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## Research

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# Tracking data and retrospective analyses of diet reveal the consequences of loss of marine subsidies for an obligate scavenger, the Andean condor

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Over the last century, marine mammals have been dramatically reduced in the world's oceans. We examined evidence that this change caused dietary and foraging pattern shifts of the Andean condor (*Vultur gryphus*) in Patagonia. We hypothesized that, after the decrease in marine mammals and the increase in human use of coastlines, condor diet changed to a more terrestrial diet, which in turn influenced their foraging patterns. We evaluated the diet by means of stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) of current (last decade) and historical (1841–1933) feathers. We further evaluated the movement patterns of 23 condors using satellite tracking of individuals. Condors reduced their use of marine-derived prey in recent compared with historical times from $33 \pm 13\%$ to less than $8 \pm 3\%$ respectively; however, they still breed close to the coast. The average distance between the coast and nests was 62.5 km, but some nests were located close to the sea (less than 5 km). Therefore, some birds must travel up to 86 km from nesting sites, crossing over the mountain range to find food. The worldwide reduction in marine mammal carcasses, especially whales, may have major consequences on the foraging ecology of scavengers, as well as on the flux of marine inputs within terrestrial ecosystems.

## 1. Introduction

Aquatic and terrestrial ecosystems are frequently linked by resources from outside their boundaries and these subsidies can influence ecological processes [1]. Marine nutrients that subsidize terrestrial ecosystems are known to influence terrestrial food webs [1–3]. Examples include the enhancement of primary productivity by nutrient inputs from seabird guano [4,5] or the numerical response of consumers (e.g. spiders, beetles, lizards, raptors, rodents and carnivores) mediated by the availability of marine-derived prey [6–10]. Most of these examples describe changes in food webs at small spatial scales, and are frequently limited to islands and coastal habitats [2,10–12]. However, it is not well known how changes in the availability of marine subsidies may determine changes in diet composition, and foraging patterns of consumers.

One particular source of marine subsidies to terrestrial food webs is through the exploitation of beached marine animal carcasses, which can represent a massive pulse of nutrients that might induce functional and numerical

responses of generalist consumers [13]. Scavengers are adapted to exploiting such clumped food resources [10], sometimes at great distances from their breeding sites. Marine subsidies have undoubtedly been an important source of nutrients to scavengers and were an important source for the critically endangered California condor (*Gymnogyps californianus*) [14]. However, increases in human populations and disturbances to coastlines all over the world, together with the overexploitation of marine fauna, have reduced the abundance of such marine subsidies [15]. In particular, the massive loss of marine mammals throughout the world by the nineteenth century [16] clearly marked a key reduction in availability of marine mammal carcasses to terrestrial scavengers.

Large soaring avian scavengers have extensive home ranges in order to subsist on ephemeral and scattered food sources such as carrion. These large home ranges are maintained, in turn, by the capacity of these scavengers to move efficiently using updrafts [17,18]. The Andean condor (*Vultur gryphus*) is the world's largest avian scavenger and lives mainly throughout the Andes in South America. This species has large home ranges that can exceed $50\,000\,\mathrm{km}^2$ [19], and is an excellent example of a species able to exploit both terrestrial and marine resources [20]. Condors may shift their diet in relation to resource availability; in fact, in recent times they have shifted from native herbivores to introduced domestic and wild ungulates [21]. There are also multiple records of condors eating from marine sources along the Pacific coast, from Peru to Tierra del Fuego, including whales, sea lions, penguins, pelicans, bird eggs and fish [22,23] (figure 1). In northwestern Patagonia, condors breed on both sides of the Andes range (i.e. in Argentina and Chile) but they seem to feed primarily in the Argentinian steppe. Thus, condors that breed in Chile typically fly dozens of kilometres to reach feeding areas [19].

