



Breeding consequences for a songbird nesting in Argentine ant' invaded land

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Abstract The consequences of ant invasions on ecosystems may only become apparent after long periods. In addition, predicting how sensitive native fauna will respond is only possible if the underlying proximate mechanisms of their impact are identified. We studied the attraction of the native and invasive ant community to artificial bird nests. Further, we studied reproduction of a wild native songbird over five consecutive breeding seasons in relation to the presence of an invasive ant species. We analysed biometric, reproductive and individual blood parameters of great tits *Parus major* breeding in invaded as compared to uninvaded sites by Argentine ants *Linepithema humile*. Great tits bred preferably in uninvaded territories by the Argentine ant. Moreover, Argentine ants were more abundant at nests in invaded sites, than any native ant species were at uninvaded sites. Further, Argentine ants recruited at the artificial nests more intensively and responded to a larger variety of nest

contents than native species. Although breeding success and adult condition did not vary in relation to invasion status, offspring quality was negatively affected by the presence of Argentine ants. Nestlings reared in invaded sites were lighter, with lower wing/tarsus length ratio and had a reduced nutritional condition and altered oxidative stress balance as measured from several blood parameters. The interspersed distribution and small distance between invaded versus uninvaded territories suggest that ant presence affects nestling condition through direct interference at the nest. Our results highlight the importance of evaluating the proximate effects like physiological parameters of the native fauna, when studying invasive ant-native bird interactions.

Keywords *Linepithema humile* · *Parus major* · Invasion ecology · Ant-bird interference · Proximate effects · Blood physiological parameters

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Introduction

Ants and birds are among the most ubiquitous and diverse terrestrial animals, and although great effort has been devoted to their study, the nature of their ecological interactions remains poorly understood. Direct interactions such as predation-prey relationships have been found to be reciprocal between both taxa (Stoddard 1936; Ridlehuber 1982; Strong 2000;

Stake and Cimprich 2003; Wiebe and Gow 2013). However, despite the differences in size, competition for resources between birds and ants has been reported through exploitative and interference competition (Haemig 1996; Aho et al. 1997, 1999; Philpott et al. 2005; Lambrechts and Schatz 2014). In general, ants are superior to birds in both types of competition, supporting one of Persson's hypotheses stating that smaller animals should be superior than larger ones in exploitative competition, especially when resources are scarce, but the opposite should be expected in interference competition (Persson 1985). Facilitative interactions between ants and birds have also been reported (Haemig 2001), for example when ants take advantage of bird nests because of microclimatic conditions, and available food resources (nestling food remains and nest-dwelling arthropods) (Mitrus et al. 2016). Likewise, birds may follow ant trails (i.e. army ants) to forage on insects flushed by ant swarms (Di Giacomo and Di Giacomo 2006), or seek ant-protection from other predators by selecting special nesting locations (Janzen 1969; Grimes 1973; Young et al. 1990; Gilardi and von Kugelgen 1991). Furthermore, interactions may not be mutually exclusive, and be context-dependent by changing from competitive or even predatory to facilitative (Haemig 1999). Additionally, the intensity of the interactions may be time-dependent and vary over the different life history stages of the taxa involved (Lambrechts et al. 2008; Boieiro et al. 2018).

Organisms can flexibly adjust their phenotype to changing conditions, primarily through physiological changes, which may in turn underlie behavioural and ultimately determine changes at an ecological scale (Piersma and van Gils 2011). Non-lethal interactions between taxa often result in subtle phenotypic changes that can carry-over and become apparent on the long-term (Monaghan 2008). However, although a wide range of interactions between ants and birds have been studied, proximate causes and consequences of most observed interactions remain unclear.

Ant invasions are known to disrupt native ant communities and modify the established interactions with birds. Studies on the effect of invasive ants on native birds has concentrated on reproduction, reporting mostly negative effects on developing chicks (see reviews by Holway et al. 2002; Allen et al. 2004; Suarez et al. 2005; Lach and Hooper-Bui 2010; but see Helms et al. 2016) (Table 1). Further, invasive ants

have been shown to reduce breeding productivity and induce behavioural shifts by direct attacks on nestlings and adults (Allen et al. 2004; Davis et al. 2008; Matsui et al. 2009; Plentovich et al. 2009, 2018). Most of these studies are based on the red imported fire ant *Solenopsis invicta*, and to other ant species known by their powerful venoms i.e. *Anoplolepis gracilipes*, *Solenopsis geminata* (Lach and Hooper-Bui 2010).

The Argentine ant *Linepithema humile* is among the five ants included in the list of the 100 world worst invaders (GISD 2018; Lowe et al. 2000). It is native from the Paraná and Uruguay river basins in South America, and it has been introduced since the nineteenth century in Mediterranean ecosystems all over the world. The species was detected for first time in continental Europe in 1890, and first reports from Spain date from 1916 (Wetterer et al. 2009). The invasive Argentine ant is known to compete with birds and other native fauna over food resources (Estany-Tigerström et al. 2010; Rankin et al. 2018). Recent evidence suggests that Argentine ants do possess venom that can impinge on small arthropods and vertebrate prey (Alvarez-Blanco et al. 2020; Welzel et al. 2018). However, in most cases only negligible effects on breeding birds have been reported so far, and seldom compared with the effects of other native ant species (Table 1).

