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Context-dependent insect predation pressure on an avian ectoparasite

Angela Salido[1,2] iD, Jesús Veiga[2,3,4] iD, Joaquín Luis Reyes-López[1] and Francisco Valera[2]

[1]*Department of Botany, Ecology and Plant Physiology, University of Córdoba, Córdoba, Spain;* [2]*Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas (EEZA-CSIC), Almería, Spain;* [3]*Department of Parasitology, University of Granada, Granada, Spain and* [4]*MEMEG, Department of Biology, Lund University, Lund, Sweden*

Abstract Context dependence arises when ecological relationships vary with the conditions under which they are observed. Context dependence of interactions involving parasites is poorly known, even if it is key to understanding host–parasite relationships and food web dynamics. This paper investigates to which extent predation pressure on an avian ectoparasite (*Carnus hemapterus*) is context-dependent. Based on a predator-exclusion experiment, predation pressure on *C. hemapterus* pupae in the host's nest for 3 years, and its variation between habitat types are quantified. Variation in precipitation and normalized difference vegetation index (NDVI) is also explored as a likely cause of context dependency. We hypothesize that predation pressure should fluctuate with such surrogates of food availability, so that inter-annual and intra-annual differences may emerge. The number of nests with significant reduction of pupae varied widely among years ranging from 24% to 75%. However, average pupae reduction in nests where a significant reduction occurred did not vary between years. No differences in predation rates between habitat types were detected. Precipitation and NDVI varied widely between years and NDVI was consistently lower around nests on cliffs than around nests on trees and farmhouses. Parallels were found between variation in predation pressure and precipitation/NDVI at a wide scale (highest predation the driest year, and much lower the 2 rainier ones), but not at the nest scale. This paper shows clear context-dependent insect predation pressure on an ectoparasite under natural conditions, and that such interaction changes in signs rather than magnitude between years. The causes for these variations require longer-term studies and/or well-designed, large-scale experiments.

Key words ants; arid areas; *Carnus hemapterus*; consumer-resource interaction; ecosystem productivity; predator–parasite; rainfall

Introduction

Interspecific interactions are known to influence distribution patterns, community structure, species coexistence, evolutionary changes and biodiversity (Hatcher *et al.*, 2006; Barraclough, 2015). Variation in the outcome (sign and/or magnitude) of interspecific interactions as a function of the biotic or abiotic context is common in nature but poorly understood (Chamberlain *et al.*, 2014 and references therein). Such variation, described as context dependency, may have major effects on individual fitness, population growth, community structure and composition, food web properties, and natural selection on species traits (see, for instance, Kokkoris *et al.*, 2002; Thompson, 2005; Miller *et al.*, 2009; Stouffer & Bascompte, 2011).

Correspondence: Francisco Valera, Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas (EEZA-CSIC), Ctra. de Sacramento s/n, La Cañada de San Urbano, Almería, E-04120, Spain. Tel: +34 950281045. Email: pvalera@eeza.csic.es

Despite the relevance of these effects, the extent of context dependency and the causes of this variation have not been given the attention they deserve (Chamberlain *et al.*, 2014 and references therein).

Context dependency has been put down to abiotic gradients (e.g., rainfall—Von Berg *et al.*, 2008; temperature—Daskin & Alford, 2012), variation in the abundance of one of the interacting species (e.g., Wootton, 1994), or the generalist versus specialist nature of natural enemies (Hassell & May, 1986). Natural ecosystems are dynamic and conditions frequently fluctuate widely over time, but context dependency is often studied along simple gradients in space and/or time, and most resource-consumption experiments have been carried out in a constant environment (Buckling & Rainey, 2002; Yoshida *et al.*, 2003; Becks *et al.*, 2010). Thus, the relative importance of different types of gradients for the generation of variation in the outcome of interspecific interactions remains largely unresolved (Chamberlain *et al.*, 2014).

The context-dependent outcome of interspecific interactions has been researched in a range of systems. Still, and probably as a result of the hitherto overlooked influence of parasites on the outcome of trophic interactions (MacNeil *et al.*, 2003; Tompkins *et al.*, 2003; Malmstrom *et al.*, 2006; Johnson *et al.*, 2010), few studies have analyzed the variation of the result of interactions participated by parasites (see, for instance, the low number of studies on parasites in the meta-analysis by Chamberlain *et al.*, 2014). Parasites can be a main character in a given interaction or a third (but meaningful) part. Parasite predation is widespread within ecosystems, and numerous vertebrate and invertebrate organisms have been reported to be highly effective at parasite consumption (Lafferty *et al.*, 2008; Thieltges *et al.*, 2008; Johnson *et al.*, 2010; Kaunisto *et al.*, 2016; Salido *et al.*, 2021). Parasite consumption (either free-living stages or parasitic ones) comprises a direct pathway through which predators can potentially shape trophic interactions and energy flow, and also lessen downstream transmission (Lafferty *et al.*, 2008; Thieltges *et al.*, 2008; Johnson *et al.*, 2010; Kaunisto *et al.*, 2016). Thus, proper understanding of host–parasite relationships, epidemiological variables and food web dynamics requires the study of (i) the effect of natural enemies of parasites; and (ii) the factors or ecological conditions influencing predation pressure (Johnson *et al.*, 2010; Thieltges *et al.*, 2013). This 2 fold approach would establish a useful predator–parasite framework to further the standing of the importance of predation on parasites for key ecological and epidemiological issues, such as pathogen transmission in natural systems. Such an approach is rare, even if variation

in the outcome of host–parasite interactions has been attested. For instance, Orlofske *et al.* (2015) proved the ingestion of free-living stages of 4 species of trematodes to be highly context-dependent, largely driven by a combination of environmental conditions in which predator and parasite interacted and their sizes. Similarly, Kaunisto *et al.* (2016) found a remarkable variation in predation pressure on a cervid ectoparasite fly between habitat types.

