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Biogeography of haemo- and ectoparasites of an arid-land bird, the Trumpeter finch

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ABSTRACT

The study of biogeographical patterns is basic to understand the processes that rule the distribution of parasites and to understand the influence that they have on host population dynamics. We tested (i) whether island dwelling host populations have lower parasite richness and higher prevalence than the mainland one; and, (ii) whether an expanding host population undergoes both lower parasite richness and prevalence than the source one. For these purposes, we studied the parasite fauna (haemo- and ectoparasites) of 398 Trumpeter finches (*Bucanetes githagineus*), an arid-adapted passerine, in three regions, the Canary Islands, south-eastern Iberian Peninsula (continental expanding) and Northwest Africa (mainland, source population). We searched for blood parasites microscopically. We studied feather lice and feather mites by scanning plumage of trapped birds. Whereas we found two haemoparasite species in the mainland/source population, one in the island and two in the expanding population, we found two ectoparasites species in the mainland/source and three both in the island and in the expanding populations. Average and total prevalence of haemoparasites were highest in the mainland/source population. Ectoparasites had the lowest prevalence in the mainland/source population. Thus, we found that blood parasites fit the biogeographical predictions whereas ectoparasites do not.

1. Introduction

Studying the diversity of parasites is particularly relevant from an ecological, evolutionary, epidemiological and conservationist point of view (Poulin, 2004; Poulin and Morand, 2000). Current studies on parasite diversity attempt to determine which factors, host or environmental-related, are the most appropriate determinants of parasite species richness (Poulin, 1998, 2004; Poulin and Morand, 2000). Works on biogeographical patterns of parasite diversity found that, besides the influence of parasite traits (Bush et al., 2009; Malenke et al., 2011; Moyer et al., 2002a), parasite distribution and richness is also linked to the ecology (habitat, migration, geographical range) of the host (Gómez-Díaz et al., 2012; Smith et al., 2004; Spurgin et al., 2012). Both factors can interact, since whereas overall species (including potential host) richness is usually lower in arid environments compared with temperate or tropical regions (Myers et al., 2000), water scarcity can limit the presence of both haemo- (Tella et al., 1999; Valera et al., 2003; but see Martínez-Abraín et al., 2004 for alternative explanations) and ectoparasites (Malenke et al., 2011; Moyer et al., 2002a).

Here we investigated large-scale patterns of the parasite assemblage of an arid-land passerine, the Trumpeter Finch (*Bucanetes githagineus*, Lichtenstein, 1823). This species is distributed along North Africa, from where it has recently expanded to the Iberian Peninsula (Barrientos et al., 2014, 2009a; Carrillo et al., 2007a). The species is also present in the Canary Islands, where populations occur long time ago (Barrientos et al., 2014). Following Poulin and Morand (2000) for studies of biogeographical patterns, we designed our study focussing on a subset of parasites from a limited number of regions/populations. More precisely, we compared two insular and one recently expanded populations with a continental, long established population (Barrientos et al., 2009a, 2014), as well-designed richness-based studies require the comparison of parasite assemblages with the source (or equivalent) population rather than with the whole range (Colautti et al., 2004). We considered two groups of parasites with different transmission modes, namely the haematozoa (life-cycle with intermediate vectors) and the ectoparasites (feather lice and feather mites, both with direct transmission). Specifically, we test the following

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hypotheses: i) parasite richness is expected to be lower in island-dwellers respect counterparts inhabiting mainland (Goüy de Bellocq et al., 2002); ii) on the contrary, prevalence in islands tends to be higher due to the expected higher host densities (Dobson, 1988); iii) birds from the expanding population are expected to undergo fewer number of parasite species and lower prevalence than those from the source population (Phillips et al., 2010; Torchin and Mitchell, 2004; Torchin et al., 2003).

2. Methods

2.1. Study area, host and parasite species

We studied the parasite assemblage of the Trumpeter finch, a small-bodied fringillid (c. 21g) distributed in arid regions from Pakistan to the Canary Islands (del Hoyo et al., 2010), in four breeding localities (Appendix 1, electronic version only): i) Errachidia (31°56′ N, 04°25′ W), placed in North Africa, representing the continental, long established population and the source for the Iberian finches (Barrientos et al., 2009a); two islands of the Canary archipelago, ii) Fuerteventura (28°35′ N, 13°58′ W) and iii) Lanzarote (28°54′ N, 13°46′ W), where the Trumpeter finch is long established (Barrientos et al., 2014). These two islands host the largest Canary populations (del Hoyo et al., 2010; Martín and Lorenzo, 2001); and iv) Tabernas (37°02′ N, 02°30′ W), placed in south-eastern Spain, by far the most important breeding locality in the more recently colonized Iberian Peninsula (Barrientos et al., 2014, 2009a; Carrillo et al., 2007a). The Trumpeter finch breeding season extends from January to May in the Canary Islands (Martín and Lorenzo, 2001), from February to July in continental Spain (Barrientos et al., 2007) and from February to June in Morocco (Thévenot et al., 2003).