We explored the effects of invasive Argentine ant presence on a breeding great tit *Parus major* population close to the southern limit of the species distribution. The great tit is a native songbird species widely distributed in forested areas throughout Eurasia (Gosler 1993). This tree-gleaning passerine feeds on invertebrates during the breeding season, and nests in natural tree-holes or artificial nest boxes, which makes it an ideal model to study ant-bird interactions in the wild. The great tit is among the most intensively studied wild vertebrates and many aspects of its breeding ecology and physiology are well known (Gosler 1993). Most knowledge comes from central and northern European populations living in temperate forests which provide optimal environmental conditions for the species, while marginal populations remain comparatively understudied. However, marginal populations are often exposed to suboptimal environmental conditions (Karvonen et al. 2012), which may render them particularly sensitive to additional ecological challenges, such as an invasive species like the Argentine ant. First, we studied ant

Table 1 Studies on the interactions between the invasive Argentine ant *Linepithema humile* and native birds

Native bird species (Scientific name)	Location	Date	Comp	Effect	Pred	Reported effect	Ref	
Allen's, Anna's, Costa's, and Black-chinned hummingbirds	<i>Selasphorus sasin</i> , <i>Calypte anna</i> ; <i>C. costae</i> ; <i>Archilochus alexandri</i>	California USA	2014	YES	YES	NO	Feeding Interference	Rankin et al. (2018)
Bulwer's petrels	<i>Bulweria bulwerii</i>	Madeira, Portugal	2014–2016	NO	YES	YES	Nestling disturbance	Boeiro et al. (2018)
Red-tailed Tropicbird	<i>Phaethon rubricauda</i>	Rapa Nui, Chile	2014–2015	NO	YES	YES	Adults disturbance	Flores et al. (2017)
Bermudian White-Tailed Tropicbird	<i>Phaethon lepturus catesbyi</i>	Bermuda Island, UK	2013–2015	NO	YES	YES	Nestling disturbance	Mejías et al. (2017)
Blue tit	<i>Cyanistes caeruleus</i>	Cataluña, Spain	2005–2007	YES	NO	NO	No significant effect	Estany-Tigerström et al. (2013)
Various insectivorous birds		Cataluña, Spain	2005–2007	YES	NO	NO	Change in bird community	Pons et al. (2010)
Barn swallow	<i>Hirundo rustica</i>	Andalucía, Spain		NO	YES	YES	Nestling disturbance	Delibes (2005)
Hawaiian goose	<i>Branta sandvicensis</i>	Hawaii, USA		NO	YES	YES	Nestling disturbance	Krushelnicky et al. (2005)
Dark-eyed Junco	<i>Junco hyemalis</i>	California, USA	1998–2000	NO	YES	YES	Nestling disturbance	Suarez et al. (2005)
California least tern	<i>Sterna antillarum browni</i>	California, USA	1989–1994	NO	YES	YES	Nestling disturbance	Hooper-Bùi et al. (2004)
Least Bell's Vireo	<i>Vireo bellii pusillus</i>	California, USA	2000	NO	YES	YES	Nestling disturbance	Peterson et al. (2004)
Hawaiian dark-rumped petrel	<i>Pterodroma phaeopygia sandwichensis</i>	Hawaii, USA		YES	NO	NO	No significant effect	Krushelnicky et al. (2001)
California gnatcatcher	<i>Poliptila melanura</i>	California, USA	1994–1995	NO	YES	YES	Nestling disturbance	Sockman (1997)

Native bird species by common and scientific name (in italics), study location and date are provided. Information on comparisons between invaded and uninvaded areas (Comp) together with the resulting effect (Effect), and whether predation was attributed to the Argentine ant (Pred). A brief description of the reported effect as well as the references are provided

attraction to artificial bird nests with different contents, to assess ant community' interspecific differences in the efficiency for finding bird nests. Second, we studied the nest-site selection and breeding success of a great tit's population in invaded and uninvaded trees by the Argentine ant over five consecutive seasons. Finally, we evaluated the consequences of breeding in Argentine ant invaded tree, on both nestlings and adults, by measuring several morphometric and blood parameters related to size, nutritional condition and oxidative stress. We hypothesized that

Argentine ants would negatively affect great tit reproduction, decrease their breeding success and offspring condition when reared in invaded sites.

Materials and methods

Study area

The study was performed in Doñana Biological Reserve (37°1' N, 6° 33' Andalucía, Spain) at sea

level and 2 km away from the coastline. The study area comprises both marshland and a matrix of an open Mediterranean scrubland containing scattered old cork oak *Quercus suber* tree stands and a small stone pine *Pinus pinea* forest. Environmental conditions in Doñana are characterized by extremely hot and dry summers and temperate winters that can be constraining for both ant and bird species inhabiting tree stands all over the area. The studied great tit population has been monitored since 2012 breeding in 75 nest boxes interspersed through the study area, comprising invaded and uninvaded tree stands.

The Argentine ant in Doñana inhabits cork oak and stone pine stands that provide the appropriate microclimate and food resources, avoiding the scrubland matrix among trees (Angulo et al. 2011). Invasive Argentine ants mostly rely on mutualistic relationships with Homoptera (Newell and Barber 1913; Tillberg et al. 2007; Powell 2008; Brightwell and Silverman 2011; Shik et al. 2014). In many cases, the Argentine ant co-opts the ant-aphid mutualism already established by native ants such as *Crematogaster scutellaris*, as found in our study area (Carpintero et al. 2007). However, the Argentine ant has generalized feeding habits and often includes animal prey or carrion depending on colonies' reproductive stage (Abril et al. 2007). The exploitation of new food items should be important in their success given their extraordinary densities in invaded areas (Helms and Vinson 2002). Because the invasion of natural areas results from inadvertent and sporadic transport by humans or other animals (Carpintero et al. 2005; Castro-Cobo et al. 2019), the Argentine ant in the study area presents a patchy and definite distribution. The arrival in 1970's and expansion of the Argentine ant has been monitored over the last decades, and the consequent retraction of the native ant community is well known (Angulo et al. 2011; Alvarez-Blanco et al. 2017).

Ant attraction to artificial avian nests

To assess the Argentine ant' use of bird nests as foraging targets, we performed an experiment in the study area in June 2014. Artificial nests have been extensively employed in ecological studies to evaluate the degree of nest predation, and despite evidence suggesting that care must be taken when comparing predation on artificial versus natural nests, the method

remains valid (Moore and Robinson 2004). Artificial nests were attached to tree trunks of 10 cork oak stands and 10 stone pine stands at 1.5 m high and with the same orientation to ensure similar sun exposure (Ardia et al. 2006). The trees were chosen according to the invasion status, so half were naturally invaded by the Argentine ant, being all interspersed within the study area (Fig ESM_1).

