

REVIEW

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# The ecological value of long-term studies of birds and mammals in Central America, South America and Antarctica

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## Abstract

This review covers long-term ecological studies in Central America, South America, and Antarctica that include at least 10 years of data on both terrestrial and marine mammals as well as birds. Specifically, we compiled long-term research on social systems, population ecology, and community ecology. Long-term research is necessary to understand decadal trends and dynamics that would otherwise go unnoticed in short-term studies. This review highlights the impact of ecological conditions as well as territoriality and conflict on social organization and structure, the role that environmental perturbations and climate change have on populations, and how interaction between biotic and abiotic factors influence entire ecological communities. It especially highlights the need for additional long-term studies to assess climate change trends and the ecological changes that will follow.

**Keywords:** Long-term studies, Social systems, Population ecology studies, Community ecology studies, ENSO, Small mammals

## Background

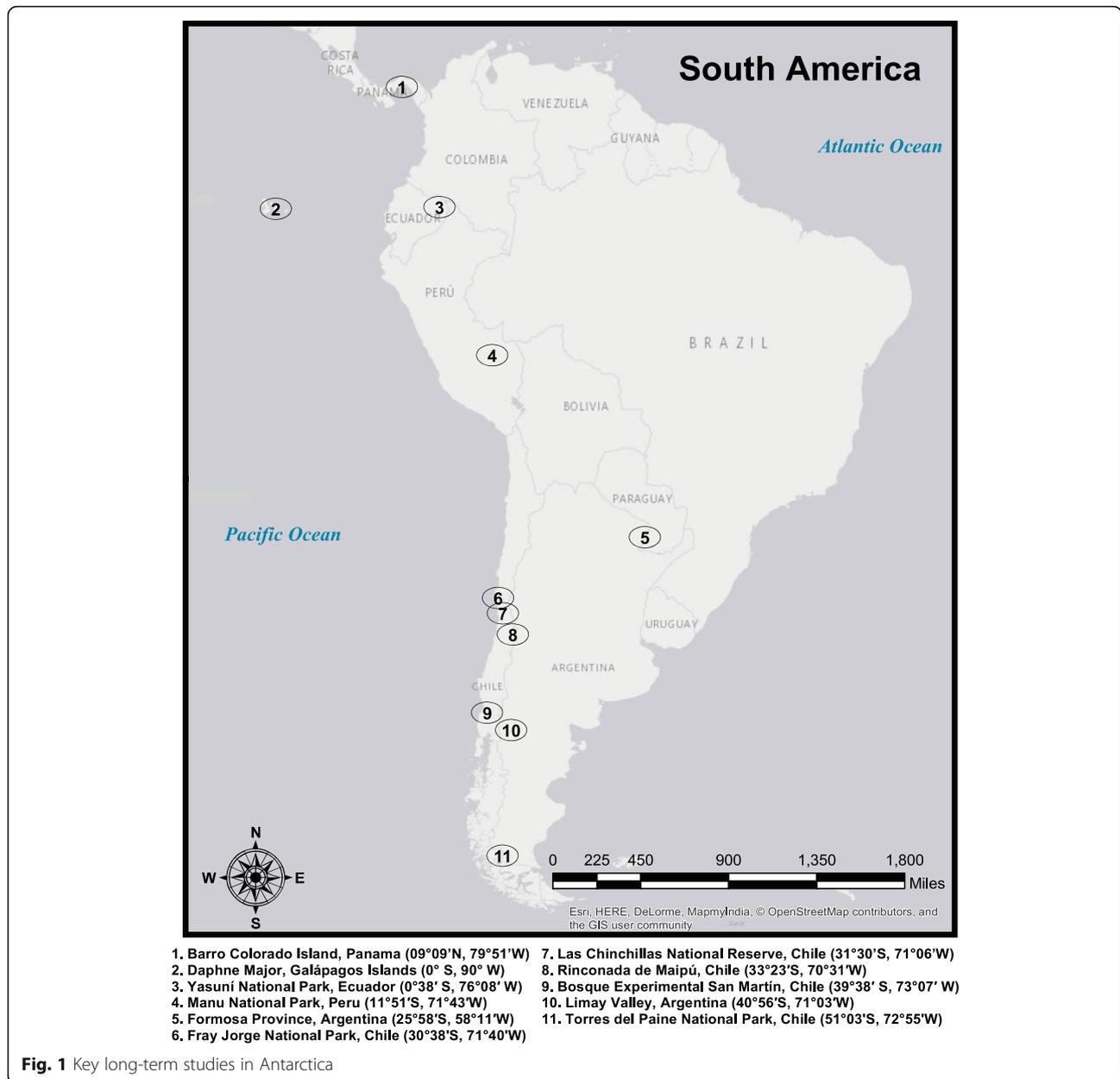
Increasingly, greater value is placed in long-term ecological studies [1–6]. Long-term studies have generated important insights into ecological processes at the population [7, 8], community [9–11], and ecosystem [12] scales and have been applied to urban systems [13]. Long-term studies have informed theory on impact of environmental change or perturbations to these processes ([7, 14–17]). Continuously collected datasets over appropriate temporal scales are required to answer specific ecological and evolutionary questions [1, 2]. For example, long-term ecological studies have shown how complex phenomena such as El Niño-Southern Oscillation (ENSO) events influence organisms at multiple scales (individual to ecosystem; [18]). Data from a long-term study of North American marmots revealed the potentially evolutionary implications of environmental change on high altitude organisms [7, 19]. Not surprisingly, patterns revealed in some long-term studies differ from those in short-term field studies resulting in challenges to existing

paradigms [14]. Thus, it is now clear that long-term datasets are essential in the development of predictive models and evidence-based management strategies [4, 20].

