

# Thriving in an arid environment: High prevalence of avian lice in low humidity conditions<sup>1</sup>

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**Abstract:** Abiotic factors have been reported to cause variation in parasite pressure among host populations, but such relationships have not been studied in detail, and conflicting evidence exists about the nature of these relationships. Here we study within- and between-population variation in chewing lice parasitization in an arid bird species, the Trumpeter finch (*Bucanetes githagineus*), and the influence of ambient humidity on parasite load. We found a high prevalence of 2 chewing lice even in particularly dry years and a positive effect of humidity on prevalence at a monthly scale. Nonetheless, our results clearly reveal that lice can become abundant at low ambient humidity conditions and that birds in arid environments are not necessarily under lower ectoparasitic pressure than birds in humid regions. We suggest that lice may adapt their life cycle to overcome the most critical period by synchronizing the more resistant phase (eggs) to the period when relative humidity is lowest (*i.e.*, summertime). We stress that studies on the effect of ecological factors on host–parasite relationships should consider detailed aspects of the life cycle of the latter and the main biological traits of the different stages of the parasites.  
**Keywords:** arid environments, host–parasite interaction, humidity, Ischnocera, Trumpeter finch.

**Résumé :** Il a été rapporté que des facteurs abiotiques puissent être responsables de variations de la pression parasitaire dans les populations hôtes quoique de telles relations n'aient pas été étudiées en détail et que des évidences conflictuelles existent à propos de la nature de telles relations. Nous avons étudié les variations du parasitisme par les poux piqueurs à l'intérieur et entre les populations d'une espèce d'oiseau des régions arides, le roselin githagine (*Bucanetes githagineus*), ainsi que l'influence de l'humidité ambiante sur la charge parasitaire. Deux espèces de poux piqueurs avaient une forte prévalence même dans les années particulièrement sèches. Nous avons aussi observé un effet positif de l'humidité sur la prévalence à l'échelle mensuelle. Néanmoins, nos résultats démontrent clairement que le poux peut devenir abondant dans des conditions de faible humidité ambiante et que les oiseaux des régions arides ne sont pas nécessairement soumis à une pression ectoparasitaire plus faible que ceux des régions humides. Nous suggérons que les poux pourraient ajuster leur cycle vital pour surmonter la période la plus critique en synchronisant leur phase la plus résistante (les œufs) à la période de plus faible humidité relative (*i.e.*, l'été). Nous insistons sur le fait que les études sur les effets des facteurs écologiques sur les relations hôte-parasite devraient considérer les détails du cycle vital et les principales caractéristiques biologiques des différents stades du parasite.

**Mots-clés :** environnements arides, humidité, interaction hôte-parasite, Ischnocera, roselin githagine.

**Nomenclature:** Eichler, 1963; Mey, 1982; Cramp & Perrins, 1994.

## Introduction

Parasites have a major influence on the ecology and evolution of their avian hosts (Loye & Zuk, 1991; Clayton & Moore, 1997). Understanding the relative contribution and interactions of factors influencing parasite pressure is essential for a better knowledge of the effect of parasites on their hosts and the evolution of host–parasite interactions. Much work has been done both on the importance of basic host features such as health status (Moller, Erritzoe & Saino, 2003; Valera *et al.*, 2004), body mass (Rózsa, 1997a,b; Krasnov *et al.*, 2004; Valera *et al.*, 2004), and morphological and physiological components of host defence (Clayton & Moore, 1997; Roulin *et al.*, 2003) and on the relevance of social, ecological, and life-history features of the host (Clayton & Moore, 1997; Tella *et al.*, 1999; Barbosa *et al.*, 2002; Krasnov *et al.*, 2004).

Parasites and their vectors are sensitive to abiotic conditions. Thus, abiotic factors may have an important influence on parasite pressure (Moyer, Drown & Clayton, 2002). Nonetheless, relatively little work has been devoted to this subject (but see Lindsay *et al.*, 1999; Talleklint-Eisen & Eisen, 1999; Moyer, Drown & Clayton, 2002 for ectoparasites and Earlé *et al.*, 1991; Freed *et al.*, 2005 for haemoparasites) probably because such questions require prolonged study periods and because not all systems are suitable for this purpose. However, in the present scenario of climate change, which is likely to have a major effect on the distribution and abundance of parasites (Sutherst, 2001), it is important to ascertain the relationship between parasites and abiotic factors in order to understand how parasites and disease risks will respond to anthropogenic climate change (Altizer *et al.*, 2006). Some parasites seem to be well suited for these studies. Permanent parasites (those completing their entire life cycle on the host), such as avian lice and feather mites, provide a suitable system for this research since the resources they need are delimited chiefly by the

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host, and thus the factors governing their ecology may be easier to identify than those governing the ecology of free-living organisms (Price, 1980).

