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Introduced species: domestic mammals are more significant transmitters of parasites to native mammals than are feral mammals

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ABSTRACT

The study of parasitism related to biological invasion has focused on attributes and impacts of parasites as invaders and the impact of introduced hosts on endemic parasitism. Thus, there is currently no study of the attributes of hosts which influence the invasiveness of parasites. We aimed to determine whether the degree of domestication of introduced mammalian species – feral introduced mammals, livestock or pets, hereafter '*D*' – is important in the spillover of introduced parasites. The literature on introduced parasites of mammals in Chile was reviewed. We designed an index for estimating the relevance of the introduced host species to parasite spillover and determined whether the *D* of introduced mammals predicted this index. A total of 223 introduced parasite species were found. Our results indicate that domestic mammals have a higher number of introduced parasites and spillover parasites, and the index indicates that these mammals, particularly pets, are more relevant introducers than introduced feral mammals. Further analyses indicated that the higher impact is due to higher parasite richness, a longer time since introduction and wider dispersal, as well as how these mammals are maintained. The greater relevance of domestic mammals is important given that they are basically the same species distributed worldwide and can become the main transmitters of parasites to native mammals elsewhere. This finding also underlines the feasibility of management in order to reduce the transmission of parasites to native fauna through anti-parasitic treatment of domestic mammals, animal-ownership education and the prevention of importing new parasite species.

1. Introduction

The ecology of invasion has occupied a core role in conservation biology, because biological invasions have become the second most significant cause of species loss (Wilcove et al., 1998; D'Antonio et al., 2001; Wilcove and Master, 2005). The study of biological invasions has historically been focused on two main fields: the attributes of invaders (Elton, 1958; Brown, 1989; Ehrlich, 1989; Cassey et al., 2004; Philibert et al., 2011) and the impact of invasions (Wright and Gribben, 2008; Strubbe et al., 2010). In the context of biological invasions, parasitism has been studied only recently and studies have focused mainly on the traits of parasites as invaders, factors that can determine their impact, and the impact of introduced hosts on endemic parasites (Keesing et al., 2006; Taraschewski, 2006; Mastitsky and Veres, 2010; Mastitsky et al., 2010; Paterson et al., 2011). Thus, the host attributes that increase the likelihood of transmitting parasites to new hosts after being introduced, or that are associated with the success in transmitting parasites to native fauna, have not been studied.

Enemy release theory (founder population effect) states that invaders lose some of their parasites during translocation (Torchin et al., 2002, 2003; MacLeod et al., 2010). Nevertheless, some parasites, particularly those with a greater impact, are able to reach a new environment (Mastitsky et al., 2010), and can then spread as the invading host spreads (Hajek and Tobin, 2011). Furthermore, the introduced parasites can be transmitted to native hosts (spillover) (e.g. see Smith et al., 2009; Thompson, 2013). For this reason, it is important to study these processes of introduction and identify factors that facilitate spillover, in order to prevent negative impacts on the native fauna.

It is known that one of the main contributing factors to the success of an invader is its relationship with humans (Elton, 1958). At one extreme, there is a small number of species that have been introduced into new ecosystems without human intent or awareness, e.g. *Rattus rattus* (rats) unintentionally introduced by ships

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(Jaksic, 1998), or *Oryctolagus cuniculus* (rabbits) which were introduced to an island in the Cauquenes Lagoon in Chile. These rabbits escaped when an extended drought drained the lagoon, thereby establishing a connection between the island and the mainland (Jaksic, 1998). At the other extreme, most species have been deliberately introduced to new ecosystems, e.g. domestic mammals. In many of these cases, there is a large amount of information about the organisms introduced, as well as the new community to which they have been introduced; e.g. reef fish (Elton, 1958).

Another contributing factor is the availability of vacant niches in the new habitat (Ehrlich, 1989). However, in the case of parasites, the decisive factor is the presence of a susceptible host, rather than the presence of a suitable niche (Taraschewski, 2006).

We hypothesise that the traits of the introduced host, specifically their degree of domestication, the dispersion and the time since introduction, play a major role in the colonisation of new territories and hosts by the parasites.