Recent syntheses of long-term studies of animals have focused largely on studies conducted in Africa, Australia, North America, and Europe [2, 21]. Long-term studies have also been an integral part of ecological research in central and South America and Antarctica ([1]; Figs. 1 and 2; Tables 1 and 2). Perhaps, the most well-known long-term study in the region is Rosemary and Peter Grant's study of evolutionary change in Galapagos finches [22, 23]. The Grants' study, 40 years in the making, has shed important insights into factors shaping phenotypic change and served as a model for long-term ecological research. Other long-term studies, including decades of research conducted at three Long-Term Socio-ecological Research (LTSER) sites in Chile – Parque Nacional Bosque Fray Jorge [24], Senda Darwin Biological Station [25] and Omora Ethnobotanical Park [26] – have contributed to theory and motivated efforts to integrate scientific and social science approaches to tackle large-scale environmental challenges [1, 27, 28]. There have also been numerous 'lower profile,' but valuable long-term studies in the region (see Table 1

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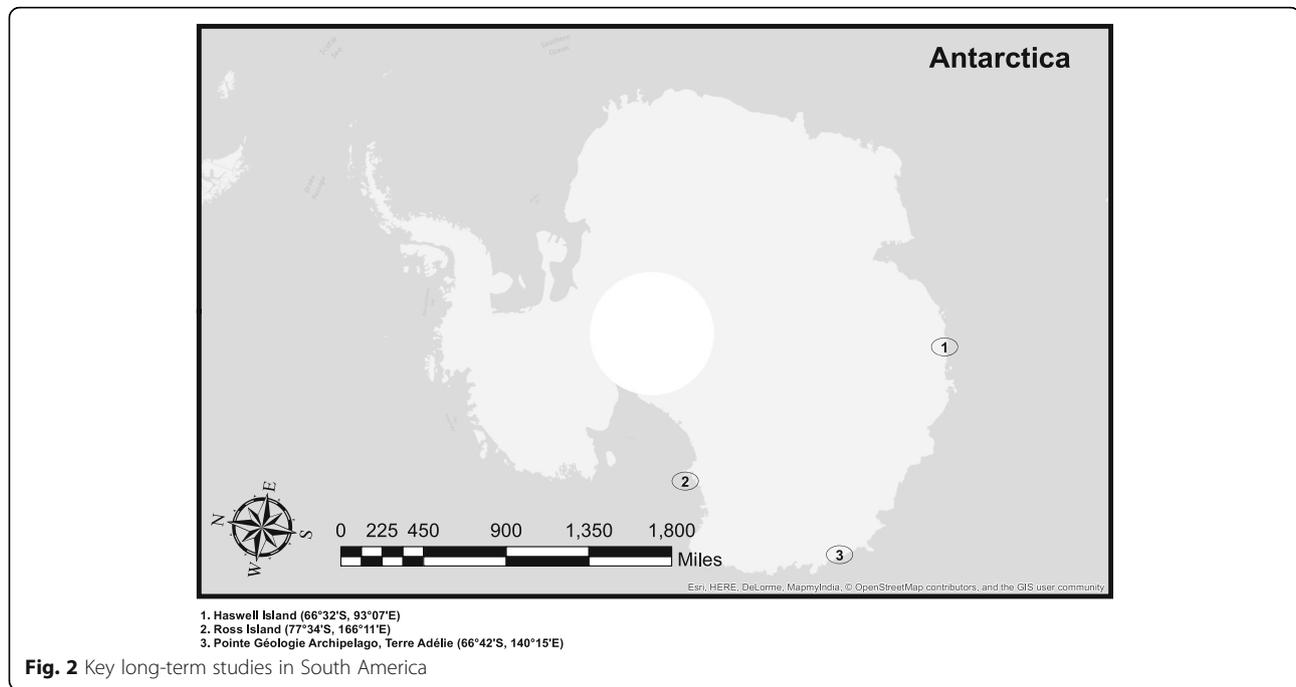
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in [1, 29, 30]). Together, these studies have answered questions about ecological and socioecological processes in semi-arid and arid shrublands, forests (old-growth mixed and evergreen, tropical forests, sub-Antarctic), grasslands (steppe), rocky intertidal, estuarine, and oceanic ecosystems [1]. Thus, there is great potential to learn broad, important concepts from this work and promote the continuation of long-term data collection in these regions.

Our objective is to highlight major advances in our understanding of ecology that have emerged from long-term studies of birds and mammals in Central and South America and Antarctica. Our review will provide the

basis of comparison to long-term studies of birds and mammals in other regions of the world and inform theory regarding the impact of decadal ecological changes and/or climate change on animal behavior as well as population and community processes. We define a long-term study as one that covers 10 or more continuous years of study. We identified long-term studies from papers that reported datasets of 10 or more years as well as series of short-term studies that make up a long-term study. We include studies in which individuals are individually marked as well as long-term monitoring studies in which individuals are not marked. A comprehensive review of all long-term studies in the



region, including plant-based population studies, is beyond the scope of this review. Rather, we aim to highlight three significant, ecological themes to which long-term field studies of birds and mammals in the region – including marine environments and Antarctica – have made significant contributions: (i) social systems, (ii) animal population and evolutionary ecology, and (iii) community ecology.

### Social ecology

Long-term studies on social systems allow us to analyze trends across generations as opposed to extrapolating data based on single-generation studies. The following studies cover factors including resource availability and other ecological conditions and their influence on mating system formation, social organization, and reproductive success from a long-term perspective.