It is generally agreed that the prevalence of avian haematozoa is lower in birds inhabiting harsh environments (Merino *et al.*, 1997; Bennett, Montgomerie & Seutin, 1992; Valera *et al.*, 2003). Whether this is also the case for ectoparasites is debatable both because of the paucity of data (but see Fabiyi, 1996; Lindsay *et al.*, 1999; Wiles *et al.*, 2000) and because there is conflicting evidence about the relationship between abiotic factors and ectoparasite infestation rate. Latta (2000) and Latta and O'Connor (2001) described a negative relationship between infestation rate of an avian ectoparasitic mite and rainfall. Fabiyi (1996) found that some chewing louse species thrived only in areas with a short humid season, whereas other species were completely restricted to areas with a long humid season. In contrast, Moyer, Drown, and Clayton (2002) found positive correlational evidence between louse abundance and ambient humidity and showed experimentally that low ambient humidity reduced the abundance of lice. They concluded that an abiotic factor, such as ambient humidity, can cause substantial variation in parasite pressure among host populations via direct effect on the parasite.

Here we investigate within- and between-population variation in chewing lice parasitization in an arid bird species, the Trumpeter finch (*Bucanetes githagineus*), and the influence of abiotic factors on infestation rate. Specifically we study: *i*) spatial and temporal variation in infestation rate of 2 chewing louse species, *ii*) host and ecological factors that could determine the prevalence and intensity of lice on birds, such as age, gender, and seasonality, and *iii*) the effect of an abiotic factor, humidity, on infestation rate. In this regard, we analyze the prevalence and intensity of parasitization of 2 Phthiraptera species within and among 2 geographically and ecologically distinct populations over 3 seasons and the variation in ambient humidity in both locations at different phases of the annual cycle over a 3-y period.

## Methods

### STUDY SPECIES

The Trumpeter finch (*Bucanetes githagineus*) is a small-bodied fringillid (21 g) inhabiting deserts and semi-deserts that recently colonized the Iberian Peninsula, which is currently the northern border of its breeding range (Carrillo *et al.*, 2007). The species became resident in southeastern Spain during the last third of the 20<sup>th</sup> century and now has a major breeding area in Tabernas (Manrique & Miralles, 1988) and some minor breeding localities in Almería province and along the Mediterranean coast (Manrique *et al.*, 2003).

Trumpeter finches breed during March–June (Manrique & Miralles, 1998; Barrientos *et al.*, in press). Two broods can be raised in a season (C. M. Carrillo, pers. observ.). Birds disperse throughout the breeding areas during July, August, and September, sometimes concentrating around drinking sites. Later on, the birds aggregate in flocks and move farther from the main breeding areas (Manrique & Miralles, 1988). Adult Trumpeter finches undergo a complete summer moult, whereas juveniles

carry out a partial summer moult (Svensson, 1992). As a result body feathers (which are the relevant ones for the lice that infest Trumpeter finches) are gradually moulted from May until September.

Chewing lice are permanent ectoparasites that seldom leave the host except to transfer among individuals, *e.g.*, between parents and their offspring (Clayton & Tompkins, 1995). Their life cycle lasts 3–4 weeks and includes the egg, 3 nymphal instars, and the adult stage (Marshall, 1981). Eggs are glued to the feathers with a glandular cement, often in locations protected from preening, the major defence of the host against lice (Marshall, 1981). Chewing lice have the potential to reduce host fitness (Clayton *et al.*, 1999) through effects on thermoregulation and feather quality (Booth, Clayton & Block, 1993). Many louse species have an efficient system of moisture uptake from the surrounding air that enables them to keep their water balance, with 43% relative humidity being the lowest critical equilibrium value so far reported (Rudolph, 1983).

### STUDY SITE

During the period 2002–2004 Trumpeter finches were captured at 2 localities in the southeastern corner of the Iberian Peninsula: Tabernas (province of Almería; 37° 00' N, 2° 33' W) and Gorafe (province of Granada; 37° 30' N, 2° 59' W), which are 120 km apart. Tabernas is the primary breeding area of the species in Spain, whereas breeding in Gorafe has been confirmed only recently (Manrique *et al.*, 2003). In contrast, hundreds of birds (mainly juveniles) aggregate in a few natural water troughs in Gorafe during summer (Fernández-Ordóñez, Martínez & Calderón, 2002; C. M. Carrillo, pers. observ.). Thus, the 2 localities hold ecologically distinct populations: a breeding population in Tabernas characterized by low-density occupation of a large area over several months and a transient population summering in Gorafe that occasionally concentrates in restricted areas to drink.

The climate in both localities is semi-arid, with long hot summers and strong fluctuations of temperature both on a daily and seasonal basis. Tabernas has an average spring–summer (March to September) mean relative humidity of 52.66% (range: 23.42–87.85%) and Gorafe has an average mean relative humidity of 50.6% (range: 20.25–85.25%) (Junta de Andalucía climatic data).

### ECTOPARASITE MONITORING

Data were collected between July 2002 and September 2004. Most data for Tabernas were obtained during the period May–September. However, the density of finches in Gorafe during breeding is extremely low (Fernández-Ordóñez, Martínez & Calderón, 2002; C. M. Carrillo, pers. observ.), and thus no bird was trapped in this location during March–June.

Birds were mist-netted, measured, weighed, aged (juvenile *versus* adult individuals), and scanned for ectoparasites. Some lice were removed from the plumage with forceps and transferred to a vial of 75% ethanol for identification. Adult breeding birds were sexed following Svensson (1992), whereas juveniles could not be reliably sexed.