Continental Chile is an ideal region for the study of biological invasion due to its biological diversity, its length and its substantially isolated nature: it has the large, arid Atacama Desert in the north, a high mountain chain to the east (the Andes), the Pacific Ocean to the west and the Strait of Magellan to the south. These natural, well-defined borders make it easy to determine which mammals are native and which ones are allochthonous, and make it difficult – but not impossible – for most terrestrial vertebrates to enter. Due to Chile's relatively isolated nature, only a small proportion of terrestrial vertebrates in this country are introduced species (Jaksic, 1998).

Chile is divided into 13 administrative regions. The northernmost regions, Arica and Parinacota, Tarapacá, Antofagasta and Atacama, are located in the Atacama Desert. From the region of Coquimbo to the south, vegetation and climatic conditions vary from semi-desert, through Mediterranean climate and cold Valdivian rainforest, to Patagonian steppe.

In Chile, protozoa, helminths and arthropods are the most frequently reported parasites in terrestrial vertebrates, and are more commonly found in mammals than in other vertebrates (e. g. see Alcaíno and Gorman (1999) for domestic mammals).

Among mammals, pets are usually confined and are treated with anti-parasitic medications. However, they may occasionally accompany their owners into the countryside where they can transmit their parasites to native mammals. Dogs and cats can also live outdoors in rural areas, increasing the risk of transmission of parasites to native species (e.g. *Echinococcus granulosus* in *Octodon degus* (degu) (Álvarez, 1961); *Hydatigera taeniaeformis* in *Leopardus guigna* (kodkod) (Fernández and Villalba, 1984) and *Phyllotis xanthopygus* (Yellow-rumped pericote) (Cubillos et al., 1991)). On the other hand, feral introduced mammals are species living in constant sympatry with native mammals, which makes the exchange of parasites likely and control almost impossible. The third group, livestock, represents animals with variable degrees of sympatry with native mammals: they are sometimes allopatric if completely confined, or can be at large during the day and confined at night. Antiparasitic control usually aims to reduce parasite burden but not eliminate it. Due to the fact that feral introduced mammals have the highest level of sympatry with native mammals – both groups living in the wild – and that their parasites are not controlled, we predicted that feral introduced mammals would exhibit the highest spillover rate of parasites.

Thus, the purpose of this work was to determine the importance of introduced mammalian species in the transmission of parasites to native mammals in Chile. We assessed whether the level of domestication (feral, livestock or pet, hereafter *D*), is significant and explored why this is the case.

2. Material and methods

2.1. Literature reviewed

We limited the concept of parasite to protozoa, arthropods and helminths. In accordance with MacLeod et al. (2010), we defined an 'introduced parasite' as a non-native parasite that arrived with and persists in the introduced host(s).

Domestic mammals (pets and livestock) considered in this work are those reported by Alcaíno and Gorman (1999) (see Table 1). Feral introduced mammals included in this study are those reported by Jaksic (1998) and Iriarte et al. (2005), apart from those whose parasites have not been studied (see Table 1). Native mammals are those reported by Yáñez and Muñoz-Pedreros (2009). In the case of *Sus scrofa* (wild boar) and *Sus scrofa scrofa* (pig) (Grubb, 2005), we considered them to be different species because they have different ecological traits: the former is feral and the latter domesticated. On the other hand, *Equus caballus* (horse), *Equus asinus* (donkey) and their hybrid (mule) are considered as a single group (*Equus* spp.) because they share both their parasites and ecological traits. In the *Lama* spp. complex, we excluded *Lama glama* (llama) because it is a domesticated native mammal, which is not a species of concern. We kept the subspecies *Lama glama guanicoe* (guanaco) because it is feral and because there is concern for its conservation. The year of introduction of feral mammals (or the first introduction) considered here is that reported by Jaksic (1998). For cases when only the decade or the century is known, we used the median year of that period; e.g. we considered 1965 for the 1960s and 1650 for the seventeenth century. The first introductions of domestic mammals are considered to be shortly after the arrival of the first Spanish conquerors in Chile (sixteenth century, i.e. 1550; see Barros-Arana, 1862).