Since 2003, the ‘Comparative Socioecology of Monogamous Primates’ study in Yasuní National Park and Biosphere Reserve in eastern Ecuador (76°08' W, 0°38' S) and Formosa Province, Argentina (58°11' W, 25°58' S) has revealed insights into ecological and social factors influencing social monogamy in primate species including owl monkeys (*Aotus azarai*), red titi monkeys (*Callicebus discolor*), and equatorial sakis (*Pithecia aequatorialis*) [31–33]. One theme that has emerged from this work is that intrasexual conflict plays an important role in social dynamics and reproductive success in some species but not others. In a study of 18 owl monkey groups in Argentina, [31] observed that individuals who mate with a single opposite-sex individual produced

25% more offspring per decade of tenure than individuals mating with multiple partners (both males and females). It was also shown that male intruders initiated the splitting up of male-female pairs and in some cases resulted in the death of expelled individuals, observations consistent with strong intra-sexual conflict in this species. In contrast, a focal study of one equatorial saki group and one red titi monkey group in Yasuní National Park suggests that intrasexual conflict is low and groups vary in social composition [32, 34]. Monkey groups are continually being tracked (e.g. [34]), which ultimately should provide greater power to place inferences about the importance of social monogamy in South American primates.

Giant otter (*Pteronura brasiliensis*) social units consist of one dominant breeding pair and their subordinate offspring (non-breeding helper adults and juveniles/infants) until males reach sexual maturity and disperse [35]. Whereas some females disperse, others remain philopatric to their natal group and ultimately, take their mother's or sister's reproductive position in the group. A long-term study (1991–2006) of these otters in Manu National Park in Peru (11°51'23" S 71°43'17" W) revealed that groups were larger and the number of offspring produced by females was greater in territories with more access to lakes, presumably due to greater availability of fish [36]. Lower quality territories in terms of size (and associated fish abundance) supported only monogamous pairs. Intriguingly, variation in group size did not predict variation in the number of offspring produced by females regardless of territorial quality and

**Table 1** Long-term studies of social systems and population ecology in central and South America and Antarctica

Genus and species	Common name	Location of study	Duration of study (years)	Individually marked?	Theme	Key reference
<i>Octodon degus</i>	Degu	North-central Chile	12 years (2004–2016)	Y	Social systems	[29]
<i>Oligoryzomys longicaudatus</i>	Long-tailed rice rat	Chile, rainforest	19 years (1979–1998)	Y	Social systems	[65]
<i>Lama guanicoe</i>	Guanaco	Chilean Patagonia	10 years (1989–1999)	Y	Social systems	[40]
<i>Pithecia aequatorialis</i>	Equatorial sakis	Ecuador	10 years (2004–2014)	Y	Social systems	[32]
<i>Pteronura brasiliensis</i>	Giant otter	Peru	15 years (1991–2006)	Y	Social systems	[36]
<i>Ctenomys sociabilis</i>	Colonial tuco-tuco	Argentina	20 years (1994–2004)	Y	Social systems	[45]
<i>Aptenodytes forsteri</i>	Emperor penguin	Antarctica	54 years (1957–2010)	N	Population and evolutionary ecology	[80]
<i>Spheniscus magellanicus</i>	Magellanic penguin	Punta Tombo, Argentina	28 years (1982–2010)	Y	Population and evolutionary ecology	[75]
<i>Apenodytes forsteri</i>	Emperor penguin	Point Geologie, Antarctica	46 years (1956–2001)	N	Population and evolutionary ecology	[84]
<i>Pagodroma nivea</i>	Snow petrel	Point Geologie, Antarctica	40 years (1963–2002)	N	Population and evolutionary ecology	[71]
<i>Fulmar glacialisoides</i>	Southern fulmar	Point Geologie, Antarctica	40 years (1963–2002)	N	Population and evolutionary ecology	[71]
<i>Pygoscelis adeliae</i>	Adelie penguin	Ross Island	41 years (1960–2000)	N	Population and evolutionary ecology	[84]
<i>Cephalorhynchus eutropia</i>	Chilean dolphin	Chile	14 years (1988–2012)	Y	Population and evolutionary ecology	[68]
<i>Phyllotis darwini</i>	Darwin's leaf-eared mouse	Chile, Auco	10 years (1987–1996)	Y	Population and evolutionary ecology	[115]
40+ marine species	See [88]	East coast of South America	38 years (1976–2013)	Y	Population and evolutionary ecology	[85]
<i>Phyllostomidae</i> bats (30 species)	See [33]	Barro Colorado Island, Panama	10 years (1975–1985)	N	Population and evolutionary ecology	[114]
<i>Geospiza fortis</i> , <i>Geospiza scandens</i> , <i>Geospiza fuliginosa</i>	Médium ground finch, common cactus finch, small ground finch	Daphne Major, Galapagos Islands	30 years (1972–2001)	Y	Population and evolutionary ecology	[22]

size. These observations suggest competition is relaxed and sociality is favored when resource availability is high [37], but that the benefits of living in groups are limited, and that cooperative breeding may be favored when resources are patchy [36].

