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Quantifying predation to insects: An experimental approach

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ABSTRACT

Predation can affect biodiversity and ecosystem processes considerably. However, its effects on threatened insects is poorly understood as predation is usually studied from the predators' rather than the preys' perspective. Human activities can severely alter predator occurrence, e.g. by livestock grazing that may attract predators. We conducted two field experiments using (1) camera traps with insect baits to identify main predators and (2) reflecting foils to investigate insect survival in relation to grazing frequency and predator presence. Our target species was the critically endangered Crau plain grasshopper (*Prionotropis rhodanica*) which has been suggested to be potentially threatened by expanding predators, such as cattle egrets (*Bubulcus ibis*), crows and lesser kestrel (*Falco naumanni*). The first experiment identified mainly crows, particularly rooks (*Corvus frugilegus*), as predators. The second experiment showed that crows and cattle egrets were positively related to grazing and negatively to insect survival (which was notably affected by crow presence). Crows and cattle egrets peaked during the early reproduction period of the Crau plain grasshopper, suggesting a potential impact on its population. Our results show that the simultaneous colonization and increase of synanthropic predator species represents a plausible threat for the grasshopper. Our novel experimental approach considering the preys' perspective should therefore encourage similar studies to quantify predation risk for threatened invertebrates. While direct effects of habitat deterioration on insect populations are well known and easy to study, secondary effects of changing predator communities should receive more attention in insect conservation.

1. Introduction

Predation can profoundly influence biodiversity and ecosystem processes: In case of disappearance of apex predators, cascading effects are known to occur in marine, terrestrial and freshwater ecosystems, which can have considerable impact on diseases, wildfires, carbon sequestration, invasive species, and biogeochemical cycles (Estes et al., 2011). On the other hand, appearance of non-native predators can also have significant consequences for wildlife and ecosystem functions. For example, predation of invasive mammalian species (e.g. cats or rodents) represents a serious threat to global biodiversity and has caused the extinction of many birds, reptiles and mammals (Doherty et al., 2016). Predation by invasive rats, mice, lizards, birds, and fishes has been identified as a direct threat to

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island endemic insects (Wagner and Van Driesche, 2010), such as wetas (Watts and Thornburrow, 2009) or damselflies (Englund et al., 2007). Different predators do not only vary in their prey, but also in hunting mode (e.g. sit-and-wait or actively hunting). Different prey response to these hunting modes (e.g. density reduction or foraging shifts) can also have substantial impact on ecosystems and is thus considered as a key functional trait (Schmitz, 2008).

Predation is usually studied based upon the diet of predators (e.g. Garcia et al., 2016; Medina and García, 2007). For insect conservation, however, it is crucial to investigate predator-prey interactions from the preys' perspective in order to understand the impact of predation on the population. Key aspects of predation risk analyses are to identify main predators of threatened insect species, to quantify predation effects and to understand which factors influence predation. Such studies may help to develop an appropriate management to increase survival probability of the target species.

One methodology that provides deeper insight into predator-prey interactions is the use of camera traps. Camera traps are usually applied for purely observational studies, for example, to obtain information on spatial and temporal activity of predator and prey populations, whereas experimental approaches on free-ranging wildlife using camera traps are still rare (Smith et al., 2020). Using camera traps with exposition of prey, simulated prey or other prey proxies allows to measure attack or survival rates and identify predators. The most popular application addressing these issues is the use of artificial nests equipped with egg dummies (i.e. chicken, quail or model eggs) to study predation effects on bird and reptile nests (Smith et al., 2020). However, camera trap experiments have also been applied, for example, using models of coral snakes (Akcali, 2019) or caterpillars (Muiruri et al., 2016), while the use of the living prey as bait is rare (e.g. Miyamoto et al., 2018).