Artificial nest structures consisted of a commercial plastic bowl grid (Copele, Spain, ref. 70516) covered with a cotton layer in which we placed different contents. Every third day we randomly alternated one of the five following contents (hereafter treatments) in each artificial nest: empty, intact eggs, cracked eggs, faeces, and cracked eggs plus faeces, so each tree experienced all treatments in different orders. In the empty treatment, no remains were added, whereas three quail eggs were added in the intact egg treatment. Cracked eggs were the same type and number of intact eggs with three holes (~ 4 mm diameter) simulating a chick piping the eggshell during hatching. We used chicken faeces (~ 5 gr) added to the cotton layer. Both treatments, empty and intact eggs were considered control treatments, without interest for the ants, since they are not able to breach the shell. For the experimental treatments we used commercial quail eggs and chicken faeces from a nearby farm. Nests with the different treatments were placed in the early morning and were visited 3, 8 and 24 h after to evaluate ant presence. Both the invasive and *C. scutellaris*, the main native ant species in the area, are mass recruitment forager species, which lay a chemical trail that guides nestmates when returning from a food source, resulting in the formation of ant trails that can be active over consecutive days (Carpintero et al. 2007). Thus, 24 h after the set-in and to avoid the bias that could occur through chemical recognition, the artificial nest was removed for one whole day and cleaned with alcohol, before being replaced the following day with a new cotton layer and treatment. During the visit we recorded the following variables in the artificial nests: the temperature (Extech 42500: Mini IR Thermometer, max resolution 1 °C), the number of ants, and whether the ants recruited to the nest or not (i.e. whether the ants made ant trails from the trunk to the artificial nest or not). We also recorded the following variables in the trunk: the total number of vertical ant trails in the trunk at nest-high, and the activity (ants/min) of the vertical

trails within 50 cm of the artificial nest (in 100 cm of the trunk perimeter).

Breeding data and sample collection

During the fall 2012 we installed 75 wooden nest boxes at ~ 1.5 m high from 25 cork oak trees separated by at least 50 m from each other (11 invaded, 14 uninvaded). During the first breeding season (2013), each tree had one nest box hanging from the trunk and two from the branches. Due to the low occupation rate (35%), from 2014 onwards the study area was expanded from 25 to 49 trees (25 invaded, 24 uninvaded), incorporating stone pines and few poplar trees *Populus sp.* Invaded trees were selected prior to the experiments whenever the Argentine ant was the only ant species observed in the tree trunk, which is the common situation whenever the Argentine ant invades this area (Angulo et al. 2011). To reduce spatial autocorrelation bias, invaded and uninvaded trees were chosen to be interspersed throughout the study area (Fig ESM_1).

Breeding parameters were recorded during routine checks that increased in frequency when active nests were detected. Due to national park restrictions some nest boxes could not be checked with the desired frequency and parameters were then estimated (see below). The breeding parameters considered were laying date (March 1st = 1), clutch size, brood size, number of fledglings, and these were used to calculate hatching success (percentage of eggs that hatched), fledgling success (percentage of hatchlings that fledged) and breeding success (percentage of eggs that fledged) to identify which breeding stages were more sensitive to Argentine ant presence. Only the first broods were considered, and laying and hatching dates were estimated when not directly recorded, by assuming continuous incubation period of 13 days and hatching synchrony. All breeding data corresponding to each year is presented in Table ESM_1.

During the breeding season in 2014, blood samples were obtained from great tit parents and nestlings. Chicks were banded, measured for body mass (g), tarsus and wing length (mm) and sampled for blood at 10 days of age. We calculated wing/tarsus length ratio as a measure of morphology and size variation that can be relevant indicator of chick development (Ricklefs and Cox 1977; Lindström 1999). Since not all chicks attained the minimum body mass for being sampled

for blood at this age, blood sampling was postponed in nests with small siblings, and days since hatching were incorporated in the analyses to control for any potential bias. Adults were captured at the nest box or with the use of mistnets after chick sampling and processed the same way. Blood samples were taken from the jugular vein using a heparinized syringe ($< 1\%$ mass) and kept cool (~ 4 °C) until they were centrifuged (4000 rpm, 20 min, 20°C). Blood plasma was separated from the cellular fraction and both were stored at $- 80$ °C until analyses.

Blood samples were analysed to study the nutritional state and oxidative balance, which can provide a measure of the physiological condition of an individual (Monaghan et al. 2009; Piersma and van Gils 2011). On one hand, nutritional state in blood can be evaluated by examining metabolite concentrations of both fat and protein metabolism and catabolism respectively (McCue 2010). Triglycerides (TGR) are the storage form of lipids, and are good indicators of fat deposition, whereas cholesterol (CHOL) is known to be a good predictor of general nutritional condition and body mass (Maceda-Veiga et al. 2015). Total proteins (TP) and uric acid (UA) are all involved in protein catabolism (Jenni-Eiermann and Jenni 1998). Further, UA is a common circulating hydrophilic antioxidant that accounts for an important portion of the antioxidant capacity in blood (Cohen and McGraw 2009). All plasma metabolites (TGR, CHOL, TP, and UA) were measured according to standard methods implemented on a Cobas INTEGRA 400 plus Chemistry autoanalyser (Roche Diagnostics Ltd. Burgess Hill, West Sussex, UK).

On the other hand, oxidative stress is generated as a by-product of aerobic metabolism damaging cell macromolecules and has been linked to diverse selective pressures on survival and reproduction (Monaghan et al. 2009). Organisms counteract oxidative stress by acquiring and producing antioxidants, and while most antioxidative activity is enzymatic, non-enzymatic antioxidants also play a relevant role in maintaining oxidative balance, particularly in blood (Pamplona and Costantini 2011). While no single measure of oxidative imbalance is available, it is commonly agreed that measurement of different antioxidative components (hydro and lipophilic), in combination with the antioxidative capacity and the oxidative damage offers more complete image of the oxidative condition of an individual (Costantini 2008;