During the breeding season, male guanacos (*Lama guanicoe*) are found either in family groups, in male-only groups consisting of non-territorial males, or as

solo territorial males [38]. Guanacos exhibit seasonal resource-defense polygyny in which males compete for access to resources required by females in order to ensure reproductive success [39]. Using a 10-year dataset of individually marked guanacos in a population in Parque Nacional Torres del Paine (51°03'S, 72°55'W), [40] determined that male reproductive success is heavily influenced by male territoriality and social structure. Most

**Table 2** Long-term studies of community ecology in central and South America and Antarctica

Community	Species	Location of study	Duration of study (years)	Individually marked?	Key Reference
Rolling pampas, agricultural lands	7 species	Argentina	24 years (1984–2008)	Y	[87]
Semi-arid rodent community	7+ species	Bosque Nacional Parque Fray Jorge, Chile	26 years (1989-present)	Y	[9]
Predator assemblage	6+ species	Auco, Chile	28 years (1987-present)	N	[104]

breeding and non-breeding males show strong site-fidelity throughout the mating season and between years. For breeding (family group) territorial males, previous familiarity with a given area seems to improve mating success [41, 42], and the probability that individuals reproduce multiple times over a lifetime in previously held territories influences site fidelity. Despite their low probability of mating, solo territorial males may exhibit site fidelity due to the difficulties of establishing territories in an unfamiliar location, and because of the uncertainty of siring offspring. Females move freely between male territories, often in the post-mating season [43], implying a polygynous mating system based on territory defense. Solo territorial males exhibit site-fidelity near territorial males and mate with females that become reproductively active late in the season. High site fidelity might indicate that there are factors other than resource availability, such as aggression, social status, and physical condition [44] that may influence guanaco mating system.

One of the most comprehensive long-term studies in South America has been Eileen Lacey's 20-year study of the social system of the colonial tuco-tuco (*Ctenomys sociabilis*), a subterranean rodent found in the Limay Valley of Argentina (40°56'S, 71°03'W) (Fig. 2). Female colonial tuco-tucos in this population share burrows with 1–4 generations of closely related females and a single immigrant male [45, 46]. Groups do not switch burrow systems between consecutive years [46], suggesting that the costs of burrow-switching are high. Similar to the subterranean bathyergid mole rats of Africa (*Heterocephalus glaber*) [47], [48] hypothesized that group living in ctenomyid rodents is associated with hard soils and patchily distributed resources. Contrary to the expectations of the aridity-food distribution hypothesis [47], solitary Patagonian tuco-tucos (*C. haigi*) in the Limay Valley live in areas with harder soils than do colonial tuco-tucos [48]. Tammore et al. [49] found that across their full geographic range, colonial tuco-tucos occur in habitats characterized by dry soil as well as wet soil, indicating that habitat specialization may not be as important as previously thought. However, spatial scale-dependent patchiness of favorable habitat may still influence dispersal in the species.

Contrary to expectations, group living results in direct fitness costs to colonial tuco-tuco females. Philopatric yearling females rear fewer offspring per capita than dispersing females and annual reproductive success of group living females is 26–40% less than expected [30]. Lifetime reproductive success and survival to a second breeding year did not differ between social strategies (disperser vs. philopatric) leading [30] to argue that ecological constraints on dispersal explains group living in colonial tuco-tucos. Although the amount of time that adults attend a communal nest increased with the number of adults in the group

[50], per capita direct fitness decreased with increasing adult group size [30], suggesting that group size benefits or benefits of communal care are minimal and/or do not exceed potential costs of living in groups.

A 12-year study (2005-present) led by Luis Ebensperger and Loren Hayes on the common degu (*Octodon degus*), a semi-fossorial rodent endemic to Chile, has generated valuable insight into ecological and social conditions influencing direct fitness consequences of group living. In contrast to colonial tuco-tucos, the availability of critical resources i.e., burrows for rearing offspring, does not have a strong influence on degu sociality [51]. Groups form as a result of philopatry and the movement of adults between social units [52], resulting in groups that lack strong kin structure [53, 54]. Initial short-term studies of 2–3 years suggested that group living resulted in direct fitness costs to females [51, 55], an extreme cost given that degus are ecologically semelparous [56]. However, analyses of an 8-year dataset suggested that the relationship between per capita direct fitness and group size is positive under conditions of low mean food but not conditions of high mean food [29]. Direct fitness of adult group members is also influenced by stability in group composition in sex-specific ways. Whereas male degus benefit the most from low female group membership stability, females benefit the most from high female group membership stability [57]. Interestingly, these findings suggest a potential sex conflict over stability of social groups. Most recently, direct fitness variation among females within multi-female groups was noted to decrease with increasing relatedness of females in groups and increasing soil hardness at burrow systems (Hayes et al. submitted). Together, these observations suggest that benefits of cooperation among females are modulated by ecological and social conditions. In particular, benefits based on mean reproductive success materialize under harsh ecological conditions and high social stability. On the other hand, benefits in terms of decreasing variance in reproductive success materialize mostly in kin groups exposed to harsh soil conditions (Hayes, LD and Ebensperger LA, unpublished data).

### Population and evolutionary ecology

Populations undergo natural fluctuations due to various factors, including climate fluctuations that can be traced in long-term studies and their influence can vary from year to year. Long-term studies can track changes in density, composition, mortality, and distributions as well as potential causes, such as climate change and density-dependent effects. The following studies examine these factors in both terrestrial and marine mammals and birds.

From 1972 to 2001, Peter and Rosemary Grant have examined morphological variance (body size and beak

size and shape) and ecology of the medium ground finch (*Geospiza fortis*) and the cactus finch (*Geospiza scandens*) on Daphne Major, Galapagos (0°25' N, -90°22' W) [22]. They were able to study natural selection and introgressive hybridization in these two species. Mean body size and beak shape were significantly different in the two species from the beginning of the study to the end. However, the two species differed on the direction of selection for net body and beak size. Natural selection on these traits led to evolution in these species due to the high heritability of these traits. There was occasional hybridization between the two study species as well as a third, the small ground finch (*Geospiza fuliginosa*), leading to additive genetic variation related to beak size and shape and body size traits. The Grants also examined the effect of an El Niño event on food availability for the finches, which led to selection for smaller beak sizes [58]. Over the decades of studying these finches, the Grants determined that the morphological evolution that took place could not have been predicted at the beginning of the study, highlighting the importance of long-term studies on understanding evolutionary trends and the effects of extreme weather events.