The Crau plain grasshopper (*Prionotropis rhodanica*) is a critically endangered insect species, for which predation has been supposed as a potential threat (Hochkirch et al., 2014). The large, flightless species is endemic to the Crau steppe, a Mediterranean stone steppe in southern France and its population declined extremely during the last two decades (Hochkirch et al., 2014). Previous studies have shown that its decline is related to sheep grazing (Bröder et al., 2019; Piry, 2018), but it remains unclear whether grazing is principally impacting the grasshopper through degradation of its habitat or whether the observed negative effect of grazing is related to grazing associated predators. Relatively little is known about predator-prey interactions in the Crau steppe ecosystem. Only a few studies on diet composition have been conducted, e.g. on ocellated lizard (*Timon lepidus*) (Tatin et al., 2013) or lesser kestrel (*Falco naumanni*) (Choisy et al., 1999).

Several potential predator species have been suggested to impact the Crau plain grasshopper population (Hochkirch et al., 2014), particularly cattle egret (*Bubulcus ibis*), lesser kestrel and crows, all of which have significantly increased in abundance during recent decades in the Crau region. Cattle egrets are well adapted to forage on grassland and closely associated with grazers (Pitt and Witmer, 2007), typically joining livestock and often occurring in large groups (Heatwole, 1965) to benefit from flushing insects. The species has spread rapidly from its original distribution in Africa to a near-cosmopolitan distribution, which was presumably facilitated by conversion of large areas to livestock pastures (Pitt and Witmer, 2007). Colonization in France started in 1957, but abundance increased extremely only since 1994 (Tourenq et al., 2000). In the Camargue wetland, an area in direct neighborhood to the Crau steppe, ca. 7.000 breeding pairs (half of the French population) were counted in 2007 (Marion, 2009). Cattle egrets typically join sheep flocks in the Crau and may thus increase predation pressure in the area (Hochkirch et al., 2014). Crows comprise another group of omnivorous birds that frequently forage in groups and sometimes also in association with domestic animals. Similarly to cattle egrets, they often forage with livestock or on pastures, which facilitates accessibility of prey, but is also related to feeding on coprophagous invertebrates. Crows are known to affect threatened bird and reptile populations due to predation of nests and young (Liebezeit and George, 2002), but crow predation as a potential threat to insects has not received much attention. In case of the Crau plain grasshopper, predation pressure coming from crows is supposed to be strong (Foucart and Lecoq, 1998), but has never been quantified. Lesser kestrel predation is not linked to grazing, but has also been suggested as a potential threat to the Crau plain grasshopper, as the insectivorous bird increased notably in abundance during the last two decades in the Crau steppe (Pilard, 2011), when the population of the grasshopper declined. The lesser kestrel population in the area harbors today half of the French population (175 of 332 breeding pairs in 2015), which was facilitated by installing nesting boxes (Pilard, 2011). The species is known to hunt preferably on large insects and particularly on Orthoptera during the feeding period of chicks (June and July) (Pilard, 2011), i.e. during the adult phase of the Crau plain grasshopper (June). Therefore, lesser kestrel is a plausible candidate species that may represent a potentially relevant predator to the grasshopper. Other insectivorous birds in the Crau are Eurasian stone-curlew (*Burhinus oedicnemus*), little bustard (*Tetrax tetrax*) and little owl (*Athene noctua*). Moreover, some native non-avian species, such as wild boar (*Sus scrofa*), red fox (*Vulpes vulpes*), European badger (*Meles meles*) or the ocellated lizard are also potential predators of the Crau plain grasshopper.

To clarify the impact of predation on the Crau plain grasshopper, we conducted two field experiments. Our objectives were (1) to identify the main predators ('camera trap experiment') feeding on large grasshoppers, and (2) to investigate grasshopper survival in relation to grazing and predator presence ('reflecting foil experiment'). The camera trap experiment was carried out on two sites, one within a subpopulation of the Crau plain grasshopper, the other one in an area where the species went extinct. We hypothesized to observe less predation in the remaining habitat of the Crau plain grasshopper compared to the area where the species went extinct, as the remaining habitat was excluded from grazing by fencing, and thus also from grazing-associated predators. In the reflecting foil experiment, we chose four study sites to test for local differences in grazing frequency, predator presence and grasshopper survival rates, taking meteorological parameters as well as daily and seasonal patterns of grazing and predator presence into account. We expected to find a strong relationship between predator presence and grazing frequency. We further hypothesized that cattle egrets are particularly related to grazing compared with other potential predators.