Finally, we conducted a review of the literature on introduced parasites present in feral and native mammals reported prior to December, 2012, and introduced parasites reported in domestic mammals from 1999 to 2012. Parasites of domestic mammals (pets and livestock) reported before 1999 and included in this work are those reported by Alcaíno and Gorman (1999). For the review, the PubMed (http://www.ncbi.nlm.nih.gov/pubmed/) and Scielo (http://www.scielo.org/) databases were searched with each of the keywords: parasite, helminth, nematode, cestode, trematode, monogenea, digenea, protozoa, coccidian, pentastomida, acanthocephala, acari, mange, lice, louse and tick, combined with 'mammal', and the name (both common and Latin binomials in English and Spanish) of mammals listed in Jaksic (1998), Yáñez and Muñoz-Pedreros (2009) and Alcaíno and Gorman (1999). For the PubMed review we also added "Chile" in the keywords. In addition we included literature provided by specialists we consulted and pre- and post-graduate theses available from Chilean universities. Finally we completed the review by searching the literature cited in all of the above studies.

Only terrestrial populations of mammals and parasites inhabiting the area from 29°S (the southern limit of the Atacama Desert) to 53° 53′ S (the Strait of Magellan) were considered. Parasites found to the south of the Atacama desert cannot cross it, which establishes the area of continental Chile south of the Atacama as an isolated territory. However, parasites found in Chile's Atacama can freely move to non-Chilean Atacaman territory in Peru, Bolivia and Argentina. This second group is excluded from the study because, since their movement is not limited, they are not representative of the isolated territory.

In order to avoid overestimation of introduced parasites, those identified to genus only in the source papers were not considered for analysis; e. g. *Sarcocystis* sp. found in *Pudu puda* (southern pudu) (Rioseco et al., 1976). The exceptions to this rule were cases corresponding to a single report of the genus; e. g. *Listrophorus* sp.

Table 1
Introduced mammals, their traits and their relevance in transmitting introduced parasites to native mammals in Chile.

Introduced host	Native catcher hosts	Domestication degree	$\sqrt{(R_h)}$	Time since introduction (year)	Estimated dispersal (km^2)	Introduced parasites	Spilled over parasites	Order[a]
Canis lupus familiaris	10	Pet	3.790	363	495,778	52	15	25
Felis catus	11	Pet	2.708	363	495,778	29	6	25
Capra hircus	10	Livestock	2.247	363	495,778	31	11	5
Ovis aries	9	Livestock	2.012	363	495,778	53	11	5
Bos taurus	8	Livestock	1.402	363	495,778	51	8	5
Equus sp.	6	Livestock	1	363	495,778	39	4	0
Sus scrofa scrofa	6	Livestock	0.837	363	495,778	32	4	5
Ovis ammon	3	Livestock	0.775	28	67,013.1	2	2	5
Mus musculus	2	Feral	1.826	413	72,379.2	7	6	68
Rattus rattus	2	Feral	1.528	413	254,986.4	8	5	68
Rattus norvegicus	2	Feral	1.155	163	254,986.4	8	2	68
Dama dama	3	Feral	0.922	58	67,013.1	4	3	5
Oryctolagus cuniculus	6	Feral	0.913	129	495,778	18	3	0
Cervus elaphus	1	Feral	0.5	58	274,714.6	1	1	5
Neovison vison	2	Feral	0	26	207,349.8	1	1	25
Lepus europaeus	0	Feral	0	117	495,778	3	0	0
Sus scrofa	0	Feral	0	48	330,697.69	1	0	5

[a] Correspond to the number of native mammalian species of the same order as the introduced mammalian species.

found in *O. cuniculus* (Alcaíno and Gorman, 1999) which is the only such report.

2.2. Index design

After reviewing the literature, we estimated the number of introduced parasites species present in each introduced host and the number of native hosts that became infected with each introduced parasite. Then we designed an index (R_{hp}) for estimating the relevance (R) of an introduced host species (h) to the success of an introduced parasite (p) in colonising native mammals. The index considers the number of introduced mammalian species that are hosts for the introduced parasite p (I) and the number of native mammalian species that are colonised by this parasite (N):

$$R_{hp} = N/I$$

Thus, the 'responsibility' of transmitting an introduced parasite to native fauna is distributed among all of the introduced hosts because any one of them could have had a role in the introduction and/or the persistence of the parasite. On the other hand, the relevance increases when the number of native hosts affected by the parasite is greater.