Ronald Sarno and colleagues' study of guanacos (*L. guanaco*) in Torres del Paine National Park (51°03' S, 72°55' W), Chile has revealed insights in demographic processes influencing population growth. Sarno and Franklin [59] found mean yearly birth mass (a predictor of reproductive success) was negatively associated with population density. Maternal condition can suffer under higher densities, which in turn impacts birth mass [60, 61] and survival [62]. Predation by Patagonian pumas (*Puma concolor*) and winter snowfall are additional predictors of offspring survival in this population ([62, 63]). Population density is an important predictor of population growth rate in a second population on Tierra del Fuego island, Chile (53°9' S, 69°3' W), that has been the focus of a long-term study. Between 1977 and 2012, there was a negative relationship between the population growth rate and abundance of guanacos [64]. The number of sheep in the study site, annual mean precipitation, and winter mean temperature do not seem to be predictors of the population growth rate of guanacos at this site.

Between 1979 and 1998, [65] conducted a live-trapping study of long-tailed rice rat (*Oligoryzomys longicaudatus*) at the San Martín Experimental Preserve near Valdivia, Chile (39° 38 S; 73° 7 W). The authors used modeling approaches to determine how feedback structure, climatic, and stochastic factors influence long-tailed rice rat population dynamics. They observed that populations experienced irregular numerical fluctuations, with first-order feedback structure regulating population change. First-order dynamics could be driven by intraspecific competition for food, space, or areas without predators. Population

growth rates were influenced by periodic flowering of bamboo (*Chusquea spp.*) and mast production. Large scale climatic variables – Southern Oscillation and Antarctic Oscillation – had non-linear direct and indirect effects on rice rat population dynamics. Decreased summer rainfall associated with El Niño events [66, 67] likely influence seed availability during the next winter, which corresponds with the breeding season of rice rats [65].

Pérez-Alvarez et al. [68] conducted a 14-year study of the Chilean dolphin (*Cephalorhynchus eutropia*), a species endemic to coastal Chile. Although there are no geographical barriers in its distribution, analysis of microsatellite markers revealed that northern [found in habitat ranging from Valparaíso (33°020 S) to Chiloé (42°000 S)] and southern populations [(from Chiloé to Navarino Island (55°140 S)] are genetically distinct. The individuals sampled were located at sites spanning the Chilean coast from 35°20' S to 52°40' S, but despite lacking a physical barrier, there is limited gene flow between the two populations [68]. Potentially, there are ecological or behavioral adaptations to the local habitats that maintain a genetic subdivision of the population.

An impressive number of long-term population monitoring studies on Antarctic seabirds have been sustained, all for 30 or more years ([69–75]; Table 1; Fig. 2). An emerging theme from these studies is that Antarctic seabird populations are sensitive to climate change [71, 76]. Herein, we highlight some of the major insights generated from long-term studies on three penguin species: Magellanic penguins (*Spheniscus magellanicus*), Adélie penguins (*Pygoscelis adeliae*), and emperor penguins (*Aptenodytes forsteri*).

Since 1982, Dee Boersma and colleagues have monitored banded individuals and marked nests in multiple study areas of Magellanic penguins (*Spheniscus magellanicus*) in Punta Tumbo, Argentina (44°02' S, 65°11' W). Using a dataset from 1984 to 1991, [16] determined that reproductive success in this population was density-dependent, and that the number of fledglings per active nest decreased with increasing nest density. This finding supports the hypothesis that the value of habitat decreases with increasing density of conspecifics [77]. Likely contributing factors included intraspecific competition and predation, both of which were significantly greater in areas with high nest density than in areas with low nest density. These correlative data were supported by the results of an experimental study showing that fledging success was higher, and that fewer aggressive interactions and less predation occurred in a plot with reduced animal density when compared to control plots [75].

Boersma and colleagues' long-term study has also revealed insights into the impact of climate change on the persistence of colonial bird populations. Using data from 1983 to 2010, [78] determined that starvation and

predation were the most important predictors of chick mortality across years in Magellanic penguins, although climate variability also negatively influenced reproductive success. The number of storms in early December, when all chicks are less than 30 days of age, increased during the period of this study. Chick mortality due to storms reached 5% during the period between 2008 and 2010. The probability of dying increased with increasing rainfall and as the minimum temperature decreased, though these relationships depended on chick age and the interactions between age squared, rainfall and temperature. Climate models predict increasing storm frequency and intensity in the future which would likely lead to increased chick mortality from storms. Chick mortality due to storms occurred disproportionately more from bush nests, which provide lower quality refuges compared with burrow nests. Finally, the synchrony of egg laying has decreased since 1983, increasing the time period that chicks are most vulnerable to storms. Thus, a potential consequence of increased climatic variation is lower recruitment in the years of especially high chick mortality and reduced population persistence.

For over 50 years, researchers have monitored populations of Adélie penguins (*Pygoscelis adeliae*) of Ross Island colonies (77°34'S, 166°11'E) and emperor penguins (*Aptenodytes forsteri*) of Pointe Géologie (Terre Adélie: 66°42'S, 140°15'E; [2]) and Taylor Glacier colony (67°36'S, 62°53'E) in Antarctica [80]. Adélie penguin populations in the southern Ross Sea have been increasing (0.067 annual growth rate, 2001–2012), though numbers remain lower than they were in early 1980s [81]. In contrast, emperor penguins have been in decline, with a 50% drop in numbers since the 1970s [71, 82]. Jenouvrier and colleagues have coupled demographic data and modeling techniques to identify factors underlying changes in emperor penguin populations at Terre Adélie. One explanation for the decline in emperor penguins is a warming event that occurred in the southern Indian Ocean during the 1970s and that reduced sea ice extent [71, 82]. A comparison of the Terre Adélie colony with another declining colony at Haswell Island (66°32'S, 93°07'E), revealed that numbers of breeding male emperor penguins correlated similarly to sea ice extent in both colonies, suggesting climate fluctuations as a main cause of population changes in the species ([83]; but see [73, 81]). Decreasing sea ice cover seems to be correlated with population declines in both species. However, Ainley et al. [84] suggested two alternative explanations for changes in population density: (i) ocean food web disturbances due to climate fluctuations, and (ii) Antarctic Oscillations, or pressure variance that influences winds and sea ice transport. Adélie penguins are sensitive to size of polynya (open water surrounded by ice) and seasonal growth rates, while emperor penguins seem

more sensitive to sea ice extent due to their breeding habits [84]. Regardless, climate fluctuations are likely to be blamed for population declines in both species.