Our microscopy study does not allow parasite identification to the species level. Instead, we worked at the genus level. Admittedly, this approach poses some limits to the interpretation of the results. In contrast it allows meaningful comparisons with previous studies (Carrillo, 2007; Carrillo et al., 2007b; Valera et al., 2003) that, in fact, enable us to test the biogeographical hypotheses mentioned above.

In consequence, we searched for the three genera of haematozoa detected to date in the Trumpeter finch: two apicomplexan, *Leucocytozoon* sp. and *Plasmodium* sp., and one microfilaria, tentatively identified as *Eufilaria* sp. We also searched for apicomplexan *Haemoproteus* sp. and euglenozoan *Trypanosoma* sp. as these parasites have been detected in several bird species following our same methodology (Valkiūnas, 2005). The genera *Leucocytozoon*, *Plasmodium* sp. and *Haemoproteus* have complex life cycles in which diptera (simuliids for the two former parasites and ceratopogonids and hippoboscids for the latter) are the main vectors (Valkiūnas, 2005). *Trypanosoma* species have also complex life-cycles and they are transmitted by a variety of simuliids (Scheuerlein and Ricklefs, 2004). *Eufilaria* species are nematodes living in the peritoneal cavity of many vertebrates that release microfilariae into the blood. They are transmitted by simuliids, ornithophilic ceratopogonids and haematophagous culicids (Anderson, 2000).

To our knowledge, the ectoparasites described for the Trumpeter finch to date are two chewing lice genera (Carrillo, 2007; Carrillo et al., 2007b), which were considered as two single taxa for the analysis purposes. *Philopterus* sp. and *Brueelia* sp. (Phthiraptera: *Ischnocera*) live in the host plumage and only leave it to transfer directly among hosts (see Carrillo et al., 2007b for details). We also searched for feather mites (Astigmata), which are permanent ectoparasites, although some authors suggest that they are symbiotic rather than parasite taxa (Blanco and Frías, 2001; Blanco et al., 2001). They have direct transmission mode whose acquisition likely occurs during periods of high host gregariousness (e.g. Blanco and Frías, 2001).

2.2. Bird sampling and parasite survey

We sampled Trumpeter finches in Fuerteventura in February 2005 (breeding), in Lanzarote during April 2005 (breeding) and in Errachidia in July 2006 (post-breeding). In Tabernas, sampling was carried out from May to September in 2004 and from May to July 2005. Haemoparasites data from Tabernas come from Carrillo (2007) and lice data from the same population come from Carrillo et al. (2007b). All birds were ringed and aged as either juveniles (first calendar year) or adults (second calendar year or more). Adult birds were sexed on the basis of plumage colouration. As parasite prevalence or load can vary between breeding and post-breeding season (Carrillo et al., 2007b), we also included this variable (breeding *vs*. post-breeding) in the analyses when appropriate.

We took blood samples by brachial venipuncture using a heparinized capillary tube. Blood was smeared immediately, air dried, and fixed with absolute ethanol. Smears were stained with Giemsa at the lab. A ×400 lens was used to look for extra-cellular parasites on all the surface of blood smears following the methodology described in Valera et al. (2003). We used the illustrations from Valkiūnas (2005) and Clark et al. (2009) to identify blood parasites. When a potential intracellular stage of haematozoa was detected, we used ×1000 to confirm or discard it. Although molecular methods have been recommended over the use of smears (e.g., Belo et al., 2012), for the aim of our comparative approach, the smear scanning method seems to be suitable because the potential biases in parasite detection are likely the same in all the studied populations. Furthermore, microscopy is essential to detect mixed infections (Valkiūnas et al., 2006).

We studied louse species following the scanning method fully described in Carrillo et al. (2007b). Basically, two persons looked for parasites and their eggs on each bird for about 5 min by examining the breast, belly, lower back, rump, head, neck and throat. Adult and eggs from *Philopterus* sp. and *Brueelia* sp. are easily distinguishable on the basis of their body size and shape (Carrillo et al., 2007b). Furthermore, they show high specificity in the places where they are found, as *Philopterus* sp. are found in the head and *Brueelia* sp. are placed in the belly or rump (Carrillo et al., 2007b). Finally, we searched for mites in every wing and tail feather. We consecutively extended wings and tail and we counted all the mites by placing the bird against the light (see Blanco and Frías, 2001 for a similar methodology).