We studied Andean condor space use and diet under the hypothesis that the current spatial patterns of condors from the western Andes range in northwestern Patagonia (Chile) have been influenced by a historical, largely marine-based diet. We hypothesized that, after the decrease in marine mammals and the increase in human use of coastlines in this region, condor diet should have changed to a more terrestrial makeup, which in turn influenced their movement patterns. To test this, we studied condor current and historical diet, and current movement patterns using two methodological approaches. We first investigated if Andean condors shifted their diets in relation to the decline of marine mammals using stable isotope analysis ($\delta^{13}$C, $\delta^{15}$N and $\delta^{34}$S) of current and historical feathers. These three complementary isotopes constitute a relatively non-invasive way of obtaining time-integrated information on assimilated diets [24–26]. Whereas $\delta^{13}$C and $\delta^{34}$S values provide information on the types of foraging habitats used, $\delta^{15}$N values have been widely used as a proxy for trophic level [27] in addition to source of feeding. Second, we further evaluated the movement patterns of modern condors using satellite tracking of individuals to determine the extent to which coastal areas are important for their foraging activities.

## 2. Material and methods

Full details of materials and methods are presented in the electronic supplementary material, S1.

### (a) Study area and study population

We worked in western Patagonia (Argentina and Chile; figure 1). This area consists of a gradient that encompasses three major biogeographic units: the Magellanic coastline, the austral forest and the steppe (from west to east; figure 1a), including the transition region between forest and steppe referred to as the forest-steppe ecotone. The Chilean Pacific coastline has been extensively used for fishing, whaling and salmon ranching and has experienced a large human population increase [28–30]. In fact, this area includes the Pacific Ocean zone where the largest numbers of whales were caught in the southern Pacific [31]. Ecotone and steppe areas have been used for extensive livestock ranching since the last century and are the regions in Argentina with the greatest amount of alien mammal introductions [21,32]. Condors in this area feed mainly from carcasses of those abundant alien domestic and wild herbivores [21].

The Andean condor is considered Nearly Threatened by the IUCN, included in CITES I, and this is mainly because of a reduction in their distribution and abundance due to human impacts [33,34]. The study area hosts one of the most abundant Andean condor populations known (greater than 300 individuals), although it is still a rare species considering their densities [35]. The western side of the region is dominated by woodlands with a very low amount of medium-to-large herbivore carcasses available, and thus condors cannot easily forage there. Moreover, condors forage by sight and hence cannot easily find carcasses under forest canopy. However, this area has a large number of cliffs that are used for breeding. Condor nests are on cliffs with shelves or caves where they lay a single egg every other year and spend more than a year to fledge the chick [36].

### (b) Condor tagging

All birds were trapped in the same area located near San Carlos de Bariloche, Argentina (41° 09′ S; 71° 16′ W). Condors were attracted to the traps using sheep carcasses. We tagged them with satellite transmitters (10 birds with patagial PTT-100 50 g Solar Argos/GPS tags, Microwave Telemetry Inc., and 13 with backpack 100 g Solar GPS–GSM CTT-1070-1100 tags, CellTrack Tech.). Those birds correspond to 13 females and 10 males. GPS tags were duty cycled to get three dimension locations every day from dawn to dusk at the maximum interval allowed by the unit (every 60 min for PTT tags, and every 15 min for CTT tags; see more details on tagging and movement estimations in electronic supplementary material, S1).