Monaghan et al. 2009). Total antioxidant capacity (TEAC) (mM/l) is a measure of the capacity of plasma to neutralize reactive oxygen species and was measured following Erel (2004). Recent studies point out that TEAC is mostly representative of the water-soluble components of the antioxidative system (Cohen and McGraw 2009). Thiobarbituric acid reactive substances (TBARS) (nmol MDA /ml) are a by-product of lipid peroxidation that reflect the oxidative damage experienced, have been measured as described in Buege and Aust (1978). We further determined the activity of four antioxidant enzymes in the cell package. Catalase (CAT) (U/mg protein), which catalyses the decomposition of hydrogen peroxide to water and oxygen and has been measured indirectly through its catalytic activity following Cohen and Somerson (1969). Superoxide dismutase (SOD) (U/mg protein), which catalyses the dismutation of the superoxide radical into oxygen or hydrogen peroxide (is an antioxidant defence) and has been measured as described in McCord and Fridovich (1969). Glutathione peroxidase (GPX) (mU/mg protein) is an enzyme family that reduce lipid hydroperoxides to alcohols and hydrogen peroxide to water and has been measured as described in Carmagnol et al (1983). Glutathione reductase (GR) (U/mg protein) is an enzyme that catalyses the reduction of glutathione disulphide (GSSG) to the sulfhydryl for glutathione (GSH), which is a critical molecule in resisting oxidative stress and has been measured as described in Cribb et al. (1989).

Sample analyses were performed at the Ecophysiology Laboratory at the Doñana Biological Station – CSIC (LEF-EBD) certified to ISO9001:2015 and ISO14001:2015 quality and environmental management systems, respectively.

Statistical analyses

The ant attraction to artificial avian nests

First, we analysed normal ant activity on tree trunks with empty artificial nests and with intact eggs. We quantified differences between invaded and uninvaded sites, tree species, the different times during the survey, ambient temperature and trunk perimeter. We used as dependent variables three estimations of ant activity in the tree trunk: the total number of vertical ant trails in the trunk relative to the trunk perimeter

(trails/m), the ant activity in all vertical ant trails in 100 cm of the trunk perimeter (ants/min) and the ant activity of the ant trail having the maximum ant activity (ants/min). We performed three independent generalized linear mixed models for each dependent variable with a Poisson distribution and logit error. Invasion status (invaded or uninvaded), tree species (pine or cork oak), the time of the survey (3, 8 or 24 h after the set-in) were considered fixed factors while temperature, and the trunk perimeter were included as covariates. We added tree identity as a random factor (each tree held all the treatments in non-consecutive days).

Second, we analysed differences in attraction to the artificial nest treatments. We calculated the relative number of ants in the artificial nest, i.e. the number of observed ants relative to the maximum number of ants observed in any of the trees and treatments from invaded – 350 ants – and uninvaded trees – 190 ants. We performed a linear mixed model on the relative abundance of ants in the nest, with treatment (five categories), invasion status, tree species as fixed factors together with their second order interactions. Ambient temperature and trunk perimeter were included as covariates and tree identity as a random factor. Finally, we explored the cases in which there was ant recruitment to any of the nest remains, analysing recruitment (yes/no) for each treatment in invaded and uninvaded trees through a generalized linear model with a binomial distribution and logit error. The dependent variable was the positive recruitments from the total survey times e.g. if ants recruited on two out of the three visits, recruitment = 2/3). We included treatment, invasion status and tree species as fixed factors, with mean temperature and trunk perimeter as covariates.

Breeding performance

Breeding parameters and nest box variables were analysed with generalized linear mixed models to test for the effects of the Argentine ant invasion status. Dichotomous variables and proportions were analysed with binomial distribution: occupation, hatching success, fledgling success, and breeding success. Discrete variables were analysed with Poisson distribution: laying date, clutch size, brood size and fledgling number. All models included the invasion status as fixed factor and nest box coordinates as covariates to

account for nest box location and tree. Latitude and longitude were rescaled by subtracting the minimum value and multiplied by a thousand to avoid convergence failure in the models. Year was included as random factor to account for interannual variation. Although nest box location was taken into consideration, all analyses were repeated excluding the first year of observations due to nest box relocation without significant differences.

Individual biometric, biochemical and oxidative stress parameters

There was a significant correlation among the different parameters studied. Larger and heavier individuals presented lower TRI in blood. Besides, heavier birds presented higher levels of CAT and lower GR, while individuals with longer wings presented higher CAT and GPX. UA was negatively correlated to TRI, CHOL and TP, which were in turn positively related to each other and TBARS. GPX was positively correlated with CAT and negatively to TRI and SOD, and GR was positively correlated with SOD (Table ESM_2a). In order to summarize biometric, biochemical and oxidative stress parameters into independent factors and reduce model overparametrization, we performed a principal component analyses data from all nestlings and adults. However, cumulative explained variance by two factors was low (0.48%) and did not improve increasing the number of factors (up to four, cumulative proportion < 0.75%, Table ESM_2b).

Thus, we performed univariate analyses on nestlings: mass, wing/tarsus length ratio, TRG, CHOL, TP, UA, TEAC, TBARS, CAT, SOD, GR, and GPX. Since all parameters could not be measured from all blood samples due to variation in volume of extracted blood, sample sizes changed slightly. We ran eight independent linear mixed models on each parameter in order to find which factors and covariates better explained the variance observed. All models included invasion status as the main fixed factor, nestling age as covariate and the nest box as random factor, and a combination of the following four explanatory variables: number of fledglings (NF), laying date (LD) and geographical coordinates (latitude and longitude). Besides, a null model was included with each dependent variable alone (without independent variables) and with the random factor. Final models were chosen

following the Akaike Information Criterion ($\Delta AIC \leq 2$). Dependent variables were transformed to follow model assumptions (TRG, CHOL, TEAC, TBARS, and GR were log-transformed and wing/tarsus ratio, SOD and GPX were square root-transformed). Lack of autocorrelation was tested for every model. Data on adults was analysed separately by sexes to avoid model overparametrization. We tested the effect of invasion status with linear models for each variable independently: mass, wing and tarsus length, TRG, CHOL, TP, UA, TEAC, TBARS, CAT, SOD, GR, and GPX. As in the precedent models, all variables were transformed to fulfil model assumptions.