Overall, we searched for haemoparasites in 366 Trumpeter finches (35 in each island, Fuerteventura and Lanzarote, 276 in

Table 1
Haemoparasite prevalence in Trumpeter finches from the three studied populations. Sample sizes are shown in brackets and 95% confidence intervals in square brackets. Since there were no differences (host sex or age, season, year or island) within populations we pooled data to obtain a single value per population. Data from Tabernas are from Carrillo (2007).

	Leucocytozoon sp.	*Haemoproteus* sp.	*Trypanosoma* sp.	*Eufilaria* sp.
Canary Islands ($n = 70$)	0.0% [0.0–5.1]	1.4% [0.0–7.7]	0.0% [0.0–5.1]	0.0% [0.0–5.1]
Errachidia (North Africa) ($n = 20$)	0.0% [0.0–16.9]	0.0% [0.0–16.9]	5.0% [0.1–24.9]	50.0% [27.2–72.8]
Tabernas (Iberian Peninsula) ($n = 276$)	0.4% [0.0–2.0]	0.0% [0.0–1.3]	0.0% [0.0–1.3]	0.7% [0.1–2.6]

Table 2
Prevalence of *Philopterus sp.* (calculated on the basis of adult, larvae and lice eggs) in Trumpeter finches from different locations, years and seasons. Sample sizes are shown in brackets and 95% confidence intervals in square brackets. When there were no (host sex or age, season, year or island) differences within a certain population we pooled the data to obtain a single value. Data from Tabernas are from Carrillo et al. (2007b).

	Breeding		Post-breeding	
Canary Islands ($n = 66$)	93.9% [85.2–98.3]			
Errachidia (North Africa)			Adults ($n = 9$)	55.6% [21.2–86.3]
			Juveniles ($n = 14$)	7.1% [0.2–33.9]
Tabernas (Iberian Peninsula)			2003 ($n = 11$)	90.9% [58.7–99.8]
	2004 ($n = 47$)	87.2% [74.3–95.2]	2004 ($n = 50$)	48.0% [33.7–62.6]

Tabernas and 20 in Errachidia; see Table 1), for lice in 398 birds (35 in Fuerteventura, 31 in Lanzarote, 309 in Tabernas and 23 in Errachidia; see Tables 2 and 3) and for mites in 205 birds (35 in Fuerteventura, 31 in Lanzarote, 116 in Tabernas and 23 in Errachidia; see Table 4).

In this paper we used i) a measure of abundance for every parasite species, namely the 'prevalence', the percentage of infested birds. When intrapopulation variation in prevalence of a given species was detected, data were treated separately. We calculated two additional measures of prevalence for the pool of haematozoa and for that of ectoparasites: ii) 'total prevalence', that is, the percentage of parasitized hosts taking into account any parasite species within each group; iii) 'average prevalence', that is, the mean prevalence averaged for all the parasites species of these two groups, including those with zero prevalence (Torchin et al., 2003). For the calculations of averaged and total prevalence, we considered only the birds in which all the parasite species (five haematozoa in one case and three ectoparasites in the other) were searched for. Thus, sample sizes for these calculations were 70 for the Canary Islands, 20 for Errachidia and 276 for Tabernas for haematozoa and 66, 23 and 111, respectively, for ectoparasites. When we compared total and average prevalence, we averaged the different values (for instance, those calculated for different host ages or years) to obtain a single value for each population, following Torchin et al. (2003). Nonetheless, the trends found following this approach are consistent with the ones obtained when using either the highest or the lowest values in each population (data not shown).

2.3. Statistical analyses

When the sample size allowed it, we studied those factors that could produce intrapopulation variation in haematozoa and lice prevalence (host gender and age, season, year or island) using chi-square or Fisher exact tests when appropriate. Concerning feather mites, sample sizes and prevalence in Tabernas did allow us to carry out more complex analyses. First, we discarded seasonal differences in prevalence (breeding 2004 *vs.* post-breeding 2004) for adults ($n = 24$ *vs.* $n = 3$), juveniles ($n = 43$ *vs.* $n = 19$) and for both age classes together by using Fisher exact tests. Then, we fitted log-linear models and tables of partial associations for fully saturated models with the software Statistica 6.0 (StatSoft 2003) to study the influence of year (2004, $n = 89$ *vs.* 2005, $n = 27$) and host age (adult, $n = 47$ *vs.* juvenile, $n = 69$) on prevalence of feather mites in this location.

