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Home sweet home: social dynamics and genetic variation of a long-term resident bottlenose dolphin population off the Chilean coast

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Coastal resident and pelagic nonresident bottlenose dolphins, *Tursiops truncatus*, have been described in north-central Chile. Using long-term residence data (over 13 years of photo-identification) and genetic mtDNA information, we analysed the social dynamics through time and the genetic variation of this long-term resident population, and evaluated its sociogenetic interaction with nonresidents. Pelagic nonresident dolphins exhibited a higher level of genetic diversity than coastal residents and a significant difference in genetic structure was detected between them. Based on the difference in haplotype numbers and frequencies between resident and nonresident populations and between resident males and females, we propose a population dynamic model in which the resident population is composed of (1) resident females (founder lineages) and some of their female descendants that were born in and remained in the group, without effective female immigration from the nonresident population, (2) resident male descendants of the founder lineage that were born in and remained in the group and (3) resident males that were incorporated from the pelagic groups. Male-biased migration from nonresident pelagic groups into the resident population likely contributes to genetic variation and therefore may help limit inbreeding in the resident population. Finally, we propose that the peripatric model of population differentiation, where resident groups are sporadically connected to the pelagic population, may explain the origin of this unique resident population of bottlenose dolphins along the Chilean coast.

Understanding the drivers and implications of animal movements have become fundamental due to their influence on population dynamics and structure (Gilliam & Fraser, 2001; Nathan et al., 2008). At the population level, movement patterns can be generally classified into three broad categories: resident, migratory and nomadic. (1) Resident, or sedentary, refers to individuals that reside in relatively small home ranges or territories, compared to the population's range (Roshier & Reid, 2003). (2) Migration is defined as a cyclic, regular long-distance pattern of movement to and from breeding and nonbreeding grounds (Roshier & Reid, 2003) and (3) nomadism denotes individuals moving along routes that vary widely or from season to season, and do not repeat annually (Mueller & Fagan, 2008). Such movements are unpredictable and are generally associated with resources that fluctuate irregularly on a multiyear scale over large geographical areas. These three categories are not mutually exclusive, meaning more than one of these patterns may occur within or among populations of the same species (e.g. Hundertmark, 1998) at the same time or at different times (Jahn, Levey, & Smith, 2004).

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Each of these movement strategies is represented within the Cetacea. The most widely studied migrant baleen whale species are the humpback whale, *Megaptera novaeangliae*, and the grey whale, *Escrhictius robustus*, however, most baleen whales are potential migrants (Forcada, 2009). Resident strategies have been reported mainly in toothed whales (here after odontocetes) including *Cephalorhynchus* dolphins (Dawson & Slooten, 1988; Hamner, Pichler, Heimeier, Constantine, & Baker, 2012; Heinrich, 2006; Oremus et al., 2012; Pérez-Alvarez, Alvarez, Aguayo-Lobo, & Olavarría, 2007; Pérez-Alvarez et al., 2015), the Amazon river dolphin, *Innia geoffrensis* (da Silva, 2009), bottlenose whales (*Hyperodon* spp.: Gowans, 2009) and the vaquita, *Phocoena sinus* (Hohn, Read, Fernandez, Vidal, & Findley, 1996). Resident dolphins tend to live in relatively small groups in protected inshore habitats. They do not range widely, probably due to the reliability of food resources. Individuals or small groups are likely better able to avoid predators than are larger groups (Gowans, Würsig, & Karczmarski, 2008). Finally, the nomadic strategy has been described for pelagic species, mainly odontocetes that travel long distances in search of food. They are often in large groups of hundreds to thousands, which may help with the detection of prey and predators (Olson, 2009). Because of the difficulty of collecting data such as photo-identification and genetic samples (Gowans et al., 2008), little is known about the population structure of these wide-ranging offshore cetaceans. It is suggested that these dolphins feed on sparsely distributed abundant food, thus reducing competition (e.g. *Stenella longirostris*: Andrews et al., 2006; Gowans et al., 2008; Karczmarski, Würsig, Gailey, Larson, & Vanderlip, 2005). Smaller *Delphinus* spp. tend to move in very large groups, while larger species such as Risso's dolphins, *Grampus griseus*, and the false killer whales, *Pseudorca crassidens*, tend to occur in smaller schools (Gowans et al., 2008). The largest odontocete, the sperm whale, *Physeter macrocephalus*, also appears to be a nomadic species and shows wide movements between areas of concentration (Mizroch & Rice, 2013; Whitehead, Coakes, Jaquet, & Lusseau, 2008).