Ants are particularly suitable study subjects in this regard. They are ubiquitous predators of many arthropods (including parasites; Duffy, 1991; Johnson *et al.*, 2010; Kaunisto *et al.*, 2016) with the potential to affect ecological communities (Cerdá & Dejean, 2011; Sanders & van Venn, 2011). For instance, Salido *et al.* (2021) recently showed that insect predation (ants being the putative predator) was an important factor regulating the abundance of a bird ectoparasite; as such, ants have the potential to influence the outcome of host–parasite relationships (see also Kaunisto *et al.*, 2012a, 2012b; Brown *et al.*, 2015).

This paper researches to which extent predation pressure on a bird ectoparasite is context-dependent. To this end, the paper looks into the system formed by the European roller (*Coracias garrulus* Linnaeus, 1758), a cavity-nesting bird breeding in nest boxes, the parasitic fly *Carnus hemapterus* Nitzsch, 1818, a widespread bloodsucking ectoparasite of many bird species (Grimaldi, 1997) and the insect predators of the latter. This system is ideal to explore the context dependency of insect predation on parasites for several reasons: (i) except for its short dispersal stage (Veiga *et al.*, 2019), the cycle of *Carnus hemapterus* occurs in the host's nest, and this facilitates research on predation through the parasite's various life stages; (ii) most of the ant species that are potential predators of this parasite are omnivorous, opportunistic, generalist species, so their impact on a given prey may depend on the abundance of various food sources; (iii) in arid and semi-arid ecosystems, water is the most important limiting resource (Friedel *et al.*, 1994; Abd El-Ghani, 1997; Pavón & Briones, 2001) and inter-annual variation in precipitation is common, and as a result, substantial differences in food availability may arise between years and may in turn influence the outcome of interactions; and (iv) the location of nest boxes in various habitat types (e.g., on trees, on human-made structures, or on sandstone cliffs) adds one more potential driver of context dependency.

First, the predation pressure on the ectoparasite is experimentally determined by means of a predator-exclusion experiment for 3 running years under natural conditions. Variation in predation pressure between

different habitat types (i.e., nest-site types) is also explored for each year. Inter-annual and between-habitats variation in surrogates of primary and secondary productivity, namely normalized difference vegetation index (NDVI) (Box *et al.*, 1989; Ustin *et al.*, 1991; Fernández-Tizón *et al.*, 2020) is also researched. We hypothesize that predation pressure on carnid pupae will fluctuate with food availability (i.e., primary and secondary productivity) both at an inter-annual level and between different habitat types. We predict the following. (i) Drier periods (i.e., low NDVI values) dampen resource availability and, thereby, indirectly drive the foraging activity of omnivorous insects and predators to utilize a wider range of resources; this results in increased predation on parasites. Similarly, decreased consumption of carnid pupae by such predators is expected in wetter seasons, when primary productivity and arthropod biomass/food quality is high. (ii) Given differences in primary productivity between habitat types, parasite predation will be higher in types associated with lower NDVI values. (iii) At a nest scale and within-year, predation pressure will be higher in nests with lower NDVI in the surroundings.

Materials and methods

Study area

The study area (∼50 km²) lies in Campo de Tabernas (Almería, SE Spain, 37°05′ N, 2°21′W). It is badlands with olive and almond groves interspersed between numerous dry streambeds (ramblas) and steppe habitats.

The climate is semi-arid Mediterranean, with a strong water deficit in summer. The average annual temperature is 18°C, with mild inter-annual oscillations and significant intra-annual fluctuations (Lázaro *et al.*, 2004). The mean annual rainfall is approximately 230 mm, with high inter-annual and intra-annual variability (Lázaro *et al.*, 2001). The study area and southeastern Spain in general are unpredictable regarding the duration of the rainy season and in the amount of rainfall, due to drastic inter-annual variation (Alba-Sánchez *et al.*, 2010).