### (c) Stable isotope methods

Historical condor feather samples from Patagonia were obtained from 24 birds (including both sex and age classes) retained in museums which were captured between 1841 and 1939 in the south of Argentina and Chile. These historical feathers came from different locations from condor distribution but we only included in our analyses those that were collected inside the home ranges of current sampled condors. Modern samples ($n = 53$; 28 adults and 19 immatures [30 females, 17 males], and 6 indeterminate) were obtained from individuals captured between 2010 and 2011 ($n = 44$, including the 23 tagged birds) in northern Patagonia (Rio Negro province; 41°09′ S; 71°16′ W) and from feathers collected between 2010 and 2013 at different condor roosts from southern Patagonia (Santa Cruz: 47°49′/50°04′ S-72°09′/71°55′ W; and Tierra del Fuego provinces 54°48′ S/68°26′ W; $n = 9$; see details on stable isotopes estimations in electronic supplementary material, S1).
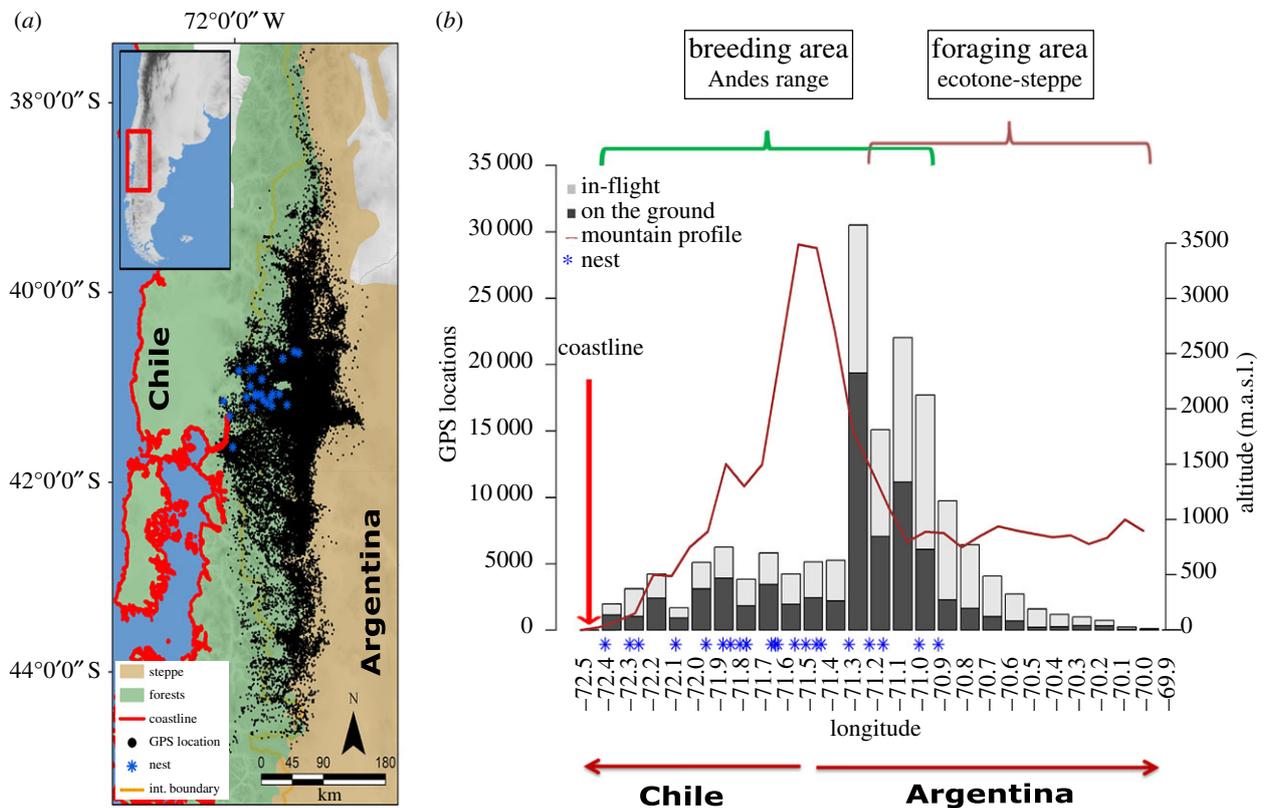
**Figure 1.** (a) Map showing the movement data from the 23 tracked adult Andean condors (13 females and 10 males) collected between October 2010 and February 2017. We include the main biogeographic biomes (forest, steppe and coastline), nest locations, and the international boundary that concur with the top of the Andes range. (b) Frequency distribution of the total condors GPS locations ($n = 159\,834$). Dark grey bars indicate the GPS data from birds roosting on a cliff or on the ground. Light grey bars indicate birds flying. Locations of the breeding areas (in longitude) are marked with blue asterisks. The location of the Chilean sea, in the Pacific Ocean, is highlighted with a red arrow. We represent the schematic silhouette of the Andes range with a violet line and its altitude over the sea level in the right axis. Note that locations from birds on the ground are concentrated on middle longitudes and they are absent in longitudes corresponding to coastline.