Two louse species (*Brueelia* sp. and *Philopterus* sp., Phthiraptera: Ischnocera) were recorded. We easily dis-

tinguished adult *Philopterus* from adult *Brueelia* on the basis of their body shape and size. Moreover, both species showed high site specificity. One hundred and thirty six out of 138 birds with adult *Brueelia* had the parasites on the feathers of the belly and/or the rump (only 11 birds had *Brueelia* on the rump). Each of the 2 remaining birds had just one *Brueelia* louse in the transition zone between the throat and the belly. Ninety-three out of 95 birds with adult *Philopterus* had these parasites on the head. The remaining 2 birds had a single *Philopterus* louse in the area between the throat and the belly. On the basis of this specificity, we assigned each parasite (adult and/or immature) to each genus according to the place where the parasite was found (*i.e.*, parasites found on head = *Philopterus*; parasites found on the belly or rump = *Brueelia*). Incorrect identification of immature lice would in any case be negligible for the calculation of prevalence since adult lice were found on all but a few of these birds (7 out of 209 birds had only immature lice on the head and 5 out of 574 birds had only immature lice on the belly).

We found 2 different types of eggs, which were easy to distinguish, even after hatching, on the basis of size, shape, and aggregation: eggs on the feathers of the throat were larger, rounded, and not clumped. Eggs attached to the feathers of the belly and the rump were smaller, oval, and clumped. We found only 2 birds with small eggs on the throat, and we found no bird with eggs of the first type on the belly and/or rump (see Foster, 1969 for similar results). We found an evident relation between the occurrence of parasites of each genus and the location of the eggs. Specifically, all 14 birds that were parasitized only with *Brueelia* (adult and/or immature) had eggs on the belly and/or the rump (just 3 birds for the latter) and none of them had eggs on the throat. Similarly, all 63 birds that were parasitized only with *Philopterus* (adult and/or immature) had eggs on the throat and none had eggs on the belly or the rump. This site-specificity is typical of Ischnocerans (Marshall, 1981) and has been specifically reported for both lice species (Ash, 1960).

Visual examination was used for quantification of feather lice. This method is an accurate predictor of louse abundance (Clayton & Drown, 2001). The adults and larvae of the 2 species of lice move slowly, and their size and the size of their eggs make them easy to spot. All birds were sampled once using a standardized method. Two persons looked for parasites and eggs on the bird for about 5 minutes. One person held the bird, and both carefully examined it in its breast, belly, lower back, and rump by gently blowing feathers away. Repeated inspections after the first 5-minute examination of birds during the study period did not result in additional detection of parasites. From September 2003 the head, neck, and throat were also explored (this accounts for differences in sample sizes between the lice species found, see Tables I and II).

In this paper we use 2 measures of abundance of lice. The first is prevalence, the proportion of birds infested with lice. Unless otherwise stated, prevalence was calculated on the basis of the presence of adult, larvae chewing lice or eggs. Nonetheless, we also report the proportion of birds infested only with eggs and only with adult/larval lice. The second measure is intensity, calculated on the basis of the

TABLE I. Prevalence of *Brueelia* sp. (calculated on the basis of the presence of adult, larvae chewing lice, or eggs) in Trumpeter finches in relation to host age and season in 2 locations during 2002–2004 (sample size in parentheses).

Location	Year	Age	Prevalence % (Sample size)	
			Breeding	Post-breeding
Tabernas	2002	Juv	0	30.0 (10)
		Ad	0	61.3 (31)
	2003	Juv	78.0 (50)	66.7 (39)
		Ad	92.6 (54)	78.6 (28)
	2004	Juv	66.7 (30)	64.3 (42)
		Ad	88.2 (17)	75.0 (8)
Gorafe	2002	Juv	0	25.0 (24)
		Ad	0	100.0 (2)
	2003	Juv	0	77.1 (166)
		Ad	0	90.0 (10)
	2004	Juv	0	23.3 (30)
		Ad	0	0

TABLE II. Prevalence of *Philopterus* sp. (calculated on the basis of the presence of adult, larvae chewing lice, or eggs) in Trumpeter finches in relation to host age and season in 2 locations during 2003–2004 (sample size in parentheses).

Location	Year	Age	Prevalence % (Sample size)	
			Breeding	Post-breeding
Tabernas	2003	Juv	0	100.0 (8)
		Ad	0	66.7 (3)
	2004	Juv	80.0 (30)	50.0 (42)
		Ad	100.0 (17)	37.5 (8)
Gorafe	2003	Juv	0	18.8 (32)
		Ad	0	0.0 (1)
	2004	Juv	0	13.3 (30)
		Ad	0	0

number of parasites per parasitized bird (Rózsa, Reiczigel & Majoros, 2000). This was assessed both for adult/larval lice and for eggs. Adults/larvae intensity depends on the number of adults and larvae counted per bird. To calculate egg intensity the number of eggs per bird was tallied and classified into 6 categories: 0–10, 11–20, 21–30, 31–50, 51–100, and > 100 eggs.