2. Materials and methods

2.1. Study context

The Crau plain grasshopper is a habitat specialist endemic to the Crau steppe, a unique Mediterranean stone steppe in southern France, representing one of the last steppe areas in Europe. The Crau steppe has been increasingly reduced and fragmented because of expansion of agriculture and industry. Today, ca. 7400 ha of the < 10,000 ha remaining steppe land are protected as a national nature reserve (*Réserve naturelle nationale des Coussouls de Crau*). Sheep grazing in the Crau steppe has a long tradition (Badan et al., 1995) and pastoral agriculture is based on transhumance, spanning an annual cycle with three stages: utilization of the Crau steppe as dry rangelands during late winter and spring (February or March until mid to late June), mountain pastures in the Alps in summer (until September or October) and meadows surrounding the Crau steppe in autumn-winter. Approximately 40,000 sheep are grazing in the Crau steppe, organized in 68 pasture zones and individually managed by shepherds, leading to spatial variation in grazing pressure.

The Crau plain grasshopper was originally widely distributed throughout the steppe, but its population experienced an extreme decline since beginning of the 2000 s (Hochkirch et al., 2014). Today, only three spatially separated subpopulations remain and the species is listed as Critically Endangered on the IUCN Red List of Threatened Species (Hochkirch and Tatin, 2016). Both sexes of the Crau Plain Grasshopper are flightless because of reduced wings. Their mobility is low (Foucart and Lecoq, 1996) and their movement rather clumsy. The large grasshopper (total adult body length males: 32–38 mm, females: 42–48 mm, Foucart, 1995; mean body weight of adult males: $2.1 \text{ g} \pm 0.02 \text{ SE}$, and females: $5.4 \text{ g} \pm 0.12 \text{ SE}$, unpublished data) has a stout body and gray-brown to reddish-brown body color, making it very well camouflaged in the Crau steppe, which is further increased by its' inconspicuous behavior, i.e. remaining mostly immobile and silent (Bröder et al., 2020). The Crau plain grasshopper is univoltine, the first nymphs appear in early April and pass five instars. Adult individuals emerge end of May (earlier than most other Orthoptera in the Crau) and only survive < 40 days (Foucart, 1995).

2.2. Experiments

In both experiments, i.e. the 'camera trap experiment' and the 'reflecting foil experiment', Migratory locusts (*Locusta migratoria*) were used as baits instead of using the Crau plain grasshopper, because of its' high conservation priority. The body size of *L. migratoria* is in the same range as the target species (male size 29–50 mm, female size 39.5–55 mm; Hochkirch and Gröning, 2008). One femur of each locust was autotomized and the wings were clipped with standard nail scissors to decrease mobility and to imitate the clumsy movements of the Crau plain grasshopper. We exclusively used males to prevent reproduction in nature.

The Camera trap experiment was performed on the study sites 'Peau de Meau' and 'Grosse du Levant' (Fig. A1). Peau de Meau maintains one of the last three remaining Crau plain grasshopper subpopulations and is entirely fenced during the grasshopper season to minimize impacts from grazing or predation by grazing-associated birds. Grosse du Levant is a neighboring site and comprises a grazed area where the grasshopper went recently (probably in 2009) extinct. The basic principle of the camera trap experiment was to dispose a bait in front of a camera trap to record predation events and identify the predator. We attached locusts to a stone using a transparent fishing line (Fig. A2) to keep the bait in the visual field of the camera trap. The maximum distance between the stone and the locust was 5 cm. The camera trap (Reconyx Hyperfire HC500) was exposed 1 m south of the bait and orientated towards north to avoid backlight (Table A1).

The Camera trap experiment was performed from 25 May to 18 June 2018 on the study sites Grosse du Levant and Peau de Meau. Each study site had three experimental stations with one camera trap and one bait. Vegetation in the Crau steppe is naturally scarce, but it is often windy which could move vegetation in front of the camera trap. To avoid perturbation and false triggering, we additionally cut vegetation close to the camera trap. The position of each station was previously chosen by calculating random points in QGIS Version 2.2 Valmiera. The bait was checked and replaced every three to four days and the position of each station was changed after three replacements. In total, 42 baits (21 samples per site) were exposed during the experiment. Information on presence or absence of the bait and notable observations, such as locust remnants in the close surroundings, were recorded before each replacement. If a bait was absent (i.e. no more attached to the stone), all camera trap photos were inspected until the moment of disappearance to identify the predator species. However, some disappearance events did not show any predators (possibly due to small predator size).