Study species

Carnus hemapterus (Diptera: Carnidae) (hereafter *Carnus*) is a 2-mm long nidicolous, hematophagous fly that infests nestlings of a wide range of bird species across the Nearctic and Holarctic (Brake, 2011). Adult flies have a winged and a wingless phase; after emergence, adults are winged, but they lose their wings as soon as they locate a suitable host (Roulin, 1998). Carnid

flies actively colonize hosts' nests during the winged phase (Grimaldi, 1997; Veiga *et al.*, 2019) and complete their cycle in their hosts' nests. Adults mate in the nest and females lay eggs in the organic debris of hosts' nest. Eggs hatch approximately 5 d later, and larvae live on the nest's organic matter (Papp, 1998). The 3 larval stages last 21 d (Guiguen *et al.*, 1983) and pupation takes place in the nest. During the pupal stage, *Carnus* undergoes a diapause that usually lasts for months (Guiguen *et al.*, 1983), even though both a short (8 d) and a prolonged diapause (several years) have also been recorded (Guiguen *et al.*, 1983; Valera *et al.*, 2006). The phenology of emergence of *Carnus* reflects their hosts', so flies emergence stops at the end of the breeding period (ca. in the first week of July) in accordance with the lack of suitable hosts (i.e., nestlings) from then onward (Calero-Torralbo *et al.*, 2013). *Carnus* parasitism can be detrimental for nestlings (Cannings, 1986; Soler *et al.*, 1999; Hoi *et al.*, 2018, but see Kirkpatrick & Colvin, 1989; Dawson & Bortolotti, 1997). Ants, spiders, and the parasitoid *Chartocerus conjugalis* (Mercet, 1916) have been previously identified as natural enemies of carnid flies in the study area (Salido *et al.*, 2021).

The European roller (hereafter roller) is an obligate secondary cavity-nesting, long-distance Palearctic-African migrant bird species. It arrives into the study area in the second fortnight of April. Insects are a significant part of roller diets (Cramp, 1998). Rollers rear a single brood per year (Cramp, 1998). Females usually lay 4–6 eggs in our study area that are laid directly on the ground of the cavity. Egg hatching is distinctly asynchronous (within-brood nestling ages are in the range of 2–10 d; Václav *et al.*, 2008; Václav & Valera, 2018). In our population, incubation takes ∼21 d, and nestlings fledge ∼22−24 d after hatching (Václav *et al.*, 2008). The latest nestlings usually fledge around mid-July.

As a result of a conservation program launched in 2005, most rollers in our study area breed in nest boxes located on trees, sandstone cliffs and human-made constructions (Valera *et al.*, 2019). Nest boxes on trees are usually isolated from other breeding bird species, the most common neighbors being open nesters (the Eurasian collared dove *Streptopelia decaocto* and common wood pigeon *Columba palumbus*). In contrast, nest boxes located on sandstone cliffs and on farmhouses are usually near natural cavities occupied by cavity-nesting birds (e.g., common kestrels *Falco tinnunculus*, jackdaws *Corvus monedula*, rock pigeons *Columba livia*, little owls *Athene noctua*, spotless starlings *Sturnus unicolor* and house sparrows *Passer domesticus*). The nest boxes on sandstone cliffs and farmhouses are usually located on devegetated surfaces, while the nest boxes on trees are

covered by dense tree canopy. The nest boxes used for this study keep the same structure (quadrangular prism), material (wood) and dimensions (height × length × width: 310 mm × 232 mm × 230 mm, entrance diameter: 60 mm, with a removable upper lid to allow nest monitoring).

Field methods and experimental design

Precipitation and NDVI. We used 2 surrogates of food availability (productivity): precipitation and NDVI.

In arid and semi-arid ecosystems, water availability determines plant growth, flowering and reproduction (Friedel *et al.*, 1994; Abd El-Ghani, 1997; Pavón & Briones, 2001). In our study area, rainfall frequency has been proven to have strong effects on flowering (Miranda *et al.*, 2009), and species-specific responses in the timing of flowering have been reported (Alba-Sánchez *et al.*, 2010). Thus, we considered the accumulated precipitation during a prolonged period: from January 1 (start of the water utilization period, see Alba-Sánchez *et al.*, 2010) to July 31 (when the experimental set up to estimate pupae predation had been completed in all study years—see below). Precipitation data for 2019, 2020, and 2021 were collected from the meteorological station in Tabernas (37°05′28″ N, 2°18′08″ W) (Red de Información Agroclimática de Andalucía, 2021).

NDVI is a remote-sensing spectral indicator that measures the photosynthetic activity of plants and is frequently used as a robust proxy of primary productivity in ecological studies (Rouse *et al.*, 1974; Tucker, 1979; Pettorelli *et al.*, 2005, 2011; Phillips *et al.*, 2008; Stegen *et al.*, 2013). NDVI is often used to predict food availability for higher trophic levels too, and is a suitable habitat-specific proxy for insectivore food availability in spring (Fernández-Tizón *et al.*, 2020). NDVI is computed from a spectral transformation of the red and near-infrared satellite frequency bands and is obtained by the formula:

$$(NIR - R) / (NIR + R),$$

where R and NIR stand for the reflectance in band 4 and band 5 of Landsat 7, respectively (Tucker, 1979; Sellers, 1989). According to the definition, NDVI values range from 0 to 1, such that higher values indicates greenness healthy vegetation (Pettorelli *et al.*, 2005).