It could be argued that prevalence calculated on the sole basis of the occurrence of louse eggs is misleading since empty or dead egg cases can remain attached to the feathers for a long time. Since coexistence of adult lice and eggs on the same individual is high from May to July (around 28–53% of parasitized birds for *Brueelia* and 79–95% for *Philopterus*, Figure 1) and chewing lice generally breed throughout the year, (Marshall, 1981) lice very likely lay during summertime. In fact, we could differentiate the occurrence of smaller, duller, hatched eggs and larger, glossy, unhatched eggs during the post-breeding season. Most birds probably carried a combination of intact eggs and shell remnants (see Foster, 1969). Moreover, since lice are capable of identifying new feathers that will not be lost (Moyer, Gardiner & Clayton, 2002) they probably lay their eggs on new feathers, whereas old, hatched eggs glued to old feathers are probably lost when those feathers are moulted. In summary, we believe that estimates of prevalence of lice that include birds with eggs only are not severely biased. Measures of intensity of parasitization on the basis

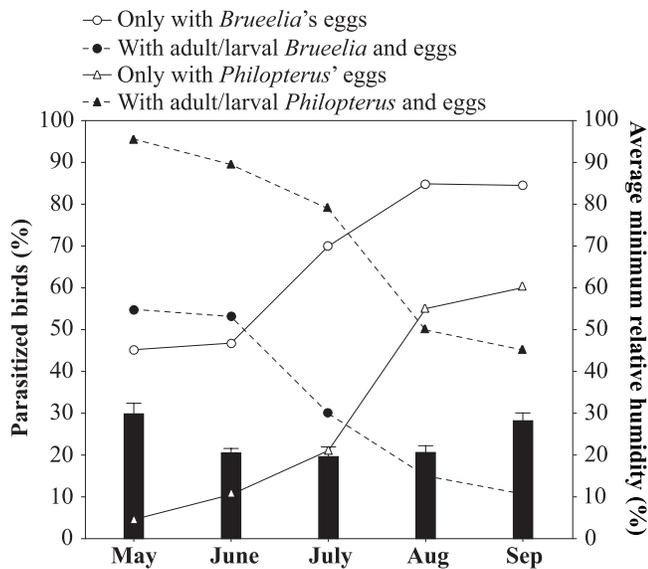


FIGURE 1. Seasonal patterns in the occurrence of life stages of *Brueelia* sp. and *Philopterus* sp. and in the average minimum relative humidity (%). Dotted lines refer to Trumpeter finches carrying adult/larval lice and eggs. Continuous lines account for finches carrying only eggs. Data are offered for each louse species separately and refer to the total number of birds parasitized by each louse species during all the study years. The number of birds parasitized by *Brueelia* and *Philopterus* in each month are respectively May: 62, 22; June: 62, 19; July: 203, 109; August: 33, 8; and September: 19, 22. Monthly humidity data (bars) are the average (+SE) of values from all the study years and locations.

of egg numbers may be biased since already-hatched eggs could be included. Nonetheless, since the bias should not vary among the cases compared (localities, years) we preferred to show the comparisons, with the warning that the reported intensity of parasitization may be overestimated.

Following Bush *et al.* (1997), we defined parasite load to encompass both prevalence and intensity.

#### METEOROLOGICAL DATA

Mean and minimum relative humidity data were obtained from the Junta de Andalucía's meteorological stations near our study areas (20 from Tabernas and 45 km from Gorafe) for the period 2002–2004.

On the basis of the rainfall and temperature pattern in our study area (Lázaro *et al.*, 2001) and the life cycle of the Trumpeter finch (Manrique & Miralles, 1988; Barrientos *et al.*, in press) the period March–June was defined as the spring season (*i.e.*, breeding season) and July, August, and September were defined as the summer season (*i.e.*, post-breeding season).

#### STATISTICAL ANALYSES

##### ABIOTIC FACTORS

Relative humidity values were not normally distributed (Lilliefors tests,  $P < 0.05$ ). Therefore, non-parametric tests (Friedman ANOVA test) were applied to the daily mean and minimum relative humidity data to look for differences among periods, years, and localities.

##### VARIATION IN PARASITE LOAD

We first looked for differences between host sexes in prevalence and intensity of parasitization across study years,

localities, and seasons. Using the program Quantitative Parasitology 2.0 (Reiczigel & Rózsa, 2001) prevalences were compared with Fisher's exact tests, whereas bootstrapped  $t$ -tests and Mood's median tests were used for comparing mean and median intensities, respectively; 4000 replications were used for estimation of 95% confidence intervals of prevalences and means and for bootstrapped  $t$ -tests. Since no significant differences were found between sexes among years, localities and seasons ( $P > 0.05$  in all cases), we pooled data from male and female birds. Therefore, we studied variation of parasite load in Trumpeter finches on the basis of age (adult *versus* juvenile), season (breeding *versus* post-breeding), and year (2002–2004). We analyzed each chewing louse species (*Brueelia* sp. and *Philopterus* sp.) separately.

Kolmogorov–Smirnov 2-sample tests were used to test for differences in intensity of parasitization on the basis of loads of louse eggs (measured in the above-mentioned categories). Unlike other tests, this one is sensitive to differences in the general shapes of the distributions in the 2 samples (Zar, 1996).

Log-lineal models were fitted and tables of partial associations for fully saturated models were used to judge the significance of associations of interest (those between prevalence and host age, season, and year) when controlling for variation due to other factors. These analyses were performed with the STATISTICA 6.0 package (StatSoft, 2001).