While a specific movement strategy has been clearly identified for some species or populations, others show a mixture of strategies. For example, some populations of pilot whales (*Globicephala* spp.) and spinner dolphins (*Stenella* spp.) have been described as nomads (Gowans et al., 2008; Olson, 2009), while others have been identified as resident populations (*Globicephala* spp. off the California coast and Hawaii; Olson, 2009), remaining philopatric and showing a complex network of social interactions (e.g. *Stenella* spp.: Karczmarski et al., 2005). Both resident and transient groups have also been described for killer whales, *Orcinus orca*. Resident killer whales form relatively large, closely related groups and forage predominantly on individual or schooling fishes. These groups range less widely than transient killer whales. Transient killer whales feed on marine mammals and form smaller groups in order to hunt their prey cooperatively. These two 'ecotypes' are morphologically, ecologically and genetically distinct populations and maintain social and reproductive isolation (Ford et al., 1998).

The bottlenose dolphin, *Tursiops truncatus*, also shows a mixture of movement strategies. It has a cosmopolitan distribution and inhabits both coastal and oceanic habitats of temperate and tropical waters. This species exhibits a wide range of intraspecific variation in ranging patterns (Bearzi, Saylan, & Hwang, 2009; Wilson, Thompson, & Hammond, 1997). In some populations, individuals are year-round residents, staying within a small home range (e.g. 15–65 km^2; Gubbins, 2002) and living in the same area for many years or for their entire life (Connor, Wells, Mann, & Read, 2000). For example, in Sarasota Bay, Florida, U.S.A., approximately 100 dolphins resided in an area of about 125 km^2 for at least 30 years (Wells, 2003). Other resident populations, with group sizes generally of tens of individuals, have been described in Texas, U.S.A. (Irwin & Würsig, 2004), Moray Firth, Scotland (Wilson et al., 1997), Shark Bay (Smolker, Richards, Connor, & Pepper, 1992) and Moreton Bay, Australia (Chilvers & Corkeron, 2001) and Fiordland, New Zealand (Lusseau, 2005).

In contrast, other larger groups of *T. truncatus* populations (mostly composed of hundreds of individuals) are nomadic with little or no site fidelity (Ballance, 1992; Defran & Weller, 1999). These groups exhibit a low level of genetic structure and are generally considered as a single genetic unit over a large geographical distance (Quérouil et al., 2007; Tezanos-Pinto et al., 2009). In this context, two 'ecotypes' have been described by Duffield, Ridgway, and Cornell (1983) as 'inshore/coastal' and 'offshore/pelagic' nomadic types, based on haematology profiles and distribution. Later studies confirmed this finding with independent lines of evidence from morphology, genetics, parasite load and diet (Hersh & Duffield, 1990; Hoelzel, Potter, & Best, 1998; Mead & Potter, 1990; Natoli, Peddemors, & Hoelzel, 2004). In particular, genetic differentiation has been detected systematically between resident and nonresident populations , while coastal populations exhibit much lower levels of genetic diversity compared to adjacent pelagic groups (Natoli et al., 2004). Based on the social and genetic conformation of resident populations, it has been proposed that pelagic populations are likely to be the source of independent founder events that have generated resident populations in coastal areas (Hoelzel et al., 1998; Natoli et al., 2004). However, there has been a lack of empirical data to test this hypothesis, to evaluate interactions between resident and nomadic populations, or to explain how these populations persist over time.

In Chile, numerous nomadic groups of *T. truncatus* are sighted along the entire coastline and follow the general pattern described worldwide (Aguayo-Lobo, Torres, & Acevedo, 1998; Olavarría et al., 2010). However, a single resident population has been reported in north-central Chile, in a small area between the Isla Chañaral Marine Reserve and the Choros-Damas Marine Reserve (29°02′–29°14′S). In this zone, long-term studies show that sympatric resident and transient bottlenose dolphins differ in behaviour, group size and site fidelity (Santos-Carvallo et al., 2018; Thomas, 2005). Some resident individuals show long residence (≥15 years) and strong site fidelity, using the area for feeding, nursing and calving, and are usually seen in groups of 15–20 individuals (range 2–40) (Gibbons, 1992; Thomas, 2005). In contrast, transient bottlenose dolphins show a lower rate of residency and are usually seen in larger group sizes of approximately 70 individuals (Santos-Carvallo et al., 2018).

In this study, using long-term residence data from a 13-year systematic photo-identification study of the resident population and genetic mtDNA information from both the resident and nonresident dolphins, we analysed the social dynamics over time and the genetic variation of a long-term resident bottlenose dolphin population off the central coast of Chile, and evaluated its sociogenetic interaction with nonresident groups. We hypothesize a contribution of genetic variability from the pelagic nonresident group to the coastal resident group as an underlying mechanism that may permit the resident group's persistence over time.

METHODS

Study Area, Data Collection and Residence Categories

A systematic long-term monitoring programme of *T. truncatus* within the Isla Chañaral (29°02′S, 71°36′W) and Choros-Damas (29°14′S, 71°32′W) Marine Reserves was undertaken from 2003 to 2015, with a gap of 3 years (2011–2013; Table 1). A total of 95 boat-based surveys were conducted (Fig. 1), using a 7 m local