapagos and Californian sea lions are separate species: genetic analysis of the genus *Zalophus* and its implications for conservation management. *Front Zool* 4:20
- Wolf JBW, Mawdsley D, Trillmich F, James R (2007b) Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Anim Behav* 74:1293–1302
- Wolf JBW, Harrod C, Brunner S, Salazar S, Trillmich F, Tautz D (2008) Tracing early stages of species differentiation: ecological morphological and genetic divergence of Galápagos sea lion populations. *BMC Evol Biol* 8:150