## 3. Results

### (a) Satellite tracking information

The tagged Andean condors bred in both the Atlantic and Pacific slopes of the Andean range with some nests very close to the coast. All of them, however, foraged almost exclusively in the eastern Patagonian steppes (figure 1a). The distance from the breeding areas to the Pacific coastline was between 2.9 and 125.9 km (mean 62.5 km, median 57.7 km). The distance from each nest to the food source in the Argentine steppe, and the distance to the possible food source in the coastline were negatively correlated (Pearson correlation test, $r = -0.91$, $p < 0.05$). From the nest site to the beginning of the foraging area, condors needed to fly an average of 32 km day$^{-1}$ (range 0 to 86 km, median 33.3 km). Moreover, the maximum distance flown from the nest to the terrestrial foraging grounds varied from 83.5 km to 176.0 km (mean 127.6 km), the birds that breed far from the beginning of the foraging area being the ones in the Argentinian steppe that tend to fly more ($R^2 = 0.40$, $p < 0.01$).

All data from birds visiting a possible feeding area (birds that landed on the ground in areas where carcasses are available) were located outside the coastline, and most of them (83%) were in the eastern side of the Andes Mountains (figure 1b). Based on all condor locations we were able to discount the possibility that the tagged condors were frequently feeding on the coast because only nine data points (from 159 834 GPS locations; 0.006%) came from birds flying over the pacific coastline (400 m wide buffer from the

border of the sea line) and none of the condor locations were on the ground in order to forage there, but in the eastern side of the Andes (Argentina) (figure 1).

### (b) Stable isotope results

Between historical and modern Andean condors, we only found significant differences in feather $\delta^{13}$C and $\delta^{34}$S values (ANOVA tests; $\delta^{13}$C, $F_{1,74} = 52.68$, $p < 0.0001$; $\delta^{34}$S, $F_{1,74} = 14.28$, $p < 0.0001$; figure 2a and table 1). Dietary estimates derived from mixing models revealed a change in the dietary habits of Andean condors between historical and modern individuals. Although terrestrial resources were the most important prey assimilated for both periods (mean ± s.d. = 91 ± 3% and 66 ± 13% for the modern and historical individuals, respectively), the marine resources were clearly more relevant for the historical samples (33 ± 13%) than for the modern samples (less than 8 ± 3%) (figure 2c).