Since we intend to explore the relationship between primary productivity and ant predation of carnid pupae contained in rollers' nests, we calculated the NDVI in a small area (see below) around nests ($n = 58$ nests occupied by rollers in any of the 3 study years) for the period April−June for 2 reasons: (i) ants commonly forage around their own nests (Traniello *et al.*, 1984; Holder Bailey & Polis, 1987; Dukas & Edelstein-Keshet, 1998), so their behavior near rollers' nests is likely affected by local productivity; and (ii) the primary production in our geographic context peaks in April–June (Paruelo *et al.*, 2005), so that food availability during the experiment (summertime) can be reflected by NDVI at that time.

The geographical location of nest boxes (Universal Transverse Mercator coordinates) was processed in QGIS 3.20.0 (QGIS Development Team, 2021) to build a circular buffer centered on each roller nest (20 m radius). The files were saved as a GeojSON format.

Satellite data were extracted and processed online in Google Earth Engine platform (GEE, via Colab). Landsat 7 ETM+ sensor data were used for this study (ImageCollection ID in GEE: LANDSAT/LE07/C01/T1_SR).

From the 3 tier categories available in Landsat Collection Level-1, Landsat Tier 1 Surface Reflectance (SR) product was the most appropriate for its high-quality characteristics, which includes atmospherically and geometrically corrected images (Mas & Soares de Araújo, 2021; Ramsey & Mavoa, 2021; Roteta *et al.*, 2021). To minimize the effects of clouds and cloud shadows and ensure high data quality, all Landsat images were masked by mask function (FMASK) algorithm (Zhu *et al.*, 2015; Foga *et al.*, 2017). Image collection was filtered spatially (circles of 20 m radius centered on each roller nest) and temporally (April, May, and June 2019, 2020, and 2021; see above). Since Landsat-7 provides images at 16-d intervals, overall 6 images were used to estimate NDVI for each year (2 per month).

Image.reduceRegion() algorithm was applied to obtain NDVI-derived descriptive statistics parameters for each sampling point. This GEE tool allowed calculation of representative values from all the pixels in each circular area (Martín-Ortega *et al.*, 2020). Mean and maximum NDVI values (".mean()" and ".max()" functions) of the 3-month period (April−June) from 2019 to 2021 were then taken as estimates of summer productivity. Only the cloud-free scenes available were used for calculation of mean values. Satellite images obtained had a spatial resolution of 30 m ($\sim$900 m^2).

Estimation of pupae predation. Pupae predation in nest boxes occupied by rollers was estimated by means of a predator-exclusion experiment (see Yusa, 2001; Piñol *et al.*, 2010 for a similar approach) in 2019, 2020, and 2021 (2019 data published in Salido *et al.*, 2021). The experiment consisted of collecting a fraction (i.e., a handful) of nest detritus (containing pupae) after the breeding season (i.e., when nestlings had already fledged

Table 1 Main characteristics of the predator-exclusion experiment: dates of detritus bagging and subsequent collection, weight (range) of bagged and exposed samples and initial conditions (clean vs. dirty) of nest boxes in each study year. Sample sizes of each category are also shown.

Year (no. nest boxes)	Bagging & detritus collection dates	Mean weight (range) bagged detritus, g [sample size]	Mean weight (range) exposed detritus, g [sample size]	Initial nest box conditions
2019 (28)	2−24/7 – 20/9−4/10	148.5 (61−228) [28]	168.2 (90−261) [28]	Clean
2020 (33)	8−24/7 – 16−28/9	173.0 (69.5−290.8) [33]	205.9 (117.6−278.3) [33]	Dirty
2021 (41)	6/7−1/8 – 21/9−5/10	161.2 (122.6−219.4) [41]	148.5 (85.9−232.1) [41]	Clean ($n = 21$) & dirty ($n = 20$)

and, therefore, adult *Carnus* flies were no longer in the nest boxes) and bagging it in a tulle sack (approximate size: 30 cm × 16 cm) to exclude potential predators of pupae. Bagged detritus was protected by a wire mess and stapled to the inner wall of the box, so both exposed and protected carnid pupae were kept in each nest box under natural conditions over the summer (approximately 2 months, see Fig. S1 and Salido *et al.*, 2021 for further details). During September−October, a sample of exposed (e.g., control samples) and of protected detritus were collected from each nest box (Table 1). The procedure was performed on 28 nest boxes in 2019 (Salido *et al.*, 2021), 33 in 2020, and 41 in 2021 (this study). As the same nest boxes were not occupied in different years, 55 different nest boxes were handled overall.

Samples were stored in individual labeled plastic bags, transferred to the Estación Experimental de Zonas Áridas (EEZA, Almería), and then sieved and scanned for carnid pupae (see below).

Clean nest boxes were settled at the beginning of the 2019 breeding season, but they were not cleaned prior to the 2020 breeding season; that is, they contained accumulated nest material from the previous season. To test the effect of nest cleaning on pupae predation, prior to the start of the 2021 breeding season, half of the nest boxes were cleaned and the second half was kept with the detritus of the previous breeding season. Information about the beginning and end of the experiment and mass of control and exposed detritus are shown in Table 1.

Control and experimental (protected) samples were sieved using a column of 2 mm, 1 mm, and 0.5 mm sieves. The sieved material was weighed and stored in zip plastic bags. Considering *Carnus* pupae size (Valera *et al.*, 2018), the material from 1 mm and 0.5 mm was mixed

and stirred to homogenize. Two or 3 subsamples of 5 g per type of sample were then selected. The subsamples were examined in November−February with a binocular loupe Leica S6D for *Carnus* pupae, identified following Papp (1998) and Valera *et al.* (2018).