All analyses were performed with R 3.3.3 (R Core Team 2017). Linear models were analysed using the function *lm*, and linear mixed models and generalized linear mixed models with functions *lmer* and *glmer*, respectively (package *lme4*, Bates et al. 2015). Variables' correlation was calculated using function *rcorr* (package *Hmisc*, Harrell and Dupont 2017), and principal component analyses with function *rda* (package *Hmisc*, Oksanen et al. 2016). Variable significance was tested with “*drop1*” function, by comparing models with or without a given variable, with likelihood-ratio test statistics (option test = “Chi”).

Results

Ant attraction to artificial avian nests

Argentine ant was the only species present at the artificial nests in invaded sites, whereas four native ant species were found visiting the nests in uninvaded sites: *C. scutellaris*, which was the most common, followed by *Lasius grandis*, *Formica subrufa*, and *Camponotus lateralis*. Normal ant activity measured in control treatments was significantly higher in invaded trees than in uninvaded trees (Table 2a), for the three variables measured: the number of vertical trails in the trunk, the ant activity in all the vertical trails in 100 cm of the trunk and the ant activity in the trail with the highest activity. The number of trails tended to increase with time since start of the experiment and as temperatures decreased, albeit not significantly. Finally, there were no differences in normal ant activity according to tree size nor tree species (Table 2a).

Table 2 (a) Ant activity in tree trunks measured as the number of vertical trails, the activity of all trails in 100 cm of the trunk, and the activity in the trail with highest activity, with respect to invasion status (invaded, uninvaded), tree species, time since start of the experiment, temperature and trunk perimeter. Ant activity was measured from trees with control treatment. (b) Ant abundance in artificial nests with respect to treatment, invasion status, tree species and their interactions. The effect of

ambient temperature and tree perimeter were also evaluated. (c) Ant recruitment in artificial nests with respect to treatment, invasion status, tree species and their interactions. The effect of ambient temperature and tree perimeter were also evaluated. Post-Hoc comparisons for treatment-effect' contrasts are presented, with the corresponding P value in bold when significant

a. Normal ant activity (in the trunk)	Number of trails (N = 102)		Ant activity (ants/min)			
	χ^2	P	All trails (N = 96)		Highest trail (N = 101)	
	χ^2	P	χ^2	P	χ^2	P
Invasion status	6.58	0.010	9.55	0.002	10.04	0.001
Tree species	0.95	0.330	2.79	0.095	1.00	0.318
Time since start	5.64	0.059	1.66	0.435	2.91	0.233
Temperature	3.69	0.055	0.11	0.745	0.48	0.489
Trunk perimeter	0.24	0.621	0.30	0.583	0.14	0.704
b. Ant abundance (in the nest)	(N = 300)		Treatment Post-hoc comparisons			
	χ^2	P	Categories		P	
Treatment	16.27	0.003	Empty nest versus Eggs		0.551	
Invasion status (Status)	10.52	0.001	Feces versus Empty		0.030	
Tree species (Tree)	3.23	0.072	Feces versus Eggs		0.019	
Treatment*Status	15.68	0.003	Feces versus Cracked		< 0.001	
Treatment*Tree	4.20	0.380	Feces versus Cracked + Feces		0.002	
Status*Tree	0.36	0.550	Cracked versus Cracked + Feces		0.959	
Temperature	3.60	0.058				
Trunk perimeter	4.58	0.032				
c. Ant recruitment (in the nest)	(N = 100)		Treatment Post-hoc comparisons			
	χ^2	P	Categories		P	
Treatment	159.75	< 0.001	Empty nest versus Eggs		0.208	
Invasion status	71.50	< 0.001	Feces versus Empty		0.020	
Tree type	0.09	0.769	Feces versus Eggs		0.307	
Temperature	10.39	0.001	Feces versus Cracked		< 0.001	
Trunk perimeter	13.94	< 0.001	Feces versus Cracked + Feces		< 0.001	
All interactions		N.S	Cracked versus Cracked + Feces		0.476	

Relative abundance of ants in the artificial nests was significantly different among treatments, between invaded and uninvaded sites but not between tree species (Table 2b). Ants visiting artificial nests were more abundant in invaded than in uninvaded trees, and in the treatments combining cracked eggs with feces or just cracked eggs over those treatments with only feces or controls (Table 2b). Again, higher temperatures decreased the relative abundance of ants, which were more abundant in larger trees (Table 2b). There were no significant interactions between tree species and treatment or invasion status. However, the response to

treatments changed with invasion status (Table 2b), and although the relative ant abundance visiting the artificial nests was higher in invaded trees, this response was different between the invasive and the native ant species (Fig. 1a). Native ants only recruited to the treatments containing cracked eggs, while the Argentine ant also recruited when only faeces were present (Fig. 1b). There was no recruitment to intact eggs or to empty nests, both considered as control treatments.

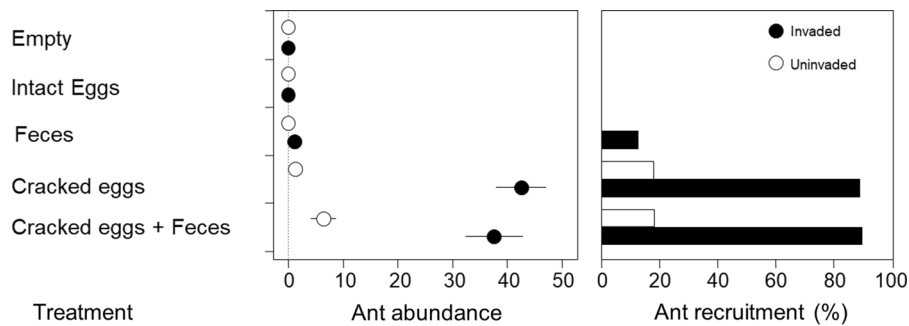


Fig. 1 Ants visiting artificial nest with different treatments in invaded (filled) and uninvaded (open) sites. Relative abundance of ants in the nest to the maximum ant number (350 and 190 ants in invaded and uninvaded sites, respectively). Ant recruitment to the nest

Breeding performance

We compiled data on a total of 355 breeding events, 169 located in invaded and 186 in uninvaded trees over five years of study (2013–2017). Great tits occupied one third of the available nest boxes on average over the five years of study ($33 \pm 2\%$, $n = 5$, Fig. 2) and significantly less nest boxes in the invaded sites compared to the uninvaded ones (LRT = 7.24, $P = 0.007$, $n = 355$, Table ESM_1, Fig. 2). Laying dates did not change between invaded and uninvaded sites (LRT = 0.09, $P = 0.762$, $n = 113$, Table ESM_1). No differences among none of the other breeding variables were found between invaded and uninvaded sites, no matter if absolute variables: success, clutch size, brood size, number of fledglings, or relative variables: hatching success, fledgling success, and breeding success (Table ESM_1) were considered.