The manner in which the occurrence of one species of chewing louse influences the occurrence of the other was estimated using the coefficient of interspecific association as described by Cole (1949). This coefficient ranges from  $-1$  (perfect negative association: the 2 species occurred together the minimum possible number of times) to  $1$  (perfect positive association: they occurred together as many times as they possibly could have). If the number of joint occurrences is exactly what would be expected under the hypothesis of independent scattering of the 2 species, no association is indicated (association value = 0). The coefficient of interspecific association expresses the realized proportion of the maximum interspecific association, which might have been obtained with the particular collections under consideration (Cole, 1949).

Spearman rank correlation tests were used to explore the relationship between monthly prevalence of each louse species and average minimum humidity of the previous month. For these analyses data from all years were considered after checking that all months of the study period (May to September) were represented at least once.

## Results

### PREVALENCE AND INTENSITY OF PARASITIZATION

Trumpeter finches were parasitized by 2 chewing louse species (*Brueelia* sp. and *Philopterus* sp., Ischnocera: Philopteridae). *Brueelia* sp. was found in all the seasons, years, and localities studied (Table I). Overall, the prevalence of adult/larval *Brueelia* was 25.5% (95% confidence interval = 0.22–0.29,  $n = 541$  birds examined), but prevalence rose to 70.1% (95% confidence interval = 0.66–0.74)

when eggs were also considered. *Philopterus* sp. also occurred in all years and localities (Table II). The overall prevalence (considering only adult/larval individuals) was 38.0% (95% confidence interval = 0.31–0.46,  $n = 171$  birds examined) and 49.7% (95% confidence interval = 0.41–0.57) when including birds with *Philopterus* eggs. The mean number of *Brueelia* and *Philopterus* lice per bird was 3.07 (95% confidence interval = 2.54–3.88) and 5.66 (95% confidence interval = 4.92–6.61), respectively.

Both louse species exhibited a positive relationship (coefficient of interspecific association,  $C = 0.52 \pm 0.11$ ,  $P < 0.01$ ,  $n = 209$ ), indicating that about half of the possible positive associations between the 2 species were realized.

SEASONAL PATTERNS IN THE OCCURRENCE OF LICE LIFE STAGES

The occurrence of adults/larvae and eggs of *Brueelia* sp. in parasitized birds (pooling data from all years) followed a different seasonal pattern (Figure 1). The proportion of birds carrying adults/larvae and eggs decreased as the year progressed such that it was significantly higher during May–June than during July–September (Proportion test,  $P < 0.01$ ). In contrast, the occurrence of birds carrying only eggs was more likely in July–September than in May–June (Proportion test,  $P < 0.01$ ) (Figure 1).

*Philopterus* sp. followed a similar pattern, although the decrease in the occurrence of parasitized birds carrying adults/larvae and eggs took place later in the season (during August and September) than in the case of *Brueelia* sp. (Proportion test,  $P < 0.01$ ) (Figure 1). The proportion of birds carrying only eggs was significantly higher in July–September than in May–June (Proportion test,  $P < 0.01$ ).

The occurrence of birds parasitized only with eggs during the study period was significantly higher for *Brueelia* than for *Philopterus* (Wilcoxon matched-pairs test,  $P < 0.01$ ). The ratio between birds parasitized only with eggs and birds parasitized with adults/larvae and eggs during post-breeding was significantly higher for *Brueelia* than for *Philopterus* (Proportion test,  $P < 0.05$ ).

INTERANNUAL VARIATION IN PREVALENCE OF CHEWING LICE

Prevalence of *Brueelia* sp. in Tabernas was affected by host age (Partial Chi-Square ( $\chi^2$ ) = 9.58,  $df = 1$ ,  $P < 0.01$ ), juveniles being less frequently infected than adult birds (Table I), and marginally significantly by season (Partial  $\chi^2 = 3.36$ ,  $df = 1$ ,  $P = 0.07$ ), tending to be higher during the breeding season than during the post-breeding season. Prevalence differed among years (Partial  $\chi^2 = 9.4$ ,  $df = 2$ ,  $P < 0.01$ ), with 2003 being the year with the highest prevalence (Table I, Figure 2).

Prevalence of *Brueelia* sp. in Gorafe was not affected by age (Partial  $\chi^2 = 2.03$ ,  $df = 1$ ,  $P = 0.15$ ), but it did vary among years (Partial  $\chi^2 = 24.38$ ,  $df = 2$ ,  $P < 0.01$ ), with a higher number of birds infected in 2003 (Table I; Figure 2).

In Tabernas, the prevalence of *Philopterus* sp. was not affected by age (Partial  $\chi^2 = 0.03$ ,  $df = 1$ ,  $P = 0.85$ ), but birds were more infected during the breeding season than during the post-breeding season (Partial  $\chi^2 = 13.2$ ,  $df = 1$ ,  $P < 0.01$ ) (Table II). There were marginal interannual differences in prevalence (Partial  $\chi^2 = 3.58$ ,  $df = 1$ ,  $P = 0.058$ ), with 2003 being the year with more birds parasitized