Prado et al. [85] used 38 years of data on marine mammal stranding along the east coast of South America to analyze shifts in distributions and mortality rates in marine mammals. Five species made up 97% of all strandings: Franciscana dolphins (*Pontoporia blainvillei*), bottlenose dolphins (*Tursiops truncatus*), South American fur seals (*Arctocephalus australis*), subantarctic fur seals (*Arctocephalus tropicalis*), and South American sea lions (*Otaria flavescens*). These species are particularly vulnerable to fishing mortality, as some species had higher stranding rates in months correlating with increased fishing, and these coastal habitats may also influence their relatively high stranding rate when to species that live in the deeper ocean. Further marine mammal stranding analysis may highlight the link between oceanic processes and species distribution patterns

Vales et al. [86] examined diets in South American fur seals (*Arctocephalus australis*) stranded between 1994 and 2011 along the coast of Brazil (from 29°19'S, 49°43'W to 31°15'S, 50°54'W). They recorded the consistent reliance by this species on pelagic fish species as a food source over the 17 years of study, noting the corresponding low consumption of demersal and benthic species. Despite an increase of trawling targeting demersal and benthic species in the area since the mid-1990s, the diet of *A. australis* has not been significantly affected. = However, the authors note that overfishing of other species could lead to negative effects on fur seals. Marine mammals may be at risk due to fishing mortality [85], as well as indirect effects caused by fishing such as increased competition for food [86]. These long-term studies will be critical for the monitoring of such effects.

### Community ecology

To date, there have only been a few long-term studies on vertebrate communities in central and South America. However, this limited number of studies has made important contributions to our understanding of the potential effects of abiotic and biotic factors and evolutionary history have on community processes. Herein, we review two long-term studies of small mammal communities in Chile and Argentina.

Since the 1970's, agricultural practices have altered the habitats in the Rolling Pampas region of Argentina (34°08'S, 59°14'W), where much of the original vegetation and food resources consumed by rodent communities have been replaced with soy and agricultural crops [87]. Live-trapping conducted over 24 years (1984–2008) revealed that the transformation of native habitat to agricultural habitat had dramatic but species-specific

effects on the native rodents in the community. Inter-annual fluctuation in the abundance of Azara's grass mouse (*Akodon azarae*), the dominant competitor in the rodent community, was attributed more strongly to variation in precipitation than changes in the physical habitat [87]. In comparison, the yellow pygmy rice rat (*Oligoryzomys flavescens*) numbers decreased within the converted agricultural areas, but increased in crop field borders. The numbers of the small vesper mouse (*Calomys laucha*), a generalist species, increased following changes in habitat [87]. Finally, invasive species including the house mouse (*Mus musculus*), black rat (*Rattus rattus*), and Norway rat (*Rattus norvegicus*) predictably became more abundant during the transformation from native to agricultural habitats [87, 88]. The observed changes in rodent community composition have been hypothesized to be driven by interspecific competition, in which dominant species such as *A. azarae* force others out into less suitable habitat (i.e. soy crop fields) through competitive exclusion of resources [88].

Since the late 1970s, Peter Meserve, Fabian Jaksic, Julio Gutiérrez, Douglas Kelt and others [9, 24, 89, 90]) have been studying small mammal community responses to environmental conditions in a thorn scrubland habitat in Parque Nacional Bosque Fray Jorge (PNBFJ), a World Biosphere Reserve in north-central Chile (30°08'S, 59°14'N). The location is impacted by El Niño-Southern Oscillation (ENSO) events every 5–7 years, allowing Meserve and colleagues to determine how dramatic, periodic fluctuations in rainfall influence both population [91] and community structure [9, 24, 90]. ENSO-related rainfall in western South America leads to a complex set of biotic responses involving bottom-up and top-down processes [89]. Bottom-up regulation involves vegetation and seed blooms, followed by small rodent increases, which lead to predator increases [89, 92–94]. Following an ENSO event between 2000 and 2002, the density of the herbivorous rodent, *Octodon degus*, increased dramatically [24, 94]. In turn, high degu densities have direct top-down effect on native herbs and indirect effects on invasive annual herbs [89, 94]. The Meserve et al. study is unique in that the investigators have monitored the response of small mammal communities to experimental manipulations of competitor density (*Octodon degus*) and predation risk for >25 years (1989-present). Not surprisingly, this study has generated >70 papers and informed a wide range of community ecology theory (see [9, 24, 89] for synthetic reviews). Most importantly, the work has supported the hypothesis that community composition is regulated by a complex interaction between abiotic and biotic factors.

An initial aim of the study developed at PNBFJ was to determine how biotic factors, such as predation, regulate the small mammal community through a shifting balance of top-down and bottom-up control [89]. The

exclusion of predators and perceived risk of predation influences some aspects of spatial ecology [95, 96] and survival of degus [89] and other small mammals in the community [89, 95]. However, and contrary to theory, predator exclusion did not have a strong effect on the abundances of other small mammals in the community, namely murid rodents and a marsupial species (e.g. [24]). Furthermore, the effect of predators on space use seem smaller compared with thermoregulatory constraints [97], yet its effect on degu abundance is greater during drought years than wet years [74].