We distinguished between nonviable pupae (broken, cracked), open pupae (after adult hatching), and apparently viable pupae (intact, closed ones). Most pupae in all samples were intact (average % ± SE: 2019 protected samples: 98.5 ± 2.0, $n = 28$; 2019 nonprotected samples: 92.6 ± 3.0, $n = 25$; 2020 protected samples: 86.9 ± 2.9, $n = 33$; 2020 nonprotected samples: 84.6 ± 3.1 $n = 33$; 2021 protected samples: 90.8 ± 0.9, $n = 40$, 2021 nonprotected samples: 88.4 ± 1.1, $n = 41$). Only intact pupae were considered to calculate the prevalence and abundance of *Carnus* in roller nests. The number of pupae obtained from each subsample of 5 g were averaged to a single value per nest and type of sample (control and experimental ones) and 95% confidence intervals for such means were calculated (see below). We assume that the difference in the number of pupae between protected and nonprotected detritus reflects pupal predation (see Orsini *et al.*, 2007; Kaunisto *et al.*, 2016; Salido *et al.*, 2021 for a similar reason).

Statistical analyses

Temporal variation in NDVI and the effect of small-scale, local habitat features (i.e., nest-site type) on the former were studied by means of repeated-measures analysis of variance (ANOVA). The dependent variable was the NDVI value around each roller nest ($n = 58$ nests, regardless of whether they were occupied over 1, 2 or 3 breeding seasons), and the independent variables

included: (i) year, cataloged as 3-level within-subject factor; and (ii) nest-site type, cataloged as 3-level inter-subject factor (tree, cliff, and farmhouse, $n = 36$, 18 and 4, respectively). The analyses covered: (i) inter-annual differences in NDVI; (ii) the influence of nest-site type on NDVI; and (iii) the interaction between these factors. The dependent variable was $\log_{10}$-transformed to achieve approximately normal distribution. Sphericity assumption was verified by Mauchly's test. *Post hoc* Bonferroni tests were performed for significant differences in NDVI between different years and nest-site types.

Given the different experimental design of each year (see rationale above), the impact of predation on carnid pupae in 2020 and 2021 was analyzed using repeated-measures ANOVAs (see Salido *et al.*, 2021 for a similar approach). The dependent variable was the mean number of pupae per 5 g sample. For 2020 the 2 independent variables were: (i) detritus treatment, considered a 2-level within-subject factor (protected and nonprotected samples); and (ii) nest-site type, considered a 3-level intersubject factor (tree, cliff, and farmhouse). Repeated-measures analyses of variance (RMANOVA) tested: (i) differences in the number of carnid pupae between protected and nonprotected samples; (ii) the effect of nest site on the intensity of pupae predation; and (iii) the interaction between these 2 factors. The effect of nest cleaning on the intensity of pupae predation and its interaction with the other factors was also checked for 2021 data. Dependency between variables (protected/nonprotected samples for each nest box) was checked by means of Spearman's correlation tests ($P < 0.01$ in all cases). Normality of the dependent variable was checked by the Wilk–Shapiro test and log-transformed variables were used when appropriate. Only nest boxes where at least 1 pupa was recorded were considered for the RMANOVA test (2020: 17 nest boxes located on trees, 12 on cliffs, and 4 on farmhouses; 2021: 27 nest boxes located on trees, 10 on cliffs, and 4 on farmhouses). The results from the 2019 breeding season were obtained from Salido *et al.* (2021).

To determine whether predation pressure had a significant effect on the abundance of pupae the 95% confidence intervals (CI) of the mean number of pupae (obtained with the different subsamples of 5 g—see above) for the protected and nonprotected samples of each nest box was calculated. The overlap between the respective CIs was then calculated. For those nests with nonoverlapping intervals the percentage of reduction of carnid pupae was obtained as the difference between the mean values of carnid pupae found in protected and nonprotected samples divided by the mean values of carnid pupae in protected samples ($\times\ 100$) (see Salido *et al.*, 2021 for a

similar approach). A significant higher number of pupae in nonprotected samples than in protected samples was found in some nests (2019: 0, 2020: 4 out of 33, 2021: 3 out of 41). We believe these cases (6.8%, $n = 102$ considering all 3 years) are not the result of biological processes, but a consequence of inefficient detritus mixing before bagging (possibly in nests where the detritus was compacted). Such nests were excluded from the analyses.

A Chi-square test was used for inter-annual differences in the number of nests where significant pupae reduction was detected. Inter-annual differences in the percentage of reduction in these nests were explored comparing their 95% CIs.

Pearson's correlations between mean and maximum NDVI values around the nest boxes and the percentage of pupae reduction in nonprotected samples were run in order to explore the relationship between resource availability and predation at the nest scale.

Statistical tests were run in R version 4.1.1. (R Core Team, 2021) and the packages EZ (Lawrence, 2016), GG-PLOT2 (Wickham, 2016), MASS (Venables & Ripley, 2002), and prevalence (Devleesschauwer *et al.*, 2014).