Statistical differences in the geographical patterns of mite prevalence were assessed with chi-square tests. In all the cases, we calculated the confidence intervals for prevalence with Clopper–Pearson tests, with 4000 replications. We used Fisher exact tests to calculate the differences in total prevalence both for haemoparasites and for ectoparasites. Unless otherwise stated, all the tests were done with the program Quantitative Parasitology 3.0 (Reiczigel and Rózsa, 2005).

Table 4
Prevalence of mites (Astigmata) in Trumpeter finches from three different populations. Sample sizes are shown in brackets and 95% confidence intervals in square brackets. As there were no differences within any population regarding host sex or age, season, year or island, we pooled them to obtain a single value.

Population	Prevalence
Canary Islands ($n = 66$)	86.4% [75.7–93.6]
Errachidia (North Africa) ($n = 23$)	0.0% [0.0–14.8]
Tabernas (Iberian Peninsula) ($n = 116$)	45.7% [36.4–55.2]

3. Results

3.1. Parasite richness and prevalence in island-dwelling vs. mainland populations

We found two species of blood parasites in Errachidia (*Trypanosoma* sp. and *Eufilaria* sp.) and a single species in the Canary Islands (*Haemoproteus* sp.) despite sample size was lower in the former (Table 1). Concerning ectoparasites, two louse species (*Philopterus* sp. and *Brueelia* sp., Tables 2 and 3) were recorded in both populations whereas feather mites were only found in the Canary Islands (Table 4).

After checking that host gender, age or island (i.e., Lanzarote *vs.* Fuerteventura) did not influence prevalence of any of the haemoparasite species (Fisher test, $P > 0.10$ in all the cases), we pooled data for all the individuals captured in each of the two populations (Errachidia and the Canary Islands). The prevalence of *Eufilaria* sp. was 50% in Errachidia whereas it was absent in the Canary Islands (Fisher test, $P < 0.0001$, Table 1). *Trypanosoma* sp. was absent in the

Table 3
Prevalence of *Brueelia sp.* (calculated on the basis of adult, larvae and lice eggs) in Trumpeter finches from different locations, years and seasons. Sample sizes are shown in brackets and 95% confidence intervals in square brackets. When there were no (host sex or age, season, year or island) differences within a certain population we pooled the data to obtain a single value. Data from Tabernas are from Carrillo et al. (2007b).

	Breeding			Post-breeding		
Canary Islands ($n = 66$)	7.6% [2.5–16.8]					
Errachidia (North Africa) ($n = 23$)				78.3 [56.3–92.5]		
Tabernas (Iberian Peninsula)	Adults			Adults	2002 ($n = 10$)	30.0% [6.7–65.3]
		2003 ($n = 50$)	78.0% [64.0–88.5]		2003 ($n = 39$)	66.7% [49.8–80.9]
		2004 ($n = 30$)	66.7% [47.2–82.7]		2004 ($n = 42$)	64.3% [48.0–78.5]
	Juveniles			Juveniles	2002 ($n = 31$)	61.3% [42.2–78.2]
		2003 ($n = 54$)	92.6% [82.1–98.0]		2003 ($n = 28$)	78.6% [59.0–91.7]
		2004 ($n = 17$)	88.2% [63.6–98.6]		2004 ($n = 8$)	75.0% [34.9–96.8]

islands while it was recorded, but with low prevalence, in Errachidia (Fisher test, $P > 0.10$, Table 1). The opposite was true for *Haemoproteus* sp. as it was found parasitizing one Canary finch, whereas it was absent in the mainland population (Fisher test, $P > 0.10$, Table 1).

The total prevalence of haemoparasites was significantly lower in the Canary Islands than in Errachidia (1.4%, $n = 70$, *vs*. 55.5%, $n = 20$, Fisher test, $P < 0.0001$), mainly due to a single parasite, *Eufilaria* sp. Average prevalence was c. 34 times lower in the island population (0.4% *vs*. 13.8%).

Concerning ectoparasites, we first checked for intrapopulation variation in parasite prevalence. We found no differences in prevalence of any ectoparasite between host genders, host ages or island subpopulations in the Canaries (Fisher test $P > 0.10$ in all the cases), and thus we pooled these data. The prevalence of *Philopterus* sp. in Errachidia was lower in juveniles than in adults (7.1%, $n = 14$, *vs*. 55.6%, $n = 9$, Fisher test, $P = 0.02$) and thus we analyzed these data separately (Table 2). Finally, the prevalence of *Brueelia* sp. did not differ between age or gender categories in this site (Fisher test $P > 0.10$ in both cases).