The reflecting foil experiment was simultaneously performed on four study sites located in the central part of the Crau steppe: 'Grosse du Centre', 'Grosse du Levant', 'Couloubri' and 'Nouveau Carton' (Fig. A1). These sites are all considered as potential reintroduction sites for the Crau plain grasshopper: Grosse du Centre and Grosse du Levant because of their vicinity to the last remaining subpopulation in the central part of the Crau steppe (Peau de Meau) to favor connection between reintroduced and remaining subpopulation; Couloubri and Nouveau Carton as these sites are close to the area where the Crau plain grasshopper was still present until 2012. All sites, except for Couloubri, are situated in the national nature reserve.

Locusts with autotomized femora and clipped wings were tagged with a self-adhesive reflecting foil on the pronotum (Fig. A2) and an individual number was written laterally on the foil (left and right). Ten male locusts with reflecting foils were released once per week at each study site. To avoid attracting predators because of high locust densities, we released always two individuals at each of five release points. The release points were arranged in a cross pattern with a distance of 25 m to each other. We tracked individuals during nocturnal controls with a torch (Halepro TG200, maximum headlight range 300 m) to detect reflections of the foil. A first control was conducted 48 h and a second one week after release. Usually two searchers were walking over the entire study area, searching from different directions and noting all locusts detected alive. Detached reflecting foils (without locusts) were also noted and

removed from the study site. All reflecting foils recovered had remnants of the pronotal integument attached, illustrating that these documented losses were caused by mortality. Each living locust or recovered reflecting foil was identified by its individual number. The search was completed when the same individuals were observed several times and no more new detections occurred. The minimum search time was 40 min per site.

The total study period of the reflecting foil experiment was seven weeks (07 May to 26 June 2018). Six cohorts of ten individuals (i.e. a total of 60 individuals) were released each in Grosse du Centre and Grosse du Levant and seven cohorts (70 individuals) in Nouveau Carton and Couloubri (Table A2). On each site, a camera trap (Bushnell Trophy Cam HD Aggressor Model 119774) was installed beginning on 22 May 2018 (see Table A1 for detailed camera trap setting) to record sheep flocks and potential predators (i.e. all insectivorous species appearing in front of the camera traps). We also noted whether predator presence was associated with grazing (i.e. recorded with sheep presence) or not. Association with sheep was classified when both, potential predators and sheep, were present in the same picture. Temporal proximity of observations was not considered as a proof of association. Time and date of each observation were recorded, permitting to calculate the number of sheep flock passages and predator visits per day and hour (from 6.30 to 21.30) (i.e. 'grazing frequency' and 'predator frequency'). We only considered days with complete camera trap surveys.

To assess variation in sheep number during the study period (caused by transhumance), we obtained data on sheep flock sizes from the Agricultural Chamber (*Chambre d'agriculture des Bouches-du-Rhône*). Only grazing zones without data gaps during the study period were used to calculate the total flock size for each study day ('sheep number') to reflect the changing sheep number in the Crau steppe. Moreover, meteorological data for each study day were purchased from [Meteociel.fr](https://www.meteociel.fr) (2018): precipitation per day (mm), daily maximum wind speed (km/h) and daily maximum temperature (°C).

2.3. Data analyses

To compare predation risk of a managed, i.e. fenced, Crau plain grasshopper population and an area where the species went extinct, we analyzed the data of the camera trap experiment using χ^2 tests for comparing frequency of absence of baits as well as frequency of predation events per identified predator species (6 different species) between the two study sites. In the latter case, p-values were computed by Monte Carlo simulations (10.000 replicates) as expected values were low. Moreover, we tested for site differences in the time until the predation event using a Wilcoxon rank sum test. To understand the relation between grazing, predator presence and survival rate of grasshoppers, we analyzed the data from the reflecting foil experiment by calculating the mean number of living and dead locusts during the first week after release and the means of grazing frequency and frequency of cattle egret, crows and total predator observations for each of the four study sites. We then used one-way ANOVAs to compare these means between the study sites. To fit the data to the model assumptions, we determined the optimal transformation exponent lambda for a Box-Cox-Transformation using the R package MASS 7.3–51.4 (Venables and Ripley, 2002). A post-hoc Tukey t-test was applied to identify differences between sites. We further applied χ^2 tests to compare the number of total predator, cattle egret and crow observations between grazed and ungrazed periods.