The demographic responses of small mammals to periodic fluctuations in rainfall vary depending on life history strategies and residency status ([90, 91, 98]). Two multiparous species with short lifespans, short gestations and large litters, Darwin's leaf-eared mouse (*Phyllotis darwini*) and the olive grass mouse (*Abrothrix olivaceus* – now *A. olivacea*) undergo rapid increases in abundance within 3–4 months after periods of high rainfall [24, 90]. High reproductive output also increases persistence of these species in drought years [90]. In contrast, the abundance of *Octodon degus* – which has lower reproductive output – increases slowly, with a 1–2 year time lag following peak rainfall [90] and is less resilient in drought years [99]. In terms of residency in the thorn scrub, there are species-specific effects of rainfall on the abundance of two opportunistic rodents found in the thorn scrubland (long-tailed pygmy rice rat, *Oligoryzomys longicaudatus*, and long-haired grass mouse, *Abrothrix longipilis*; [100]). *O. longicaudatus* is characterized as being sporadic and with long periods of absence from the thorn scrubland [76]. In comparison, *A. longipilis* exhibit much less pronounced periods of increase during wet years [76]. All species used nearby mesic habitats during periods of drought [79].

Since the early 2000s, an increase in rainfall and a decline in the inter-annual variation of rainfall in Meserve and colleagues' study site has resulted in fewer pronounced periods of drought. Consequently, there has been a major shift in small mammal composition. *Octodon degus* abundance has become more stable and less temporally variable [24] contributing more to small mammal biomass in the thorn shrubland [24, 90, 99]. This change can have critical consequences to the community for multiple reasons. First, degu herbivory and behavior has complex effects on plant diversity including negative impacts on perennial plant diversity through degu herbivory [24]. In contrast, degu runway development and digging is thought to have a positive effect on the density of annual plant seed densities [94, 101]. In this way, the abundance of degus has indirect effects on other small mammals by increasing or decreasing the availability of food and cover (critical for shade, safety). Additionally, degus are superior competitors than most

of the other small mammals in the community [97]. Based on giving up densities (GUDs), the foraging of some species, such as *Abrothrix olivaceus*, is less efficient in areas in which degus have access [97]. Taken together, long-term studies at PNBFJ have highlighted how abiotic and biotic ecological conditions interact at different levels and temporal scales to influence demography and space use of small mammals.

Studies lead by Fabian Jaksic, Mauricio Lima, Matias Arim, and Ariel Farias at Las Chinchillas National Reserve, near Auco, Chile (31°30'S, 71°06'W) focused on vertebrate predator assemblages. Arim et al. [102] studied diets of 6 predatory species [burrowing owl (*Speotyto cunicularia*), Magellan horned owl (*Bubo magellanicus*), austral pygmy owl (*Glaucidium nanum*), barn owl (*Tyto alba*), American kestrel (*Falco sparverius*), and culpeo fox (*Lycalopex culpaeus*) to monitor food chain lengths based on diet composition and trophic position. The authors' scale designated a predator with a diet of only herbivorous prey as having the lowest possible trophic position, while a diet of only nonherbivorous prey would indicate the top most trophic position. They discovered an overall positive association between precipitation and food chain length, which may not have been uncovered on a short-term scale. These studies also have revealed effects linked to long-term fluctuations in climate. Previtali et al. [89] Lima et al. [103] and Farias and Jaksic [29] determined that increased small-mammal abundance, and thus predator food availability, correlated positively with increased rainfall (corresponding with El Niño events). Farias and Jaksic [105, 106] compared empirical data with models and identified two divergent predatory species groups in Las Chinchillas National Reserve, one which mostly fed on small mammals, and another with a more varied, generalized diet. Changes in the functional structure of this assemblage can be attributed to the relationship between species composition and abundance of main and alternative prey. The two predatory species groups will vary their diets depending on mammal prey availability having higher niche overlap in extremely favorable or extremely scarce prey resource conditions, and less overlap during moderate prey shortages [106]. Similarly, Farias and Jaksic [104] showed how functional diversity of the predator assemblage in Las Chinchillas National Reserve is influenced by changes in taxonomic composition as well as behavioral responses by the predatory species.

**Summary of major insights** This selective review of long-term studies in central and South America and Antarctica highlights the advantages of long-term studies over short-term studies. Overall, these advantages are materialized at different scales of analysis or themes:

*Social systems:* Long-term studies of animal social systems in Central and South America have generated valuable insights into the role of sexual conflict in social monogamous species, and the influence of ecology on the formation and reproductive consequences of social systems. For example, giant otter social organization may be influenced by resource availability, and guanaco and primate mating success is tied to territoriality and social structure. Another major theme that has emerged is that there is contradictory evidence on how ecology influences social systems. On the one hand, short-term studies of *C. sociabilis* and *O. degus* suggest that ecological conditions do not influence the formation of groups. However, a long-term study of *O. degus* has shown that harsh conditions influence the direct fitness consequences of group living [29], suggesting that researchers need to rethink how we examine the effects of ecology on the reproductive consequences of social systems.

*Population and evolutionary ecology:* Long-term studies of population ecology, largely in Antarctica, have provided valuable census data for modeling the impact of environmental perturbations on populations. However, in guanacos, population density seems to have the largest influence on survival. Rice rats seem to be affected by vegetation and its response to extreme weather events [107]. Current models project high probabilities of extinction in seabirds due to climate-mediated effects on sea ice levels [108]. Other factors, including ENSO effects and snow falls [109], impact seabird colonies in Antarctica, suggesting that weather variation caused by climate change should also be monitored on a long-term scale. The Grants' groundbreaking study of Galapagos finches would not have been observed on a smaller time scale.