Our data do not allow suitable comparisons of lice prevalence between the Canary Islands and Errachidia since data were collected in different seasons and years. However, we found a different pattern for the two species. Prevalence of *Philopterus* sp. in the Canary Islands during the breeding season was significantly higher than those found in Errachidia during post-breeding (for adults: 93.9%, $n = 66$, *vs*. 55.6%, $n = 9$, Fisher test, $P < 0.01$; for juveniles: 93.9%, $n = 66$, *vs*. 7.1%, $n = 14$, Fisher test, $P < 0.0001$; Table 2). In contrast, prevalence of *Brueelia* sp. in the Canary Islands during the breeding season was significantly lower than the one found in Errachidia during post-breeding (7.6%, $n = 66$, *vs*. %, 78.3%, $n = 23$, $\chi^2 = 44.5$, df = 1, $P < 0.0001$; Table 3).

The differences in mite prevalence between populations are obvious since prevalence in the Canaries was as high as 86% whereas Errachidia birds were not infected ($\chi^2 = 55.2$, df = 1, $P < 0.0001$; Table 4).

The total prevalence of ectoparasites was higher in the Canary Islands than in Errachidia (100%, $n = 66$, *vs*. 82.6%, $n = 23$, Fisher test, $P < 0.01$). Average prevalence was almost two fold higher in the Canary Islands (62.6% *vs*. 36.6%).

3.2. Parasite richness and prevalence in expanding vs. source population

We found two blood parasites both in the expanding (*Leucocytozoon* sp. and *Eufilaria* sp., Table 1) and in the source population (*Trypanosoma* sp. and *Eufilaria* sp.). Concerning ectoparasites, *Philopterus* sp. and *Brueelia* sp. were recorded in both populations (Tables 2 and 3) but mites were only found in Tabernas (Table 4).

The prevalence of haematozoa in Tabernas was very low for the two species recorded (<1%, Table 1). The prevalence of *Eufilaria* sp. was significantly lower in Tabernas compared with Errachidia (0.7%, $n = 276$, *vs*. 50.0%, $n = 20$, Fisher test, $P < 0.0001$) whereas that of *Trypanosoma* sp. was marginally lower (0.0%, $n = 276$, *vs*. 5.0%, $n = 20$, Fisher test, $P = 0.07$) (Table 1).

The total prevalence of haemoparasites was significantly lower in Tabernas than in Errachidia (1.1%, $n = 276$ *vs*. 55.5%, $n = 20$, Fisher test, $P < 0.0001$), again mostly due to *Eufilaria* sp. Similarly, average prevalence in Tabernas was 46 times lower than the one assessed for the source population (0.3% *vs*. 13.8%).

The intrapopulation differences in prevalence of ectoparasites in Tabernas were: (i) birds were more infected by *Philopterus* sp. and *Brueelia* sp. during the breeding season (Tables 2 and 3); (ii) *Philopterus* sp. and *Brueelia* sp. prevalence differed between years (Tables 2 and 3); (iii) *Brueelia* prevalence was lower in juveniles than in adults (Table 3). Concerning feather mites, prevalence in Tabernas in 2004 did not differ between seasons neither for adult, for juvenile birds, or for both age classes together (Fisher test, $P = 0.20$; $\chi^2 = 0.4$, df = 1, $P = 0.51$; $\chi^2 = 2.4$, df = 1, $P = 0.12$, respectively). Year and host age had no significant effect on mite prevalence in Tabernas either (interaction year-prevalence, partial chi-square, $\chi^2 = 0.7$, df = 1, $P = 0.40$, and interaction host age-prevalence, partial chi-square, $\chi^2 = 2.3$, df = 1, $P = 0.13$).

Our data do not suggest a lower prevalence of *Philopterus* sp. in the expanding population as the lowest prevalence recorded in Tabernas was similar to the highest one from Errachidia during the same season (48.0%, $n = 50$, *vs*. 55.6%, $n = 9$, Fisher test, $P = 0.73$; Table 2). Concerning *Brueelia* sp., prevalence during post-breeding was significantly lower in Tabernas than in Errachidia in a single case (for adult birds in 2002, 30.0%, $n = 10$, *vs*. 78.3%, $n = 23$, Fisher test, $P = 0.02$; Table 3). For the remaining cases (juveniles in 2002, adult and juveniles in 2003 and 2004) prevalence was similar in both populations (chi-square or Fisher tests when appropriate, $P > 0.10$ in all the cases; Table 3).

The comparison between the expanding and the source population renders similar total prevalence of ectoparasites (93.5%, $n = 111$ in Tabernas *vs*. 82.6%, $n = 23$, in Errachidia, Fisher test, $P = 0.10$), whereas average prevalence was nearly two fold higher in Tabernas (63.7% *vs*. 36.6%).