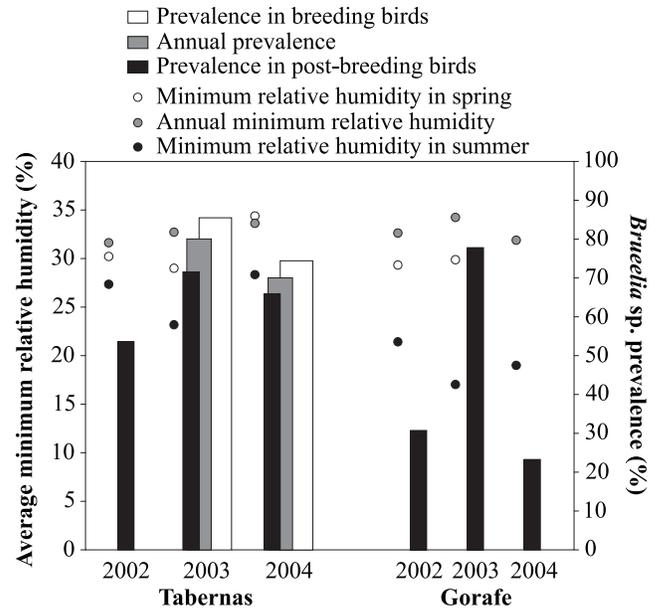


FIGURE 2. Average minimum relative humidity (%) and *Brueelia* sp. prevalence (calculated on the basis of the presence of adults, larvae chewing lice, or eggs) in several years and localities. Humidity data (dots) are offered for 2002–2004 in spring (March–June), summer (July–September), and for the whole year in both study sites. *Brueelia* sp. prevalence (bars) is shown for those periods, years, and localities for which data were available (see Methods).

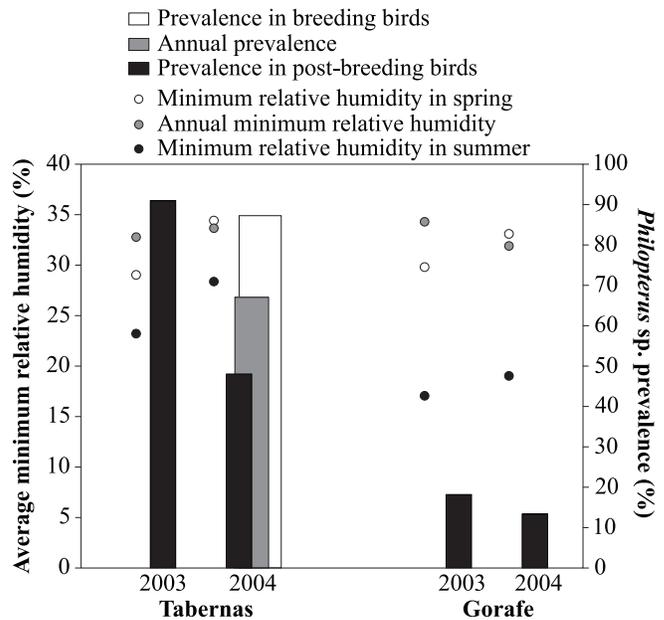


FIGURE 3. Average minimum relative humidity (%) and *Philopterus* sp. prevalence (calculated on the basis of the presence of adults, larvae chewing lice, or eggs) in several years and localities. Humidity data (dots) are offered for 2003–2004 in spring (March–June), summer (July–September), and for the whole year in both study sites. *Philopterus* sp. prevalence (bars) is shown for those periods, years, and localities for which data were available (see Methods).

(Table II, Figure 3). In contrast, in Gorafe, prevalence of *Philopterus* sp. did not vary between years ( $\chi^2 = 0.67$ ,  $df = 1$ ,  $P = 0.67$ ) (Table II, Figure 3).

Overall, 2003 was the year with the highest prevalence for both louse species in both localities, with the apparent exception of *Philopterus* sp. in Gorafe.

#### GEOGRAPHIC VARIATION IN PREVALENCE OF CHEWING LICE

Prevalence of *Brueelia* sp. in juvenile birds during post-breeding did not vary between localities (Partial  $\chi^2 = 1.45$ ,  $df = 1$ ,  $P = 0.23$ ) (Table I). In contrast, the prevalence of *Philopterus* sp. for the same age class and period was significantly higher in Tabernas (Partial  $\chi^2 = 25.49$ ,  $df = 1$ ,  $P < 0.01$ ) (Table II).

#### VARIATION IN INTENSITY OF PARASITIZATION

Variation in intensity of parasitization was investigated in those cases for which enough data were available, namely intensity of parasitization by *Brueelia* on *i*) juveniles during post-breeding in Tabernas in 2003 versus Gorafe in 2003 and *ii*) birds trapped in 2003 versus 2004 in Tabernas. For the latter analysis we pooled data from different age classes and seasons since the proportion of individuals for each age category and period did not differ (Proportion tests,  $P > 0.05$  in all cases).

The intensity of parasitization of *Brueelia* sp. (considering only eggs) on juveniles trapped during the 2003 post-breeding season did not differ between localities (Tabernas: median = 15.0, kurtosis = 2.7,  $n = 24$ ; Gorafe: median = 15.0, kurtosis = 3.7,  $n = 127$ ; Kolmogorov–Smirnov 2-sample test,  $P > 0.10$ ).