## 4. Discussion

Our results show that Andean condors reduced their niche breadth from historical time (nineteenth century) to the present (figure 2). We hypothesize that this fact should be at least in part due to the reduction of the marine food resources. Marine mammal carcasses are a huge nutrient pulse which have been and still are in some cases an important source of nutrients for scavengers [10,14], thus subsidizing terrestrial food webs and enhancing their
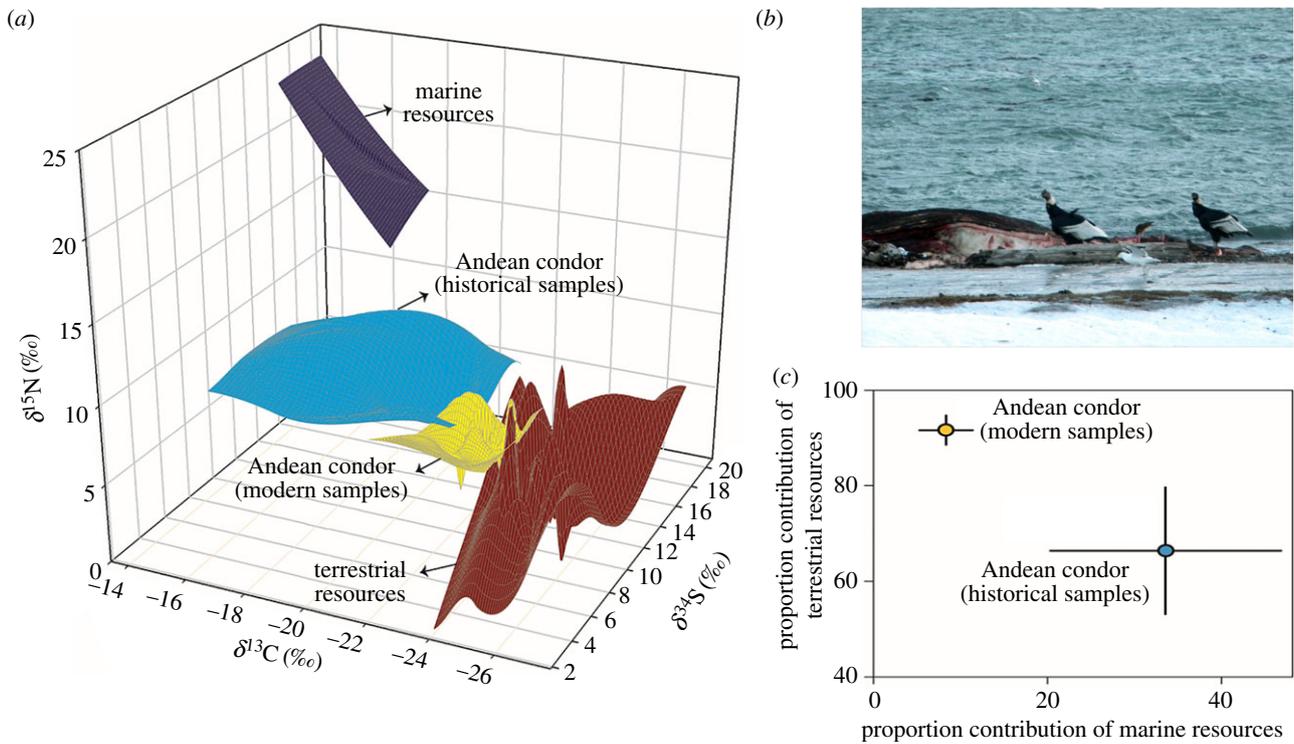
**Figure 2.** (a) Three-dimensional mesh plot showing the isotopic space of historical and modern Andean condor samples, and marine/terrestrial resources based on their $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$. Marine and terrestrial resources are corrected for trophic discrimination values and for tissue-related differences. (b) Andean condors feeding on a whale in Tierra del Fuego Island, the southern tip of Patagonia, Argentina (July 2012; photo: Maria Constanza Marchesi). (c) Mean and standard deviation of the estimated contribution of terrestrial and marine resources to the diets of modern and historical Andean condors based on the results of the SIAR models.

productivity [1]. Our isotopic mixing models revealed that marine resources such as whales and sea lions were part of the diet of the Andean condors from a century ago but are largely irrelevant today. It is well known that changes in the distribution and composition of potential food sources may produce several modifications in the behaviour of consumers [37–39]. Reduction in niche breadth in the last century has been also observed in a carnivore mammal, the Weddell seal (*Leptonychotes weddellii*), associated with the shift in the marine ecosystem structure [40].

Our conclusions that marine subsidies declined in condor diet are supported primarily by the $\delta^{13}C$ and $\delta^{34}S$ data, two isotopes that differ between terrestrial and marine resources. For $\delta^{13}C$, a similar isotopic result as that of historical samples could be expected for a carnivore that fed on herbivores consuming large amounts of C4 plants historically (i.e. enriched in $^{13}C$). However, C4 plants are (and were) absent from the study area, and the first C4 species are located several hundred kilometres away from the main areas visited by condors [19,41]. We expected $\delta^{15}N$ values in historical samples to be higher than modern samples in keeping with a greater abundance of marine foods but this was not the case. However, that result can be explained by the possibility that historical marine inputs were largely from baleen whales at a comparatively lower trophic level, which have lower $\delta^{15}N$ values than other whales [42]. Natural $\delta^{15}N$ values in marine isoscapes [43] and in baleen whales in high latitudes in southern Oceans have a lower $\delta^{15}N$ compared to the ones coming from lower latitudes [44]. Taken together, these facts suggest the change in the proportion of the diet coming from marine sources as the main explanation for our results. However, further $\delta^{15}N$ investigation of terrestrial and marine dietary items is warranted.