Finally, the overall relevance of the host h in the spillover of parasite species (R_h) is the sum of the indices (R_{hp}) of this host among all introduced parasites it hosts:

$$R_h = \Sigma R_{hp}$$

Methodologies for estimating the number, density or biomass of introduced mammals vary in the literature; e.g. (i) Lobos et al. (2005) estimated the relative density of rodents as the number of captured rodents * 100/capture effort (traps per night), which varied from 24% to 80%; (ii) Acosta-Jamett et al., 2010 estimated the density of dogs as animals * km^{-2} which varies from 1 to 1,544 within an administrative region, and (iii) the Instituto Nacional de Estadísticas (INE) counted the total number of animals (livestock) in each administrative region (INE, 2007, 'Cuadro' 12; in http://www.ine.cl/canales/chile_estadistico/censos_agropecuarios/censo_agropecuario_07_comunas.php. Last accessed: September 23, 2013). There is no single established methodology for estimating the population size of all introduced mammals in the literature. Therefore, we used the distribution of introduced mammals, estimated as the sum of the areas of the administrative regions (km^2, see Alvarado and Moya, 2007) spanned by each introduced mammal (see INE, 2007, 'Cuadro' 12 for livestock, Lobos et al. (2005) for rodents, Jaksic et al. (1998) for other feral mammals, and all regions for pet; Table 1) to indirectly assess the effect of the host population size on the index.

2.3. Statistical analysis

ANOVA and regression models were used to estimate the importance of D (feral, livestock or pet), the number of introduced parasites, the time elapsed since the introduction of the mammals, their dispersal and the number of native species of the same order as the introduced mammalian species in the R_h index.

For dichotomised variables, t-tests were used.

In order to achieve the assumptions of the analysis, we used the converted dependent variable $\sqrt{(R_h)}$.

In order to determine the effect of phylogenetic proximity, we also used the Fisher exact test to compare proportions of parasites transmitted to native mammals between introduced mammals that belong to the same order as a native species and mammals that do not (feral mammals only). The number of species of each order was obtained from Iriarte (2008).

Statistical analyses were made using the Rcmdr-package v.1.6-3 in the R environment (R Core Team, Vienna, Austria). Model parameters of complex models and their F-values are given in the Supplementary Tables S2–S4. $P \leqslant 0.05$ was considered significant.

3. Results

3.1. Data summary

A total of 237 introduced parasite species were found among the 17 introduced mammals. Supplementary Table S1 shows the list of introduced parasites, their introduced hosts and native hosts if they exist, but does not include parasites reported in Alcaíno and Gorman (1999) unless they have been found in native hosts, introduced feral hosts or subsequent reports in domestic mammals.

Ovis aries (sheep) and *Bos taurus* (cattle) were the host species with the largest number of introduced parasite species (53 and 51, respectively). *Canis lupus familiaris* (dog), *O. aries* and *Capra hircus* (goat) were the species with the largest number of parasites transmitted to native mammals (15, 11 and 11, respectively). *Felis catus* (cat), *C. hircus* and *C. l. familiaris* were the species whose parasites were transmitted to the largest numbers of different native species of mammals (11, 10 and 10, respectively). Finally, *C. l. familiaris* was the species with the highest $\sqrt{(R_h)}$ index (3.79), followed by *F. catus* (2.71), *C. hircus* (2.25) and *O. aries* (2.01) (Table 1).

3.2. Data analysis

When summarising data by *D*, the pet group was the group with the highest mean $\sqrt{(R_h)}$ index (3.25), followed by livestock (1.37); feral mammals had the lowest index (0.76). The ANOVA output was significantly different among groups ($F(2,14) = 11.43$, $P = 0.001$) and the regression model

$$\sqrt{(R_h)} = \beta_0 + \beta_1 * D \quad \text{(a)}$$

(*feral* as base level, *pet* and *livestock* as dummy variables; β_i are the parameters) showed significant difference only between *feral* and *pet* ($P = 0.001$) (Supplementary Table S2).

The *t*-test found that domestic mammals (pets and livestock as one group) showed a significantly different (higher) $\sqrt{(R_h)}$ index than for feral animals (1.846 and 0.76 respectively) ($t\ (15) = 2.55$, $P = 0.022$).

Simple regression models (parameters omitted) indicate that both the number of introduced parasites and the time since introduction are significantly and positively associated with $\sqrt{(R_h)}$ as unique variables ($F(1,15) = 12.02$, $P = 0.003$ and $F(1,15) = 14.91$, $P = 0.002$, respectively), but the estimation of the dispersal as described above is not significantly associated with the index ($F(1,15) = 1.5$, $P = 0.240$).