4. Discussion

4.1. A large-scale overview of parasitisation patterns

We have found a general low prevalence of blood parasites in all the study areas, what agrees with works reporting low prevalence of blood parasites in arid habitats (Tella et al., 1999; Valera et al., 2003). Yet, other authors have reported very variable or even high prevalence (e.g., Belo et al., 2012; Illera et al., 2008; Spurgin et al., 2012). Various hypotheses may account for the scarcity of avian haematozoa in arid-adapted birds: (i) birds inhabiting arid habitats may have a natural resistance to blood parasites or, alternatively, species with poor immunocompetence may have been displaced to arid habitats, where the prevalence of haematozoa is low (Tella et al., 1999). This can be the case of the Trumpeter finch, for which low prevalence of haematozoa has been reported (Valera et al., 2003; Yakunin and Zhazyltaev, 1977) and absence of pox virus infection (Smits et al., 2005), suggesting that this species is resistant to some pathogens; (ii) absence of suitable vectors in arid habitats, as blood parasites need of intermediate hosts with certain water requirements to complete their larval phase (Hille et al., 2007; Valera et al., 2003); (iii) low host densities could account for the absence of parasitemia (Hille et al., 2007); (iv) not time enough for the co-evolution of host, vectors and parasite to have occurred (Earlé and Underhill, 1993). Finally, although not exclusively for arid-adapted birds, local particularities can account for notable differences. For instance, Carrete et al. (2009) found that Lesser Short-toed Lark (*Calandrella rufescens*) feeding in farms had higher risk of contracting diseases from poultry compared to those with natural feeding habits.

Ectoparasites have direct transmission modes (e.g., Carrillo et al., 2007b), and, consequently, higher transmission efficiency as they do not depend on hosts. Thus, it is expectable that factors different from climatic ones can also limit their presence. Indeed, whereas ectoparasite richness seems to be limited by abiotic factors in extreme environments, like arid habitats, it seems to be governed by species competition in benign ones (Malenke et al., 2011). Consequently, ambient humidity plays a key role in structuring ectoparasite communities, limiting the range of the poorly arid-adapted species in a similar way than it does with free-living

organisms (Bush et al., 2009; Malenke et al., 2011; Moyer et al., 2002a), but also driving temporal changes in parasite prevalence (Carrillo et al., 2007b).

Regarding the Trumpeter finch, the only blood parasite with high prevalence was *Eufilaria* sp. in Errachidia, which reaches high prevalence even when compared with studies from habitats more favourable for its vectors (e.g., Haas et al., 2011). In contrast to some studies describing low prevalence of ectoparasites in arid habitats (see above), we have found moderate to high prevalence of ectoparasites all over the study area (see also Carrillo et al., 2007b), with the exception of mites, which were absent in Errachidia. Overall, we found that blood parasites fit the predictions of our biogeographical hypotheses whereas ectoparasites do not, what suggests that the former have more limitations to establish themselves in new regions colonized by their hosts, likely because intermediate host are lacking (Colautti et al., 2004; Torchin et al., 2003). Our data support the idea that parasites with direct life-cycles could overcome the founder effect more easily in such new ranges (Dobson, 1988; Dobson and May, 1986).

The genus *Eufilaria* sp. has been found in several families of passerines in the Palearctic (e.g., Haas et al., 2011). These parasites are known to be transmitted by various dipterans including genera *Simulium* and *Culicoides* (Anderson, 2000). The high prevalence of *Eufilaria* sp. in Errachidia, its minimal occurrence in Tabernas and its absence in the Canaries could be due to: i) *Eufilaria* sp. is absent in Tabernas and the Canaries and thus cannot be transmitted to the Trumpeter finches. This explanation implicitly assumes that infected birds found in Tabernas (2 out of 276 birds) came from other areas. Genetic analyses support the occurrence of these movements from African to Iberian quarters (Barrientos et al., 2009a); ii) birds coming from Africa to the Iberian Peninsula and the islands are the healthiest, non-parasitized ones. This is also likely since it has been shown that birds that have better immune response disperse further (Snoeijs et al., 2004) and they are also more resistant to blood parasites (González et al., 1999); iii) the suitable vectors do not occur (or they do at very low densities) outside Errachidia (Valera et al., 2003). Smits et al. (2005) underlined the general scarcity of mosquitoes in the Canary arid habitats as well as the low level of hippoboscid flies parasitizing the Canary passerines. The aquatic larvae of many haematophagous insect species of the above mentioned families require habitats that are usually scarce in arid environments (Minakawa et al., 2005). However, birds from Errachidia were trapped in an oasis (with clean, permanent water that can allow a development of haematophagous species that are rare in the other habitats, Baz, pers. com.). Nevertheless, the high prevalence of *Eufilaria* sp. in Errachidia must be taken with caution as sample size is moderate, although it is above a reasonable threshold for parasite studies (Jovani and Tella, 2006). These authors suggest that sample sizes around 10–20 individuals guarantee representativeness in a similar way to larger sample sizes (Jovani and Tella, 2006).