Results

Inter-annual variability in precipitation and NDVI and effect of nest-site type on NDVI

Precipitation in 2020 was twice as much as in 2019, and in 2021 it was 3 times as much as in 2019 (Table 2). Consequently, there was significant inter-annual variation in NDVI ($F_{2,110} = 62.5$, $P < 0.001$, Fig. 1), so that 2019 had significantly lower values than 2020 and 2021 (Bonferroni test: $P < 0.001$ in both cases), but there were no differences between 2020 and 2021 (Bonferroni test: $P > 0.20$).

Nest-site type had a significant effect on NDVI ($F_{2,55} = 17.2$, $P < 0.001$, Table 2), as nests had significantly lower NDVI values on cliffs than on trees and farmhouses (Bonferroni test, $P < 0.001$ in both cases). The interaction between nest-site type and year was significant ($F_{4,110} = 2.9$, $P = 0.02$). NDVI around nest boxes on farmhouses was higher in 2021 than in the other years (Table 2).

Impact of predation, nest-site type, and nest cleaning on the abundance of carnid pupae

Experimental exclusion of predators in the dry year 2019 resulted in a significantly higher number of pupae in protected samples (Salido *et al.*, 2021; Table 3).

Table 2 Surrogates of productivity in the study area: accumulated precipitation (mm) from January 1 to July 31. Mean normalized difference vegetation index (NDVI) (and SE) calculated for circles of 20 m radius centered on each nest box ($n = 58$ nest boxes, of which 36 were on trees, 18 on sandstone cliffs and 4 on farmhouses).

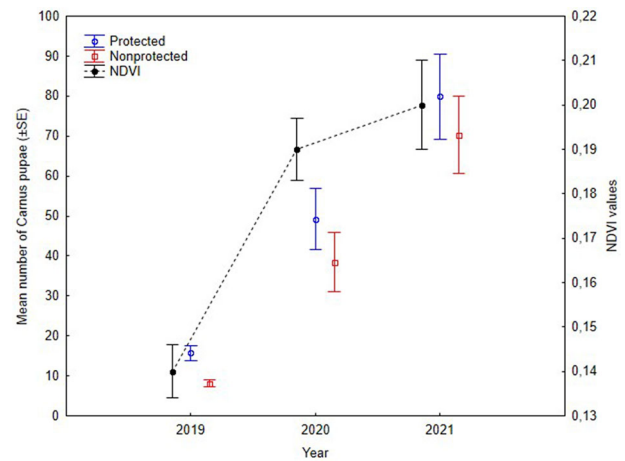| Year	2019			2020			2021		
Precipitation (mm)	63.2			138			198.8		
	Cliff	Tree	Farm	Cliff	Tree	Farm	Cliff	Tree	Farm
Mean NDVI ± SE	0.10 ± 0.008	0.15 ± 0.007	0.17 ± 0.017	0.15 ± 0.008	0.21 ± 0.008	0.22 ± 0.015	0.15 ± 0.012	0.21 ± 0.011	0.32 ± 0.041

Fig. 1 Inter-annual variation in normalized difference vegetation index (NDVI) (mean values ± SE calculated for circles of 20 m radius centered on each nest box, $n = 58$ nest boxes) and in the effect of antipredator protection on the mean number of intact carnid pupae (± SE) (2019: 28 nests, 2020: 33 nests, 2021: 41 nests). 2019 data are by Salido *et al.* (2021).

In the wet year 2020, the experimental exclusion of predators was also significant (i.e., more pupae in protected than in nonprotected samples: $F_{1,26} = 6.3$, $P = 0.02$). However, nest-site type had no significant effect on pupae abundance ($F_{2,26} = 0.76$, $P = 0.48$) (Table 3). The interaction between nest-site type and the protection treatment was not significant either ($F_{2,26} = 1.11$, $P = 0.34$).

In the wettest year (2021), the experimental treatment did not influence pupae abundance ($F_{1,32} = 0.48$, $P = 0.49$; Table 3), and nest-site type had only a marginal effect ($F_{2,32} = 3.14$, $P = 0.06$). Similarly, nest cleaning did not influence pupae abundance ($F_{1,32} = 0.34$, $P = 0.56$). No interaction effect was significant (P-value > 0.30 in all cases).

Inter-annual comparisons in the effect of predator exclusion

The number of nests where significant pupae reduction occurred in nonprotected samples (i.e., no overlap between the 95% CIs of the mean number of pupae in both types of samples), varied significantly between years ($\chi^2 = 21.3$, $P < 0.001$), being remarkably higher in 2019 (Table 4). However, the mean percentage of reduction in such nests did not differ between years (i.e., overlap between the 95% CIs; Table 4).

Table 3 Mean number (± SE) of intact pupae in protected and nonprotected samples in 2019, 2020 and 2021. Sample size in brackets (note that each nest provides 1 protected and 1 nonprotected sample, so that the number of nests is equal to the number of samples of each type—see Materials and Methods section). 2019 data are by Salido *et al.* (2021).