The estimation of the parameters of the most complex model

$$\sqrt{(R_h)} = \beta_0 + \beta_1 * D + \beta_2 * p + \beta_3 * time + \beta_4 * \text{dispersal} \quad \text{(b)}$$

where *D* presented *feral* as the base level and *livestock* and *pet* as dummies comparing variables, *p* is the number of introduced parasites, *time* is the time since the introduction, *dispersal* is the estimation of the dispersal described above; and β_i are the parameters of the model – indicates that *time* and being *pet* versus being *feral* are significant positive predictors of $\sqrt{(R_h)}$, *dispersal* is a significant negative predictor, but *p* and the difference between livestock and feral mammals are not significant (Supplementary Table S3).

Further analyses of collinearity using simple models demonstrated that *p* is positively associated with *D* ($F(2,14) = 12.59$; $P = 0.001$), *time* ($F(1,15) = 15.04$, $P = 0.002$) and *dispersal* ($F(1,15) = 15.66$, $P = 0.001$), and there was no significant association between *D*, time and dispersal in pairwise tests.

All of the above suggests that *p* is associated with *time* and *dispersal* together. The model

$$p = \beta_0 + \beta_1 * time + \beta_2 * \text{dispersal} \quad \text{(c)}$$

shows that both variables are positively and significantly associated with *p* (Supplementary Table S4).

In summary, analyses of collinearity allow us to state that *D* is associated with *p*, and *p* is associated with *time* and *dispersal*.

On the other hand, in a simple model, $\sqrt{(R_h)}$ is associated with the number of native species of the same order after correction using the domestication criterion (domestic versus feral) ($F(1,15) = 7.65$ $P = 0.014$).

The order Lagomorpha is represented only by introduced species (*O. cuniculus* and *Lepus* (*Eulagos*) *europaeus* (hare)); in contrast, the orders Artiodactyla, Carnivora and Rodentia are represented by native and introduced species. Lagomorpha showed a significantly lower proportion of transmitted parasites species to native mammals than the other feral introduced mammals together (1/17 and 9/20, respectively; one-tailed Fisher: $P = 0.039$).

4. Discussion

Ecologists have worked for many decades to determine which traits of a species are important in predicting whether or not the species will be a successful invader and will spread following introduction to a new habitat (Brown, 1989; Ehrlich, 1989; Cassey et al., 2004; Taraschewski, 2006; Philibert et al., 2011). We focused on host attributes of parasites and tested whether the introduced mammals' degree of domestication is an important factor in the transmission of parasites to native hosts and why this is the case. Contrary to our predictions, pets were the most important group of introduced mammals in the transmission of parasites to native mammals, followed by livestock. Statistical analysis of data suggests that this is due to the larger number of introduced parasites of domestic mammals, the time since introduction and the dispersion of these mammals. Statistical analyses also indicate that only *dispersion* is not significantly associated with the index in a simple model and it is negatively associated in the complex model. This could be due to a low resolution of the estimation of this variable and its behaviour after the inclusion of the other variables in the model. However, the positive association of *dispersion* with the number of parasites suggests that this variable is an important positive predictor of relevance.

The enemy release theory states that introduced species (hosts) will lose many of their enemies (parasites) during the introduction process but, in spite of this, some parasites manage to arrive with their hosts and persist in the new environment. Consequently, the larger the number of introductions of a new host species, the larger the number of parasites species it may introduce. Most introduced feral mammals in Chile were introduced on only a few occasions (Jaksic, 1998) e.g. only one introduction of *Castor canadensis* (American beaver) on the Argentinian side of Lake Fagnano, in 1946, was necessary for them to spread to the Chilean side of Tierra del Fuego, and then, through the Strait of Magellan, to continental Chile; *Neovison vison* (American mink), imported from Argentina, escaped from confinement in Chile on one occasion after 1967 and were feral by 1971 (Jaksic, 1998). Given the low number of occasions on which they have been introduced, feral introduced mammals in Chile are expected to have few introduced parasite species.

On the other hand, most domestic mammals, whether pets or livestock, have been introduced for a longer time and are being introduced continually. Therefore, they represent a large number of introduction processes. There is a long history of importation of mammals, from times when technologies and scientific knowledge may have been insufficient to prevent the introduction of parasites. We therefore posit that the larger number of introduction processes of domestic mammals is one cause of a larger number of introduced parasite species. In addition, the longer the period of time since their arrival, the larger areas they cover and, therefore, the larger number of individuals also increases the possibility that parasites will be transmitted to native mammals. Thus, both the larger number of parasite species and the higher possibilities of transmission result in higher indices. This result concurs with that of Hayes and Barry (2008), who concluded that the number of arriving/released individuals is associated with establishment success in some invader species.