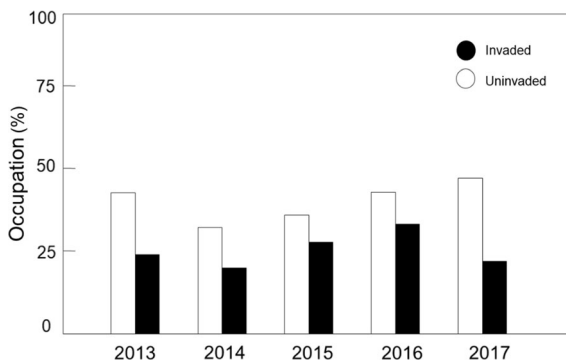


Fig. 2 Great tit nest box occupation in invaded (filled columns) and uninvaded (open columns) trees over the five years of study (2013–2017)

Individual parameters

From the 12 variables analysed, we found that in half of them the best model selected by the AIC included the invasion status (Table 3, Fig. 3, Table ESM_3). Nestlings from invaded sites were lighter (LRT = 13.98; $P < 0.001$) and smaller, with a lower wing/tarsus ratio length (LRT = 5.07; $P = 0.024$) (Table 3; Table ESM_3). TRI (LRT = 5.24; $P = 0.022$), TP (LRT = 8.20; $P = 0.004$) and TBARS (LRT = 4.87; $P = 0.027$) were all lower, whereas GPX (LRT = 6.07; $P = 0.014$) was higher in invaded compared to uninvaded sites after accounting for differences in nestlings age, laying date fledgling success or location (Table 3; Table ESM_3). No direct relation to the invasion status was detected for the other variables: TEAC, UA, CAT, SOD and GR (Table 3). We obtained data on 64% of the females and 54% of the males that bred with success in our study area. However, sample size remained limited and no differences between adults breeding in invaded and uninvaded sites were found in any of the variables studied: mass, tarsus and wing length, TRG, CHOL, TP, UA, TEAC, TBARS, CAT, SOD, GR, and GPX (All $P > 0.05$; Table 3).

Discussion

Argentine ants displaced the native ant community, were more efficient in finding artificial avian nests and recruited in larger numbers and into nests with larger variety of edible contents than their native counterparts. Great tits breeding in the area chose to nest preferentially in uninvaded over invaded trees,

Table 3 Morphological variables and biochemical blood parameters from nestlings and adult breeding great tits *Parus major* from 2014 breeding season

Variable name	Nestlings		Adult females		Adult males	
	Invaded	Uninvaded	Invaded	Uninvaded	Invaded	Uninvaded
Mass (g)	14.5 ± 0.25 (27)	15.2 ± 0.32 (42)	16.6 ± 0.9 (3)	17.1 ± 0.3 (4)	16.5 ± 0.5 (3)	16.2 ± 0.2 (3)
Wing length (mm)	36.9 ± 1.11 (27)	39.3 ± 1.16 (42)	69 ± 2 (3)	68 (4)	71 ± 1 (3)	74 ± 1 (3)
Tarsus length (mm)	18.6 ± 0.17 (27)	18.8 ± 0.18 (42)	19.23 ± 0.43 (2)	19.17 ± 0.19 (4)	20.01 ± 0.20 (3)	19.36 ± 0.41 (3)
Triglycerides (mg/dl)	1.98 ± 0.05 (27)	2.08 ± 0.05 (42)	136.68 ± 29.2 (3)	170.25 ± 38.56 (4)	140.21 ± 7.8 (3)	150.11 ± 27.5 (2)
Cholesterol (mg/dl)	404 ± 51.4 (22)	627 ± 64.5 (39)	188.76 ± 24.1 (3)	204.52 ± 12.37 (4)	203.77 ± 8.5 (3)	227.55 ± 14.1 (2)
Total protein (g/dl)	171 ± 12.4 (18)	200 ± 9.3 (38)	2.25 ± 0.24 (3)	2.27 ± 0.09 (4)	1.90 ± 0.21 (3)	2.26 ± 0.38 (2)
Uric acid (mg/dl)	1.73 ± 0.07 (20)	2.00 ± 0.05 (39)	15.81 ± 3.76 (3)	24.02 ± 4.21 (4)	21.47 ± 3.58 (3)	17.11 ± 3.45 (2)
TEAC (mM/l)	19.1 ± 1.73 (19)	19.3 ± 1.27 (36)	3.20 ± 0.93 (2)	3.45 ± 0.59 (3)	3.31 ± 0.57 (3)	3.05 ± 0.03 (2)
TBARS (nmol MDA/ml)	3.61 ± 0.20 (18)	3.90 ± 0.21 (30)	11.62 ± 0.68 (3)	12.42 ± 0.37 (4)	11.31 ± 1.27 (3)	17.07 ± 2.50 (3)
Catalase (U/mg prot)	11.4 ± 0.54 (23)	12.1 ± 0.58 (39)	35.05 ± 5.45 (3)	39.70 ± 2.85 (4)	36.53 ± 2.24 (3)	32.21 ± 1.80 (3)
SOD (U/mg prot)	23.7 ± 1.61 (24)	26.7 ± 0.90 (41)	10.84 ± 5.75 (3)	10.25 ± 1.99 (4)	13.48 ± 1.78 (3)	20.54 ± 9.11 (3)
GR (U/mg prot)	22.0 ± 2.24 (23)	19.7 ± 1.65 (40)	140.00 ± 15.3 (3)	155.00 ± 8.7 (4)	170.00 ± 5.8 (3)	136.67 ± 12.0 (3)
GPX (mU/mg prot)	178 ± 7.64 (24)	172 ± 3.7 (41)	117.62 ± 18.1 (3)	124.46 ± 15.1 (4)	123.85 ± 20.5 (3)	77.70 ± 17.22 (3)