Our historical and recent data on condor diet based on isotope analyses come from the same area, covering almost the entire Western Patagonia. Tagged condors covered large areas of most Patagonia in their daily movements (figure 1a), and the areas they do not cover in their movements were specifically sampled. Our result on the almost complete terrestrial condor modern diet evaluated by isotope analyses agrees with other diet studies in the same area. For example, diet evaluated by pellets collected between 1992 and 2009 in northwestern Patagonia suggests that currently at least 98% of condors food is composed by terrestrial mammals [21,45]. Similar results were found in northern condor distributions in Argentina [46]. Apart from this, condor contour feathers take weeks to grow and we collected feathers that grew at different times of the year and used the complete feather to best represent diet. Feathers from historical and current condors were contours, so if they had any seasonal pattern of growing this should be at similar times of the year thus reducing any temporal bias in our comparisons. Moreover, our GPS data on current condor movements show condors flying close to or over the coastline, but a complete absence of fixes on the ground at the coastline. This result also suggests that the birds are not currently using this area for feeding, and supports the evidence collected by stable isotopes.

Reductions in marine food subsidies to the terrestrial system have been accompanied by a non-negligible increase in human populations and their use of the coastline, which may have enhanced the deterioration in those areas as suitable foraging habitat by condors [15]. In fact, the crowded coastlines in some areas of Chile have increased the conservation problems of marine and associated terrestrial wildlife [28]. Condors tend to avoid landing in human-influenced

**Table 1.** Mean ($\pm$ s.d.) isotopic values of historical and modern Andean condors and their main trophic resources collected in the Patagonian area (isotopic values corrected; see Material and methods).

| species | n | $\delta^{15}N$ (‰) | $\delta^{13}C$ (‰) | $\delta^{34}S$ (‰) |
|---|---|---|---|---|
| *Andean condor* | | | | |
| historical samples (1841–1939) | 24 | 10.08 $\pm$ 0.82 | −22.14 $\pm$ 2.31 | 7.66 $\pm$ 2.42 |
| modern samples (2010–2011) | 53 | 9.82 $\pm$ 0.62 | −24.44 $\pm$ 0.72 | 5.48 $\pm$ 2.13 |
| *terrestrial resources* | | | | |
| guanaco (*Lama guanicoe*) | 2 | 6.27 $\pm$ 0.59 | −24.74 $\pm$ 1.44 | 5.71 $\pm$ 2.27 |
| horse (*Equus ferus*) | 3 | 4.01 $\pm$ 0.55 | −24.05 $\pm$ 0.42 | 8.96 $\pm$ 1.28 |
| hare (*Lepus europaeus*) | 17 | 3.31 $\pm$ 1.01 | −25.39 $\pm$ 0.78 | 4.49 $\pm$ 3.17 |
| sheep (*Ovis aries*) | 5 | 5.80 $\pm$ 0.85 | −24.93 $\pm$ 0.27 | 5.64 $\pm$ 0.92 |
| cow (*Bos taurus*) | 1 | 4.06 $\pm$ 0.67 | −24.53 $\pm$ 0.42 | 7.99 $\pm$ 1.44 |
| red deer (*Cervus elaphus*) | 5 | 4.85 $\pm$ 1.37 | −25.18 $\pm$ 0.97 | 5.32 $\pm$ 0.71 |
| *marine resources* | | | | |
| blue whale (*Balaenoptera musculus*) | 3 | 14.27 $\pm$ 2.02 | −16.19 $\pm$ 1.35 | 17.71 $\pm$ 1.98 |
| sea lion (*Otaria flavescens*) | 1 | 19.8 | −13.8 | 16.9 |

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areas, particularly for feeding purposes [47]. Therefore, anthropogenic use of coastlines may also have led to the reduction of the feeding event in the coastlines, as it occurs in other parts of the Andean condor distribution [23], and in other species and regions of the world [15].