Habitat type	2019		2020		2021	
	Protected	Nonprotected	Protected	Nonprotected	Protected	Nonprotected
Tree	16.6 ± 2.8 (16)	8.1 ± 1.4 (16)	45.6 ± 12.4 (15)	39.0 ± 12.8 (15)	64.4 ± 9.6 (26)	56.5 ± 8.7 (26)
Cliff	12.7 ± 2.5 (8)	7.5 ± 1.9 (8)	49.7 ± 9.9 (12)	33.2 ± 6.3 (12)	81.2 ± 27.9 (8)	72.9 ± 24.5 (8)
Farmhouse	18.0 ± 2.1 (4)	9.4 ± 0.6 (4)	72.7 ± 23.2 (2)	64.1 ± 42.2 (2)	178.8 ± 26.5 (4)	154.7 ± 33.5 (4)
All pooled	15.7 ± 1.8 (28)	8.1 ± 0.9 (28)	49.2 ± 7.7 (29)	38.4 ± 7.4 (29)	79.9 ± 10.6 (38)	70.3 ± 9.6 (38)

Table 4 Number of nests (%) where significant pupae reduction (nonoverlapping 95% confidence intervals) was recorded in nonprotected samples. Mean percentage of carnid pupae reduction (± SE and 95% confidence intervals) in nests where significant reduction was found is also shown. Sample size (no. of nests) is shown in brackets. 2019 data are from by Salido *et al.* (2021).

	2019 ($n = 28$)	2020 ($n = 29$)	2021 ($n = 38$)
Nests (%) with significant pupae reduction in nonprotected samples	21 (75.00%)	10 (34.48%)	9 (23.68%)
Mean % reduction (± SE) in nests with significant reduction [95% CI]	51.9 ± 2.4 [8.4−15.9] ($n = 21$)	51.23 ± 3.83 [8.3−22.1] ($n = 10$)	36.89 ± 7.61 [15.4−43.8] ($n = 9$)

Relationship between NDVI and pupae reduction

A broad pattern emerges from the 3 study years, such that the higher the NDVI, the higher the number of pupae and the smaller the difference in the number of pupae between protected and nonprotected samples (Fig. 1). However, at the nest scale, no relationship was found in any of the study years between the mean NDVI values around the nest and the percentage of pupae reduction in nonprotected samples (considering the nests where significant reduction was detected) (Pearson's correlations, $P > 0.10$ in all cases). This was also the case when considering maximum NDVI values.

Discussion

The outcome of interactions frequently varies as a function of the biotic or abiotic context. Yet, context dependency in nature is poorly described and our understanding of the relative importance of the factors behind such variation is modest, partly because context dependency is often studied along simple gradients and/or in constant environments (Buckling & Rainey, 2002; Yoshida *et al.*, 2003; Becks *et al.*, 2010; Chamberlain *et al.*, 2014).

Context dependency in parasite-participated systems has been scantily considered (but see Orlofske *et al.*, 2015; Kaunisto *et al.*, 2016). This paper investigates context dependency of parasite predation in an arid environment where fluctuations of key ecological factors are common. The predator-exclusion experiment was found to have a significant effect on the number of ectoparasites in 2019 and 2020, but not in 2021. More importantly, predation pressure varied between years: it was strong in 2019 (an average reduction of 50% in carnid pupae abundance occurred in 75% of nest boxes within a few months, Salido *et al.*, 2021), milder in 2020 (mean reduction of ca. 51% of pupae in 34% of nest boxes), and even milder in 2021 (an average reduction of just 32% of pupae in 24% of the nests). Proper understanding of such results relies on correct comprehension of the factors accounting for context dependency, which frequently include abiotic gradients (Von Berg *et al.*, 2008; Daskin & Alford, 2012) as well as other influences (e.g., Hassell & May, 1986; Wootton, 1994). This paper explores inter-annual variation in precipitation (the most important limiting resource in arid and semi-arid ecosystems; Friedel *et al.*, 1994; Abd El-Ghani, 1997; Pavón & Briones, 2001) and, consequently, in primary and secondary productivity by

means of NDVI (a robust proxy for insectivore food availability in spring, Fernández-Tizón *et al.*, 2020). A similar pattern was found to the pattern of predation pressure at a broad scale: 2019 was a dry year with low vegetation cover and primary productivity (e.g., NDVI). In contrast, 2020 was a wet year and 2021 a particularly rainy one. As a result, primary productivity was significantly higher in both years than in 2019. These results are in agreement with our prediction that food availability is likely to influence predation pressure, because predation pressure (high in dry 2019, moderate in wet 2020 and low in wettest 2021) relates to precipitation profile. Yet, since our study is observational, caution is advised. Data from more years or an experimental approach is necessary to confirm the relationship suggested by this study.