We found no differences in the number of adult/larval *Brueelia* in parasitized birds from Tabernas between 2003 and 2004 (median values: 1.0 and 2.0, respectively, Mood's median test,  $P = 0.22$ ,  $n = 53$  and 30, respectively). We obtained the same result when comparing the number of *Brueelia*'s eggs in parasitized birds (2003: median = 15.0, kurtosis = -0.3,  $n = 133$ ; 2004: median = 40.0, kurtosis = -0.6,  $n = 66$ ; Kolmogorov–Smirnov 2-sample test,  $P > 0.05$ ).

#### SPATIO-TEMPORAL VARIATION IN ABIOTIC FACTORS

The average mean and minimum daily relative humidity varied significantly among years: 2003 was the year with the lowest values for the summer period (July–September) in Tabernas and Gorafe (Friedman ANOVA  $\chi^2$  tests,  $P$  values  $< 0.05$  in both cases and for both variables; Figure 2). This was also true for spring (March–June) in Tabernas ( $P < 0.01$  for both variables, Figure 2). During all 3 years the mean and minimum daily relative humidity for the summer period was significantly higher in Tabernas than in Gorafe (Wilcoxon Matched Pair tests;  $P$  values  $< 0.01$  in all cases and for both variables; Figure 2).

The average mean and minimum relative humidity decreased as the season progressed, such that summer values were significantly lower than spring values in all years and localities (Mann–Whitney tests,  $P$  values  $< 0.05$  in all cases and for both variables; Figure 2). When data were pooled for all years and locations we obtained a maximum difference of 10.25% relative humidity in the average minimum relative humidity between May and July (Figure 1).

#### PARASITE LOAD AND ABIOTIC FACTORS

We found no relationship between prevalence of *Brueelia* sp. and year-to-year changes in minimum humidity

(average minimum humidity values for spring–summer in Tabernas and only for summer in Gorafe) (Spearman rank correlation,  $r_s = 0.14$ ,  $P = 0.78$ ,  $n = 6$  [2 localities and 3 years]). The scarce data did not allow us to test this association for *Philopterus* sp.

In contrast, we found a significant relationship between humidity and prevalence at a shorter time scale. The monthly prevalence of both *Brueelia* and *Philopterus* was significantly and positively correlated with the average minimum relative humidity of the previous month (*Brueelia*:  $r_s = 0.59$ ,  $P = 0.027$ ,  $n = 14$ ; *Philopterus*:  $r_s = 0.79$ ,  $P = 0.036$ ,  $n = 7$ ). This was also the case when we calculated prevalence only on the basis of the occurrence of adult and/or immature lice ( $P < 0.05$  for both species).

## Discussion

This study reports widespread parasitization by chewing lice in the Trumpeter finch. Two Ischnoceran lice, *Brueelia* sp. and *Philopterus* sp., were found at a high prevalence in 2 ecologically distinct populations dwelling in arid areas. Previous studies have reported the occurrence of *Philopterus* sp. and *Brueelia* sp. in closely related bird species living in arid environments, *Rhodopechys obsoleta* and *Bucanetes mongolicus*, respectively (Mey, 1982; Fedorenko, 1984). We also show within- and between-population variation in chewing lice parasitization in this arid-zone bird in relation to host characteristics (age, gender), ecological features (seasonality), and abiotic factors (relative humidity).

Concerning host characteristics, we found no effect of host gender on lice parasitization (Marshall, 1981; but see Potti & Merino, 1995). Overall, age did not affect lice parasitization either (see Calvete *et al.*, 2003 for similar results), with the single exception of adults being more parasitized with *Brueelia* sp. than juveniles in Tabernas (see Petrie, Cotgreave and Stewart (1996) for similar results, but see Millan *et al.*, 2004 for higher parasitization of lice on juveniles). Host-age-related differences in prevalence of *Brueelia* in Tabernas but not in Gorafe nor in prevalence of *Philopterus* in Tabernas may be explained by differences in time of exposure to the parasite (Petrie, Cotgreave & Stewart, 1996) (juveniles summering in Gorafe may have already been exposed to the parasite long enough to reach the same infestation level as adult birds) and/or by differential efficiency of grooming ability for different body parts (belly, head) as juveniles grow (Marshall, 1981).

Our results also reveal spatio-temporal variation in infestation rate. Prevalence of *Brueelia* sp. was highest in both localities during 2003, the driest year, and prevalence of *Philopterus* sp. was also highest in Tabernas in that year. Prevalence of *Brueelia* sp. during summertime did not differ between localities (Table I), whereas the prevalence of *Philopterus* was higher in Tabernas at this time of the year (Table II, Figure 3). In contrast, we found no significant difference in intensity of parasitization in any of the cases investigated, including different years and localities varying in relative humidity. Since we found no relationship between year-to-year variation in humidity and prevalence of lice, interannual variation in the latter may have been related to characteristics of the host populations (*e.g.*, fluctuation in relative humidity).

tuations in host population size or quality of host resources; Hoi *et al.*, 1998; Whiteman & Parker, 2004).