Mean ± SE raw values are presented for individuals from invaded and uninvaded areas. Significant differences from the independent models are presented in bold. See main text for a description of each variable

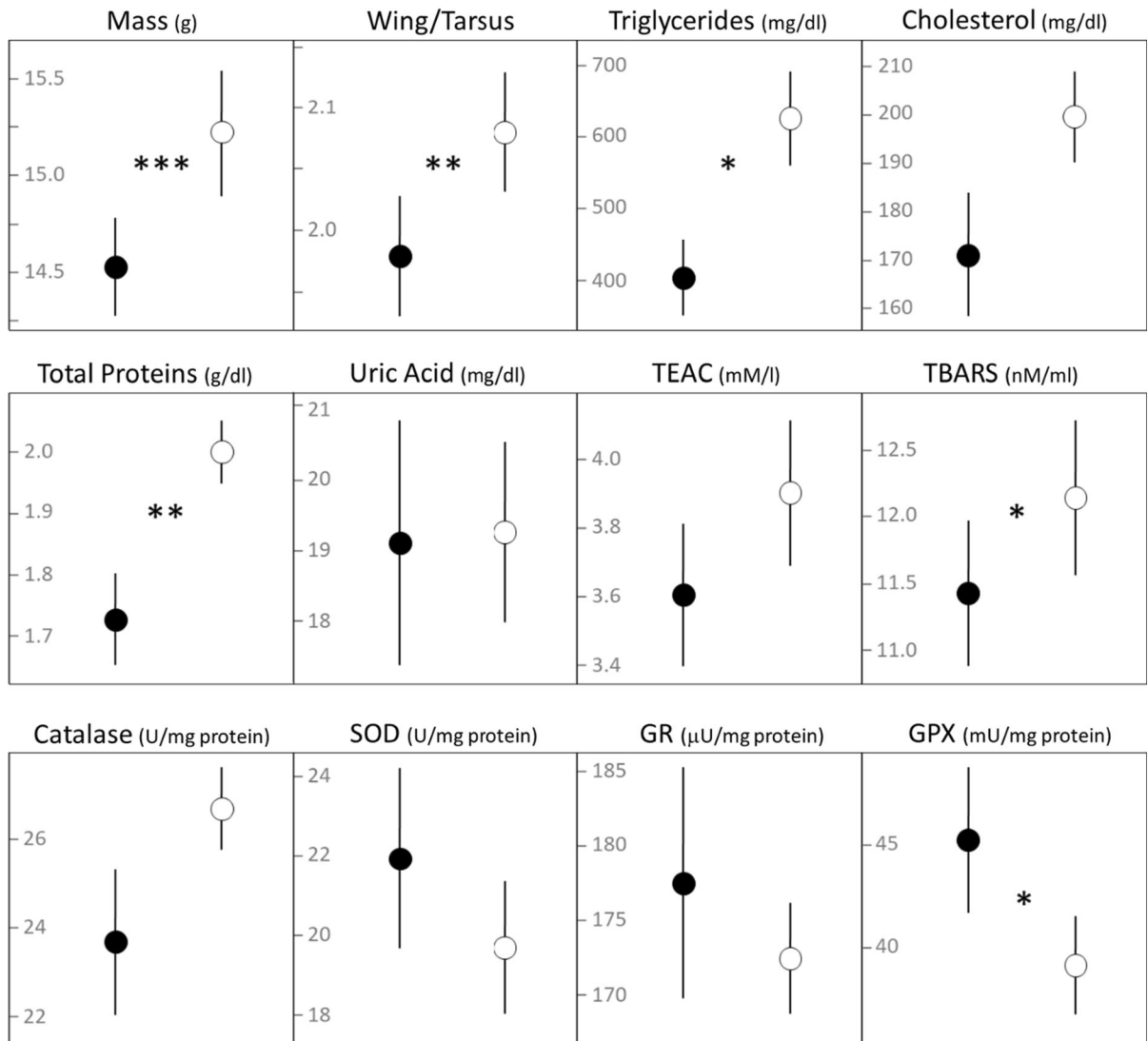


Fig. 3 Nestling biometric measurements and blood parameters measured related to nutritional and oxidative stress balance from invaded (filled) and uninverted (open) areas (mean ± SE).

Enzymes as Catalase, SOD, GR, and GPX are showed in enzymatic units per mg protein (U/mg protein)

although breeding parents nesting in uninverted trees showed no significant differences in condition nor breeding success with parents nesting in invaded trees. However, those parents breeding in invaded trees raised nestlings with an impaired nutritional condition and altered oxidative balance as compared to nestlings from uninverted trees.

Invasive Argentine ants displaced the local ant community and were more abundant than native ants, a pattern repeatedly observed in previous studies (Carpintero et al. 2005; Estany-Tigerström et al. 2010;

Angulo et al 2011; Alvarez-Blanco et al. 2017). Further, we did not detect any case of Argentine ant breaking any eggshell from the breeding great tit population or the experimental eggs studied, unlike other invasive ants e.g. *S. invicta* or *Solenopsis xyloni* (Hooper-Bui et al. 2004; Suarez et al. 2005; Seymour 2007). However, we found that Argentine ants were more abundant and recruited more frequently than native ants when the artificial nest contained cracked eggs, in agreement with previous studies (Suarez et al. 2005; Varela et al. 2018). Consequently, for hole-

nesting passerines, breeding in Argentine ant invaded trees implies an increased exposure of their nestlings during their most sensitive developmental period.