In our system, ants are the most likely predators of carnid pupae (Salido *et al.*, 2021). Most of the ant species found in roller nests are omnivorous, opportunistic and generalists in their dietary habits, and include insect predation as a part of their trophic ecology (López-Sebastián & Tinaut, 2004; Pereira *et al.*, 2004; Ottonetti *et al.*, 2008). As a result, ants may have increased predation on carnid pupae during the dry year (i.e., the one with lower food resources). In fact, ants are known to be influenced by environmental conditions (i.e., climatic factors) and resource availability (Fellers, 1989; Hahn & Wheeler, 2002; Kaspari & Valone, 2002), and accordingly change their dietary and foraging habits (Herbers, 1989; Offenberg, 2001; Sanders & Gordon, 2003). In addition, as nutritional needs change through the developmental stage of the ant colony, a given resource can become more or less valuable at any given time (Kay, 2002; Portha *et al.*, 2002; Abbott *et al.*, 2014). For instance, during the brood stage, ant workers search for high-protein food to boost larval growth (Dussutour & Simpson, 2009; Cook *et al.*, 2010). Given that predation accounts for most of ants' protein intake, *Carnus* pupae in dry years may prove a valuable resource to satisfy dietary demands in times of protein shortage. Thus, parasite gatherings in specific places (e.g., nest boxes) may become an attractive or rewarding resource for ants to predate upon opportunistically in order to supply their nutritional needs, when other food sources are lacking (Salido *et al.*, 2021). In contrast, in rainy years, with higher food availability, ants' impact on a given prey (e.g., carnid pupae) may be lower. Hassell and May (1986) pointed out that the broad diet of polyphagous, generalist predators is likely to buffer the negative effect of fluctuations in a given food source. Such fluctuations can have important consequences for a given prey type, in that it may become preferred in the absence of alternative prey. This may be precisely the case of carnid flies in dry years in our study area. Al-

though our study suggests that the relationship between food availability and predation pressure seems to hold for ants in general, species-specific studies would help to make more precise predictions that would make it easier to test this relationship. This also applies to other parasitic predators such as spiders or beetles (Šustek & Jurik, 1980).

Our results also agree with the ones obtained by Chamberlain *et al.* (2014), whereby abiotic gradients are rich sources of variation in the outcome of pairwise species interactions (see also Maziarz *et al.*, 2022 for a similar system to the one under study here). However, the suggested relationship between primary productivity and predation pressure did not hold at lower spatial scales in this study. We hypothesized that differences in primary productivity between habitat types could result in different predation pressures, parasite predation being higher in habitat types associated with lower NDVI values. NDVI values were consistently lower around nest boxes on cliffs. This makes sense, because cliffs are usually along frequently dry watercourses with little herbaceous vegetation. Yet, neither Salido *et al.* (2021) nor this study report a significant effect of habitat type on the predation pressure on carnid pupae. Similarly, no correlations can be reported here between predation pressure and NDVI values at the nest scale. Probably, such relationships are more difficult to find at small scales, given the probably high variability in many other meaningful factors such as the number of ant nests around nest boxes, their distance to nest boxes, the composition of the ant community and competition phenomena, abundance of local, alternative food sources, to mention some of them.

Regardless of the cause of temporal oscillations in predation pressure on parasites, such fluctuations may have major consequences for hosts. Carnid flies can be detrimental for nestlings (Cannings, 1986; Soler *et al.*, 1999; Hoi *et al.*, 2018, but see Kirkpatrick & Colvin, 1989; Dawson & Bortolotti, 1997). Therefore, a high predation pressure can be beneficial both during the current year and in the future (due to depletion of carnid pupae in nests that are reoccupied the following year). Therefore, the association between birds and insects preying upon parasites could be considered as a mutualism. Some bird species have been reported to prefer nesting near ants, because ants offer protection against predators (Hindwook, 1959; Young *et al.*, 1990; Gibson *et al.*, 2019). Our study suggests that such benefits fluctuate between years. As most of the ants (the main putative predator) visiting rollers' nests are generalists (Salido *et al.*, 2021), mutualism between breeding birds and ants is bound to be opportunistic and context-dependent. A meta-analysis study by Chamberlain *et al.* (2014) revealed that

predation varied more in magnitude, but less in sign change, along abiotic gradients than other interaction classes did. This suggests that predation interactions can vary in interaction strength, but are more constrained (than other classes of interactions) against changing signs. This is because the interaction rarely deviates from being beneficial to predators and detrimental to prey. However, our results suggest that predation did change sign in our system, whereas interestingly, the mean percentage of reduction in nests with significant predation (i.e., magnitude) did not differ significantly between years (Table 4). In-depth studies on ant communities and ecological factors around nests may provide insights on the factors determining the magnitude of predation.

In conclusion, insect predation on parasites fluctuates between years. This implies that parasites, ants, and birds may be in a dynamic balance: some years may favor the predator and some others may favor the parasite. Since the incorporation of parasitism in food webs, research has largely focused on parasite effects on their hosts, rather than on the role of parasites as a rich resource and the environmental conditions that might be involved in parasite vulnerability to be consumed (Wood & Johnson, 2015). We suggest that the study of the effect of natural enemies of parasites, and of the factors influencing predation pressure is key to understanding significant ecological and epidemiological issues such as pathogen transmission and disease dynamics in natural systems. Further research should identify factors potentially driving predation on parasites, and explore predator and prey properties mediating the role of parasites as prey in terrestrial ecosystems.

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Disclosure

The authors declare no conflicts of interest.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Experimental set up: bagged detritus (containing *Carnus hemapterus* pupae) was protected by a wire mess and stapled to the inner wall of the nest box.