One of the main findings of our study is the high prevalence of 2 lice species in a bird species living in an arid environment. Moyer, Drown, and Clayton (2002) found that birds in arid regions had fewer lice than birds in humid areas and showed experimentally that low ambient humidity reduced the abundance of lice. They suggested that low humidity decreases ectoparasite pressure since lice are unable to maintain their water balance below 40% relative humidity (Rudolph, 1983). Our results show a different picture. We found high prevalences of both louse species (25.5% and 38.0% for *Brueelia* and *Philoaterus* sp., respectively, and 70.1% and 49.7%, respectively, when considering also eggs) in 2 populations where minimum relative humidity values under 40% occurred in 80% (Gorafe) and 75% (Tabernas) of summer days. By comparison, Clayton, Bush, and Johnson (2004) indicated, after a thorough review of studies performed in a variety of habitats (many of them more mesic than ours), that the prevalence of species of *Brueelia* tends to be low (< 10%) (see also Clayton, Gregory & Price, 1992, and Hahn, Price & Osenton, 2000). Moreover, we found high prevalences in particularly dry years (Figures 2 and 3). These results are not necessarily incompatible with the positive relation between prevalence of both louse species and the minimum average humidity of the preceding month found in this study. In our opinion, these findings show that humidity favours lice in dry environments but that they can cope with arid climates.

We also found a seasonal effect in the prevalence of *Philoaterus* and *Brueelia* (marginally significant for the latter) such that lower values were found during the post-breeding season. Seasonal fluctuations in louse parasitization load have been described in several studies, associated with the transmission of lice to juveniles (Ash, 1960) or with the effect of feather moulting (see Moyer, Gardiner & Clayton, 2002 and references therein). In our case, the decrease in the prevalence of chewing lice matches a pronounced decrease in humidity (Figure 1) in summer compared to the level of humidity in spring and partly coincides with the moult of body feathers. This seasonal effect is also evident when analyzing the occurrence of the different phases of the life cycle of lice. Whereas the percentage of birds carrying adult/immature lice and eggs decreases from May to September, the percentage of birds carrying only eggs increases. This suggests that adult/immature lice vanish. Most birds trapped during July–September are juveniles that undergo a partial moult affecting mainly the body feathers. “Disappearance” of adult lice may be due to death (*e.g.*, due to harsh climate) and/or to the fact that they are more difficult to detect during moulting (Moyer, Gardiner & Clayton, 2002). The increase in the percentage of birds carrying only eggs may be a correlated effect of the disappearance of adults. However, it may also be that lice adapt their life cycle to overcome the most critical period (*i.e.*, summertime) by synchronizing the more resistant phase (eggs) to the period when relative humidity is lowest (Figure 1), since louse eggs are not influenced by humidity (Saxena *et al.*, 2004). Some results accord with this

last possibility. Whereas the prevalence of *Brueelia* during post-breeding did not vary between localities, the prevalence of *Philoaterus* at this time was higher in the more humid Tabernas. In this season, prevalence of *Brueelia* is due mainly to the occurrence of eggs (80% of individuals), whereas around 50% of birds parasitized by *Philoaterus* carry adults/larvae (Figure 1). Thus, if adult/larval stages are sensitive to low humidity (see below), it makes sense to find higher prevalence of those stages in more humid habitats.

The effect of abiotic factors on ectoparasite prevalence has seldom been studied (but see Lindsay *et al.*, 1999; Talleklint-Eisen & Eisen, 1999; Wiles *et al.*, 2002; Moyer, Drown & Clayton, 2002). In contrast to the findings of Moyer, Drown, and Clayton (2002) our results suggest a positive effect of humidity on prevalence of lice but also show high prevalence of lice in arid habitats. Latta (2000) and Latta and O'Connor (2001) found for feather mites, a species of the same ecological guild as lice (Rózsa, 1997a), a negative relationship between infestation rate and rainfall. Specifically, mites were far more common in a dry desert thorn scrub than they were in higher-elevation and more moist habitats. Moreover, they showed that many of the infested species had distributions that spanned multiple habitat types. Similarly, Fabiyi (1996) found a high plasticity in geographical distribution patterns of certain species of chicken lice in Nigeria, with some species completely restricted to areas with a long humid season, whereas others thrived only in areas with a short humid season. Therefore, it may be that there are louse species specially adapted to different climates, such that humidity is not as restrictive a factor as suggested by Moyer, Drown, and Clayton (2002). The significant reduction of louse prevalence and abundance reported by Moyer, Drown, and Clayton (2002) can probably be explained by the severe experimental conditions imposed on the lice (17% relative humidity over 6 weeks), which are unlikely to occur in the wild even in the driest deserts (*e.g.*, relative humidities between 40% and 80% occurred during the night in the Atacama Desert; see Dose *et al.*, 2001).

Finally, other aspects, such as host selection of favourable habitats during critical periods (Tieleman & Williams, 2002), which would in turn favour the parasite, and/or parasite strategies (moving along the host looking for favourable microhabitats; Wiles *et al.*, 2000) could help parasites to cope with low relative ambient humidity.

In summary, we agree with Moyer, Drown, and Clayton (2002) that abiotic factors can cause some variation in parasite pressure among host populations, but our results show that the effect of humidity can vary in different louse species (see Merino & Potti, 1996) and that lice do not necessarily do poorly when humidity is low. Lice (*i.e.*, parasites) may have several means to overcome unfavourable conditions, and timing some phases of their life cycle to cope with the less favourable conditions can be an important and widespread strategy (Foster, 1969; Marshall, 1981). We therefore stress that studies on the effect of ecological factors on host–parasite relationships should consider detailed aspects of the life cycle of the latter and the requirements of the different stages of the parasites.

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