The absence of mites in Errachidia population is striking as these parasites are abundant in the other two populations, and it could be again influenced by the moderate sample size. It could be also argued that visual examination of ectoparasites during molt (i.e., during post-breeding season) tends to underestimate parasite loads (Moyer et al., 2002b). However, where we could study both seasons in the same year, we found higher prevalence of mites in post-breeding compared with breeding (in Tabernas, 54.5%, $n = 22$ *vs*. 42.6%, $n = 94$, respectively). Abiotic factors have been argued to explain differences in parasite prevalence between populations (Fromont et al., 2001; Malenke et al., 2011). For instance, a moderate level of water vapour in the air is a key trait for the survival of feather mites (McClure, 1989). Whereas the relative humidity reaches moderate to high values both on the aridest islands in the Canaries (for example, year-round mean c. 70% for Lanzarote, Graf et al., 2008) and Tabernas desert (mean 81% at dawn in August 2005, mean 88% at dawn in October 2005; Junta de Andalucía, Meteorological data), inland localities in North Africa reach clearly lower values (c. 35% at dawn in August, c. 60% in October, Guernaoui et al., 2006). Thus, the lower relative humidity in inland localities of the African continent could be restricting the distribution of mites in these extremely dry ecosystems. Although birds were captured in an oasis as it has been stated above, and then relative humidity in these places could be higher, Trumpeter finches prefer dry habitats using the oasis just for drinking (pers. obs.). Relative humidity can also affect geographical differences in lice (Malenke et al., 2011), since the above mentioned values fall under the critical level for this group (c. 45%, Rudolph, 1983). Since *Philopterus* seems to be more sensitive to dryness than *Brueelia* sp. (Carrillo et al., 2007b), geographical differences in abiotic factors like relative humidity could also account for the differences in *Philopterus* sp. prevalence between Errachidia and both the Canary Island and Tabernas populations.

4.2. Island vs. mainland

Several works have found a poorer parasite assemblage in islands compared with mainland (Fromont et al., 2001; Goüy de Bellocq et al., 2002; Segovia et al., 2007). Overall, we found a similar richness in the island population compared with the mainland one. It is remarkable that different parasite species were found in each population. Whereas the absence of some species with low prevalence (e.g., most of haematozoa) could be explained by the low sample size, this cannot be argued for *Eufilaria* sp. (50% prevalence in Errachidia and absent in the Canary Islands, where more individuals were sampled), or for mites (86% prevalence in the Canary islands and absent in Errachidia).

In contrast to the general agreement about the reduced number of parasite species expected for island-dwelling vertebrates, there is not a clear pattern for prevalence. Host density seems to be an important factor, but its values are not always higher in island populations, what influences the differences in parasite prevalence between island and mainland populations (Dobson, 1988; Fromont et al., 2001; Hakkarainen et al., 2007). Unfortunately, we have no data on Trumpeter finch density in North Africa. However, its density in the Canary Islands (<3 birds/10 ha in any of the 23 sampled localities, Carrascal and Alonso, 2005) is fairly lower than that from Tabernas (21 birds/10 ha, Carrillo, 2007). Although birds can concentrate when feeding on maize supplied for goats in farms in the Canary Islands (Carrete et al., 2009), we did not sample these places. Furthermore, it is unlikely that bird density can explain the contrasting patterns observed in two ecologically similar parasites like *Philopterus* sp. and *Brueelia* sp. We found a higher prevalence of haemoparasites in mainland (Errachidia) than in the islands, but this result is due to the high prevalence of a single species, *Eufilaria* sp. Concerning ectoparasites, this comparison is probably affected by the different dates of sampling. Carrillo et al. (2007b) found that the prevalence of *Brueelia* sp. and *Philopterus* sp. in south-eastern Iberian Peninsula decreased significantly along the season, with lower values during summertime (July–September). Considering that the same pattern could be found in Errachidia and Canary populations, it is therefore plausible that the prevalence of *Brueelia* sp. is higher in Errachidia (78% in summertime) than in the Canary Islands (8% during breeding). However, this is not the case for *Philopterus* sp. as a hypothetical seasonal decrease of prevalence in the Canary Islands similar to the one observed in Tabernas (c. 45%, Table 2) would render a value (c. 52%) close to the prevalence observed in the post-breeding period in Errachidia (56%, Table 2). An alternative explanation could be that island hosts are