Argentine ants may affect breeding bird communities indirectly by competing for food sources and directly by disturbing parents and nestlings. Great tits from our studied population preferably chose nesting locations free of Argentine ants, implying that individuals were able to obtain relevant information before breeding commenced and avoided this invasive species. Insectivorous bird species often use habitat structural cues of resource availability when selecting nesting locations (Marshall and Cooper 2004), and the presence of certain ant species could be among such cues. Some studies have shown that interference competition between birds and ants promote changes in bird behaviour, which avoid foraging in trees with ant activity (Haemig 1996; Aho et al. 1997; Philpott et al. 2005). Argentine ant presence in the breeding territory of a Mediterranean population of a closely related *Paridae* species, the blue tit *Cyanistes caeruleus*, reduced the arthropod biomass from the invaded tree canopy, from which these tree-gleaning species feed on (Estany-Tigerström et al. 2010). However, such effects did not affect the native bird community (Pons et al. 2010) or the blue tit breeding performance (Estany-Tigerström et al. 2013). Likewise, breeding parameters of great tits in our study were not influenced by Argentine ant invasion status, as neither were the body size or physiological parameters of the breeding parents. Although our sample size calls for caution with interpretation, our results are in line with previous studies (Krushelnicky et al. 2001; Estany-Tigerström et al. 2013). Argentine ant presence did not affect the overall great tit breeding performance, which may suggest that parents were unlikely segregated by condition due to the invasive ant presence, and the potential detrimental effects were below a detrimental threshold and/or partly compensated by parental effort.

Bird breeding failure has been often attributed to Argentine ant direct disturbance, although solid evidence is surprisingly scarce (see Table 1). While some studies described nests infested by ants that were feeding on chicks' corpses (Mejías et al. 2017; Sockman 1997; Suarez et al. 2005) or on hatching eggs (Boieiro et al. 2018), most evidence of direct predation by the Argentine ant appears to be anecdotal (when not just a mere suspicion) (Delibes 2005;

Flores et al. 2017; Hooper-Bui et al. 2004; Peterson et al. 2004). Throughout the breeding season we observed ants feeding on dead chick corpses (see Fig. ESM_2). However, only in two occasions ants were found to disturb alive chicks with the subsequent nest failure, and these were Argentine ants not native ant species. Other studies from similar habitats reported observations of native ant species, the *C. scutellaris*, which is the main native ant in our uninvaded trees, disturbing or preying on blue tit nestlings (Lambrechts et al. (2008). However, taking together the evidence published so far, it appears that the Argentine ant has a low direct impact on breeding birds in comparison with other invasive ant species (see the reviews of Holway et al. 2002; Suarez et al. 2005).

Nevertheless, we found great tits nesting in invaded sites reared poorer quality offspring, with lower body mass and wing/tarsus ratio. Birds nesting in areas infested by other invasive ants such as the red imported fire ant and the invasive European fire ants *Myrmica rubra* were adversely affected by impaired chick growth rates or body condition (DeFisher and Bonter 2013; Ligon et al. 2012). Further, *S. invicta* may impinge directly on chicks by stinging and/or altering their behavioural pattern (Giuliano et al. 1996; Pedersen et al. 1996), or indirectly by increasing the foraging distances of their parents (Ligon et al. 2012). The European fire ants also increase the erratic breeding behaviour of adults, which may hinder embryonic development (DeFisher and Bonter 2013). Effects on bird offspring have been also reported from the native ants *Formica rufa* spp, their abundance being adversely associated to body mass, tarsus length, and subcutaneous fat index of treecreeper *Certhia familiaris* offspring (Jäntti et al. 2007). Thus, our results are in line with these previous studies. Nestlings from invaded sites suffered from an impaired condition, with lower nutritional values in both lipids and proteins, which constitute the primary physiological fuel and structural units most needed in early development (McCue 2010). Furthermore, nestlings from invaded sites showed an altered oxidative balance. Paradoxically, chicks with impaired nutritional condition exhibited less oxidative damage (TBARS) and higher antioxidant enzyme values (GPX). These results may be explained by the lower growth rates experienced by nestlings from invaded sites, which in turn may induce lower oxidative stress

(Costantini 2008; Monaghan et al. 2009). Alternatively, it could be possible that Argentine ants may indirectly benefit developing nestlings by controlling nest-dwelling ectoparasites presence (Gibson et al. 2019). Conditions during early development can have long-term consequences carried over into adulthood (Monaghan 2008), potentially affecting whole cohorts simultaneously (Lindström 1999), which certainly deserve further studies.

There are multiple non-mutually exclusive explanations behind the differences in nestling condition detected. First, it could be possible that better parents occupied uninvaded trees and displaced lower quality parents to invaded trees. Thus, chicks from those parents would enjoy better genetic background and/or parental care, although we did not find any substantial differences between parents breeding in invaded compared to parents from uninvaded trees. Secondly, it could be possible that Argentine ants did influence habitat suitability by indirect exploitative competition, as found by Estany-Tigerström et al. (2013). Therefore, parents even with the same quality, would struggle to provide the same parental care as parents from uninvaded trees. However, in our study system this possibility seems unlikely given the spatial scale and interspersed distribution of the tree stands with different invasion status (Figure ESM_1). Invaded trees can be just few meters distance from uninvaded trees, much lower distances than the ones great tit travel on nestling feeding bouts (Naef-Daenzer 1994). Finally, it is still possible that a decreased parental investment due to ant disturbance to adults, and/or direct ant disturbance at the nest, generating stress and disturbed development may explain the pattern observed.

Although the overall great tit breeding parameters were unaffected by the presence of the Argentine ant, we found significant effects on the offspring quality. Our contrasting results with previous studies (Estany-Tigerström et al. 2013) suggest that great tits in this marginal population may be unable to fully compensate for the disturbance experienced by the presence of the Argentine ant. Whether these subtle physiological effects on offspring may be carried over into adulthood with potential long-term consequences remains to be studied. Thus, our results suggest that the subtle impacts of invasive species might act in synergy with other global change drivers, such as climate, making certain populations more sensitive than others.

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Author contributions PAB, JB, XC and EA designed the experiment. PAB and OGJ collected the data. PAB, JB and EA analysed the data and wrote the manuscript. All authors critiqued the manuscript for intellectual content.

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Availability data and material Data will be made available upon reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures were conducted according to local ethical committee guidelines. The experimental procedures were approved by the national authorities (CEBA-EBD 11-36b, CSD2008-00040, 1043/MDCG/mect, 2014-1073-00000613-FQH/MDCG/mect, 2015-1073-00001494-FQH/MDCG/mect and 2015-1073-00003362-JPCD/MDCG/mes).

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