In spite of the above, we expected that feral introduced mammals would have a higher relevance because they have a higher rate of contact. This was not found to be the case, and three causes are possible. First, the phylogenetic distance between host species is frequently recognised as a barrier for the host switching of parasites (e.g. Perlman and Jaenike, 2003; Davies and Pedersen, 2008; de Vienne et al., 2009); thus the phylogenetic distance of some mammals of this group with native mammals reduced the number of parasites able to successfully infect native mammals. For example, *O. cuniculus* and *L. europaeus* are widely spread in the territory and are hosts to a large number of introduced parasites (Table 1). However, Chile has no native lagomorphs and this would cause them to share significantly lower numbers of parasites species with native mammals. This is confirmed by the association between the number of native mammalian species of the same order as the introduced mammal and the relevance of the introduced mammal. Second, sometimes introduced and native mammals are related, but there are no or few studies on the native species. This could be due to their small population sizes, which makes studying them difficult. e.g. there is only one study focused on parasites of *Hippocamelus bisulcus* (Patagonian huemul) in Chile (González-Acuña et al., 2009), which is susceptible to the parasites of domestic ungulates. Third, sympatry and the case of rodents: there are many studies on parasites of native rodents (e.g. Poupin, 1896; Babero and Cattan, 1975; Durette-Desset et al., 1976; see Cattan and George-Nascimento, 1982 for a review), but only two studies were expressly done in sympatry with introduced rodents (Franjola et al., 1995; Landaeta-Aqueveque et al., 2007).

In contrast, the higher relevance of *C. l. familiaris*, *F. catus, C. hircus* and *O. aries* can be explained ecologically by several factors. Firstly, their management, which allows sympatry of these species with many native species, especially as sheepdogs and flocks roam freely over large areas and are confined only at night (Silva-Rodríguez et al., 2010). In addition, in some rural localities, free-ranging dogs are common; e.g. 67% of the population in the Coquimbo Region (Acosta-Jamett et al., 2010) and close to the 90% in the Los Lagos Region (Silva-Rodríguez, 2006; thesis available at: http://www.carnivoreconservation.org/files/thesis/silva-rodriguez_2006_ dvm.pdf, last accessed November 29, 2013). This free-ranging condition could have different ecological implications in comparison with confined dogs – for instance, they could shed eggs or oocysts in areas also used by native canids. This highlights the importance of the sympatry with native fauna for parasite transmission. Second, many flocks and agricultural areas are located on the edges of fragmented habitats and are frequently visited by native fauna. These agricultural regions can also be sources of visits to native habitats by domestic mammals (e.g. landscape studied in Fontúrbel et al. (2010)). Third, dogs often visit native habitats when accompanying their owners; not all native landscapes are protected areas nor are protected areas truly free from domestic animals (e. g. Acosta-Jamett et al., 2010). In addition to this, it is known, although not reported in scientific literature, that there are feral populations of dogs and cats in wild habitats in Chile interacting with native fauna (see http://estudiocarnivoroschile.files.wordpress.com/2013/07/perro-ataques-en-snaspe-anc3a1lisis-28-8-12.pdf, last accessed on November 12, 2013, for a governmental report on protected areas). Several studies elsewhere have reported different parasites in feral populations of dogs and cats (e.g.: Morrison et al., 1988; Horak et al., 2004); however there is no study on parasitism in Chilean feral populations of these species. Given the unknown size of these populations and their parasites it is not possible to estimate their importance in the spillover of parasites. Fourth, native mammals do not only live in native environments; many of them have colonised or survived in farming systems (e. g. Silva-Rodríguez et al., 2010), where transmission from domestic mammals is more readily achieved. Finally, there is a closer phylogenetic relationship between these mammals and many native mammals; e.g. in Chile there are several native canine (*Lycalopex* spp.) and feline species (e.g.: *Puma concolor* and *L. guigna* among others, see Table 1). This explains why most of the parasites in our study identified as spillovers are hosted by carnivores and artiodactyls; our data agree with Pedersen et al. (2007), who stated that 88% of mammals threatened by infectious disease belong to these orders.