particularly susceptible to parasite infections due to their impoverished genetic diversity, including their high inbreeding levels (Whiteman et al., 2006) or their little variable MHC (Bollmer et al., 2011). Nevertheless, on one hand, the populations here studied show similar values of inbreeding (Barrientos et al., 2009a). On the other hand, there are no studies on Trumpeter finch immune system or genetic-related traits to test the second hypothesis. Finally, it is worth mentioning that some authors have found that competition can shape ectoparasite communities (Bush and Malenke, 2008; Bush et al., 2009; Malenke et al., 2011). In this sense, a high haematophagous ectoparasite load, as the one here reported for the Canary Islands, could lead to a competitive exclusion of blood parasite vectors, reducing haemoparasite prevalence (Martínez-Abraín et al., 2004).

4.3. Expanding vs. source population

We found no support for lower parasite richness in expanding population for haemoparasites. The number of ectoparasite species was even higher in the expanding population, as mites were not present in the source population. However, we found support for lower prevalence in the expanding population as expected for haemoparasites, although this is, again, mainly due to the high prevalence of *Eufilaria* sp. in Errachidia. In contrast, the prevalence of ectoparasites was not lower in the expanding population. Differences in sample size between sites does not seem to influence our data, as trends are opposite for haemo- and ectoparasites. The high density of Trumpeter finches found in the expanding population and the relatively favourable climatic conditions (see above) could be favouring the spread of parasites with direct transmission and subject to climatic constrains like louse species (Carrillo et al., 2007b) and mites. On the other hand, the longer a species is established in its new range, the more parasites it should accumulate (Torchin and Mitchell, 2004). Phillips et al. (2010) found that whereas Cane toads (*Bufus marinus*) in the expansion vanguard are virtually free of parasites (Lungworms *Rhabdias pseudosphaerocephala*, a parasite with direct cycle), these nematodes arrive to the expansion front 1–3 years after toads themselves. Thus, it is possible that the time elapsed since the Iberian Peninsula was colonized (several centuries ago, although population differentiation with North Africa could already have occurred in that continent, Barrientos et al., 2014), is long enough to allow an enrichment of Iberian bird parasite fauna. Furthermore, the continuous flow of hosts from North Africa (Barrientos et al., 2009a) can also contribute to soften parasite bottlenecks. Indeed, the reproductive output of the Trumpeter finch, a parameter commonly related with the level of parasitism (e.g., Fitze et al., 2004), is similar between our expanding and source populations (Barrientos et al., 2009b). Finally, it is possible that parasites with different transmission modes respond in dissimilar ways when their host expands its range. In their studies with naturally expanding White-winged doves (*Zenaida asiatica asiatica*), Glass et al. (2002a,b) found some helminth species in a recently established population that were not previously detected in the core one. However, no new haemoparasite species was found in the new quarters (Glass et al., 2002a,b).

4.4. To what extent are our results sensitive to common biases affecting similar biogeographical studies?

Two main biases are common in biogeographical studies on parasites (Colautti et al., 2004; Goüy de Bellocq et al., 2002; Poulin and Morand, 2000; Torchin and Mitchell, 2004), namely: i) the different research effort conducted within every population because hosts and their parasites are usually better studied in their original ranges rather than in the new ones; ii) mainland/source populations whose hosts have larger geographical ranges (and more localities sampled) have been used. We think that our results are free of such biases because: i) sampling effort was higher in the island and in the expanding population than in the mainland/source one; ii) our data do not come from various sources or publications, rather we obtained the information with a standard methodology.

It could be argued that the *parasite fauna* (*sensu* Poulin, 2004) here studied is too small to detect differences, since we recorded only seven parasites and we could not identify them beyond the genus level. However we studied seven out of eight of the haemo- or ectoparasite species (or taxa) recorded to date parasitizing Trumpeter finches, as we found no *Plasmodium* sp. in our study. Studies employing biogeographical focuses similar to ours have also used parasite faunas of similar richness (Bush et al., 2009; Glass et al., 2002a,b; Malenke et al., 2011). Also, parasite infections are expected to be higher at sites with larger richness of related host species (Poulin and Morand, 2000; Torchin and Mitchell, 2004). Among passerines, 12 breeding species co-occur in the Canary Islands, 35 in Tabernas and 38 in Errachidia (del Hoyo et al., 2010). Thus, differences in potential host richness in the Canary Islands respect mainland could account for the higher prevalence of haematozoa in the later, but, however, this cannot explain the differences between Errachidia and Tabernas or differences in ectoparasites. In conclusion, our results suggest that (i) there is a geographic-related variability in Trumpeter finch parasitemia; (ii) parasites with different transmission modes work different.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2014.03.005.

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