*Community ecology:* Despite a paucity of long-term studies on community ecology, Jaksic and colleagues' work in Las Chinchillas National Reserve and Meserve and colleagues' work in Parque Nacional Bosque Fray Jorge have had major impacts on our understanding of community processes. Jaksic, and Lima have given insight specifically to how ENSO rainfall influences bottom-up community structure ([91]; [92]). Most critically, the work suggests that changes in rainfall patterns, mediated by climate change, can have unexpected consequences at regional and local scales, an idea that is supported by other long-term studies in other arid regions of the world [110, 111]. A major take home message of Meserve and colleagues' long-term

study is that the previous view that predators and herbivores have predictable and strong impacts on communities is overly simplistic. More likely, biotic interactions are modulated by abiotic conditions, namely the amount and evenness of rainfall [24]. Understanding these dynamics is critical to predicting how other perturbations, such as overgrazing and invasion of exotic species, influence communities.

### Challenges and future directions

Long-term studies involve some important challenges to researchers. Some of these are highlighted by how our ability to place causal inferences about biological processes being monitored may be compromised by lack of continuity in the data sets. For instance, the emperor penguin study at Taylor Glacier includes a 12-year period (1976–1987) during which census data were not collected. Consequently, Robertson and colleagues ([80]) were not able to explain the reason for the observed population decline because they lacked critical demographic data. The lack of a complete dataset in this study highlights the enormous challenges that researchers face in maintaining a long-term study. Long-term studies are daunting, carrying significant professional risks to project leaders. Gaps in data collection, such as those reported in Robertson et al. [80], can occur for a number of reasons, including natural events that prevent access to sites or decimate populations (e.g. volcanic eruptions, storms, droughts, earthquakes). Changes in the local political landscape, land use practices, or access to sites can also prevent work from being accomplished or require changes in location, as two of us (Loren Hayes and Luis Ebensperger) experienced following a permitting decision made by a national park service administration (CONAF-Chile). Inevitably, gaps in funding or institutional support, or changes in personnel also may impact the ability of research teams to keep a long-term study going. For example, funding cycles only last 3–5 years; thus, maintaining a long-term study site involves researchers spending time writing new grants proposing new hypotheses to justify long-term monitoring.

Effective long-term studies generate new questions and change paradigms (see [89]). Consequently, researchers engaged in long-term studies need the resources and logistical support required to change or add to research protocols in ways that do not compromise the consistency and quality long-term datasets. For example, in 2008, Meserve et al. added new experimental plots and began using other plots previously used for food addition experiments (Meserve et al. 2001). The changes were made in part, so that they could monitor the effect of increasingly invasive lagomorphs on vegetation [24]. We now know that the exclusion of lagomorphs resulted in changes in some perennial shrubs [24], which could in

turn, influence spatial ecology of small mammals that forage or nest underneath shrubs.

Long-term field studies are powerful because they can track changes to natural systems before and after natural and anthropogenic disturbances. Although there are several long-term studies tracking the effects of natural disturbances such as ENSO on natural systems in Central and South America (e.g., [24, 58, 112]), studies of human effects on birds and mammals are rare [71, 87]. Understanding human impacts on natural systems probably requires the simultaneous monitoring of species in protected areas and human-impacted areas within the same ecosystem. One such study in South America, a > 25 year study of coastal communities in the protected area of Las Cruces, Chile and nearby human-impacted coastline [113], has provided valuable information on how human activity has changed coastal ecosystems. More research like La Cruces study, while logistically challenging and expensive, is needed to inform conservation policy.

### Conclusions

While the risks of long-term studies are high, the benefits to researchers and more importantly, the quality of science that we do, can be substantial [5]. Long-term ecological research in central and South America and Antarctica has uncovered new information that otherwise would not have been recorded and informed behavioral, ecological, evolutionary theory as well as conservation biology. Some studies, such as a long-term study of Phyllostomidae bats in Panama [114], are excellent examples of how long-term studies can integrate levels of analysis. Ultimately, the integration of data from multiple long-term study sites, such as Parque Nacional Bosque Fray Jorge and Parque Nacional Las Chinchillas (both in Chile), may allow a broader understanding of how rainfall influences populations and communities.

This review has revealed a consistent theme, where ecological conditions shape social systems, populations, and communities, but in more complex ways than previously thought. Within a single season or a few seasons, it may not be possible to detect the effects of environmental variation at these levels, as factors such as resource availability and patchiness, rainfall, predation, weather and climate vary year to year and decade to decade as a result of other factors. Long-term research also allows us to assess how different life history and social strategies respond to these environmental changes. Future efforts to build long-term datasets will improve scientific understanding in numerous ways including, increasing the quality of data available for comparative studies, providing necessary data for conservation efforts, and generating baseline data from which future changes can be measured. Thus, we hope that this review motivates interest and investment in future long-term studies in the region.

**Abbreviations**

ENSO: El Niño-Southern Oscillation; GUD: Giving-up density; LTER: Long-term ecological research; PNBFJ: Parque Nacional Bosque Fray Jorge

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MTJ contributed to writing of the social ecology section as well as edits to other sections. MKS contributed to the writing of the community ecology section and made the figures. KC contributed to the writing of the evolutionary and population ecology section. KN edited all sections, formatted the manuscript, and contributed citations. LE contributed to writing of the manuscript as well as edits of drafts. LDH conceived of the review topic and contributed to the writing of the manuscript. All authors read and approved of the final manuscript.

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