We did not find studies on parasites of pets, other than dogs and cats, in Chile. In contrast, there are reports on introduced parasites in other pet species overseas. e. g., introduced *Mesocricetus auratus* (hamsters) in Japan have been found to be parasitised by three species of *Syphacia*. These three *Syphacia* spp., together with the parasites found in other domesticated rodent pets, comprise a total of 13 species of helminths found in domesticated rodents in Japan (Hasegawa et al., 2008). The nematode *Dentostomella traslucida* parasitises the introduced *Meriones* (*Pallasiomys*) *unigiculatus* (Mongolian gerbil) in Brazil (Pinto et al., 2003). In these two cases, hamsters and gerbils – the studied hosts – were bought in pet stores. In Chile, there are hamsters, gerbils and many other allochthonous mammals for sale as pets. The fact that there have been no recorded findings of their parasites in native fauna suggests that these parasites, if they do exist in Chile, have not spilled over. Gerbils and hamsters are usually confined to an intra-domiciliary environment without possible contact with native fauna and there is no evidence of feral colonisation of these species. This suggests that the contact or at least occasional sympatry of introduced mammals with native ones is important in the transmission of parasites.

This study was executed in a region with insular characteristics for mammals; however it is not completely isolated. There is a limited movement of mammals through the Andes mountain chain and through the Strait of Magellan (Jaksic, 1998), which has allowed the arrival of alien mammals firstly introduced to Argentina (see above).

The finding that domestic mammals are more relevant in the transmission of parasites is important due to the fact that the main domestic mammals are essentially the same species distributed worldwide – dog, cat, cow, sheep, goat, horse, pig – and they can become the main transmitters of parasites to native mammals elsewhere. This finding is also important because it enhances the feasibility of management in order to reduce the transmission of parasites to native fauna. This management must include anti-parasitic treatment for pets and education about responsible pet ownership, especially for those pet owners who are likely to bring their pets on visits to wild environments. Since the anti-parasitic treatment of livestock, if it exists, is usually aimed at reducing, but not eliminating, parasites, management becomes more difficult. Management should be aimed at reducing the contact rate with native mammals and reinforcing the anti-parasitic treatment at times when either contact or sympatry is unavoidable, such as during seasonal translocations of flocks. Another important management goal is the prevention of the introduction of parasitised mammals (e. g. uncontrolled illegal importation), in order to avoid the introduction of new parasites species.

Despite the high relevance of *C. l. familiaris* in the transmission of parasites to native mammals, the most important impact of *C. l. familiaris* on native fauna is predation – e.g. on *H. bisulcus* in Chile (Povlitis, 1983), followed by disease transmission, mainly rabies and canine distemper virus, as reported by Hughes and Macdonald (2013). Thus, in addition to this work, our results indicate the need for increased consideration of dogs not only as a source of disease in public health programs but also as a significant issue in biological conservation plans.

Continental Chile, from the southern limit of the Atacama Desert to the southern end at the Strait of Magellan comprises an important variety of different ecosystem climates and eco-regions, from the arid desert, through several mediterranean climate zones and cold rainforests to Patagonian steppe (see Di Castri, 1968). Most of these environments are represented in the literature that served as sources for this work. This diversity of ecosystems and the worldwide origin of introduced mammals suggest that our results are likely to be extrapolated to other areas with similar characteristics: a large number of introduction processes of domestic mammals, farms located near wild habitats, wild habitats visited by domestic mammals and domestic habitats visited by native mammals. In all of these ecosystems it is possible for domestic mammals to have a high impact on native mammal populations through parasite transmission to native mammals. In areas with lower isolation and higher colonisation rates of feral introduced mammals, and hence a higher number of parasite introduction processes, these mammals could be of greater relevance in the transmission of parasites to native mammals. However, given the multifactorial nature of this process, more studies are necessary to assess the real importance of isolation as a factor.

Our results suggest that domestication is not an important factor in the spillover of parasites in mammals per se, but rather, that the important factors are the number of parasites introduced by a host species, the time since the host species' arrival and their dispersal. Our results also suggest that domestic mammals become important in the spillover of parasites only if they are not isolated from native mammals. It appears that the small number of parasite species and the phylogenetic differences with native mammals are the reasons that feral mammals have low relevance in parasite transmission. The fact that domestic mammals are more relevant also implies a greater feasibility of implementing control strategies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ijpara.2013.12.002.

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