A non-mutually exclusive alternative explanation for the change in condor diet would be the increase in the consumption of terrestrial food due to changes in herbivore abundances in recent times. The huge introduction of domestic livestock and exotic species from the end of 1800 to the Argentine Patagonia replaced native guanacos (*Lama guanicoe*) and choiques (*Rhea pennata*), among others [21,32]. The large abundance of livestock tends to be associated with high productivity areas such as Patagonian meadows, which are preferred by foraging condors [48]. A relatively stable introduced food source could be attractive for condors from both sides of the Andes range, and particularly for the ones that depended on less predictable sources of carcasses of marine animals. However, livestock in the Argentine steppe replaced guanacos, which were historically present in their millions in the same areas and available to condors [49]. Most importantly, livestock units increased from the end of 1800 to 1950 but then decreased to similar numbers of the beginning of the twentieth century, so livestock figures were relatively similar between historical and recent condors [50]. Thus, the change in biomass of livestock carcasses might have not been as important as would be needed to produce the observed change in the movements of condors.

Regardless, the Andean condor dietary shift we documented has probably had major consequences for their spatial ecology. Historically, Andean condors inhabiting both slopes of the Andes range in Patagonia may have exploited both terrestrial and marine food sources. However, changes in the abundance of marine subsidies [31] in the last century imply that birds breeding in the western side of the Andes range are now breeding far from their current main food source, which consists of carcasses of terrestrial animals. There is no information on the exact location of historical condors breeding areas, and no data on movement of this species exist from historical times. Nonetheless, as their food sources changed, their movement patterns should have changed reflecting the changes in prey locations. Indeed, modern Andean condors rely almost exclusively on wild and domestic terrestrial herbivores from the Argentine [21,46] (this study).

Andean condors have not changed most of their historical distribution in northwestern Patagonia [20,33]. However, condors breeding closer to the Western coast (Pacific Ocean) in Chile should have changed their habitat use because they spend much time in the Argentine steppe, but not in the Pacific coast. Individual condors are expected to reduce commuting and foraging time when possible. However, they now must travel farther (from 45 to 86 km), and cross over the mountain range, to reach a site with access to enough terrestrial carcasses. To cross those mountains they move from a few hundred to more than 3000 m.a.s.l., fly against strong frontal winds (sometimes more than 100 km h$^{-1}$), and cross the Valdivian temperate rainforest, which is one of the rainiest areas of the world (almost 4000 mm year$^{-1}$ [51]). Therefore, it could be expected that today condors nesting on the Pacific side expend more time and energy (e.g. [52]) than their historical counterparts and those individuals breeding on the eastern side of the Andes. In fact, this condor population has a telomere spatial structure determined by the distance from breeding areas to the current feeding areas, which may suggest some constraints in relation to the distances needed to reach feeding areas (i.e. the distance to the food source might have physiological consequences, probably in the form of reduced lifespan or influencing the spatial distribution of the age of the birds; [53]). The species is threatened and its distribution has been reduced in several areas [33], but no demographic data exist for the study area. Thus, implications of higher distances to food sources and changes in the composition of the diet may have for this species merits special attention in future studies.

Our work highlights the significance of marine subsidy losses to terrestrial systems in a world where marine

biodiversity is declining and coastlines are becoming increasingly impacted by human use. The reduction of marine subsides in modern condors can be linked to the massive loss of marine mammals throughout the world [54]. In the Southern Hemisphere commercial harvesting reduced several whale species almost to extinction. Declines of whales by whaling have been important, especially for the low trophic-level baleen whales (more than 90% for some species, and a decrease in biomass available of more than 80%) [55]. Importantly, during the last century the abundance of those species was pronounced in the southern Pacific, particularly in our study area [29,31,56,57] . Our work suggests an effect of the loss of marine inputs to Andean condors and emphasizes the need for better understanding of the true ecological significance of the marine subsidies to terrestrial systems in general.

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