The R package vegan 2.5–6 (Oksanen et al., 2019) was used to perform a principle component analysis (PCA) to illustrate potential inter-correlations of the following daily covariates: precipitation, maximum wind speed, maximum temperature, date, sheep number, grazing frequency and frequency of cattle egret and crow observations. Data were scaled by their proportional eigenvalues because of their different units. We additionally calculated the percentage of surviving locusts compared to the last count (i.e. release or last nightly inspection) for each cohort during the first week after release (hereafter 'survival rate') and used environmental fitting (with the function `env.fit`) to test for significant correlation of the survival rate with the PCA functions based on 1000 permutations.

Binomial Generalized Linear Models (GLMs) with logit link function were applied to model survival rate in response to the variables site, interval length (2 or 5 days between controls), date, grazing frequency, frequency of crow and cattle egret observations, sheep number and temperature. We first generated saturated models including only variables that were not correlated with each other (Spearman's rank correlation, variables not included if $r > 0.4$ or $r < -0.4$ and $p < 0.05$). Least significant predictor variables were then successively dropped from the model. The package MuMIn 1.43.6 (Bartoń, 2019) was used to calculate AICc values and model weights. Models were ranked based on AICc. Explained deviance [i.e. ((null deviance - residuals deviance) / null deviance) * 100] was additionally calculated for each model. To verify model assumptions, residuals were plotted versus fitted values, versus each covariate in the model and versus each covariate not included in the model. The selected model was tested with a Hosmer-Lemeshow goodness-of-fit test with the package `glmtoolbox` 0.1.6 (Vanegas et al., 2023).

To visualize daily and seasonal variations in grazing frequency and predator presence, hourly and daily numbers of observations were plotted over daytime (from 6.30 to 21.30) and study period. Linear regression models were then applied to test for linear relationships between the number of predator and grazing observations on a daily and seasonal scale. All statistical analyses were carried out in R 3.6.1 (R Core Team, 2019).

3. Results

3.1. Camera trap experiment

In total, 57% of the baits (24 of 42) were absent when experimental stations were checked. In Peau de Meau 67% (14 baits) of the baits were absent, in Grosse du Levant 48% (10 baits); the site difference was however not significant (χ^2 -Test: $\chi^2 = 0.67$, $df = 1$, $p = 0.414$). Time until predation was $32 \text{ h} \pm 5 \text{ h}$ standard error (SE) and mean bait presence did not differ significantly between sites (Grosse du Levant: $29 \text{ h} \pm 7 \text{ h}$ SE; Peau de Meau: $34 \text{ h} \pm 7 \text{ h}$ SE; Wilcoxon rank sum test: $p = 0.585$). In Peau de Meau, 86% of the

missing baits were absent because of confirmed predations (12 baits), in Grosse du Levant 60% (6 baits). In five cases (once for Peau de Meau and four times for Grosse du Levant) the reason of absence was not recorded by the camera trap (possibly due to small predator size).

In total, 17 of the 18 observed predation events (i.e. 94%) were caused by birds, only one bait was predated by a spider. Among bird predators, 82% were crows: 41% rooks (*Corvus frugilegus*); 24% western jackdaws (*C. monedula*); 18% carrion crows (*C. corone*). Predation by lesser kestrel was observed once, by Eurasian stone-curlew twice. No predation event by cattle egrets was observed in the camera trap experiment. Predator species composition (i.e. rooks, western jackdaws, carrion crows, lesser kestrel, Eurasian stone-curlew and spider) did not differ significantly between sites (χ^2 -Test: $\chi^2 = 6.91$, $p = 0.276$).

3.2. Reflecting foil experiment

On average 36.0% ($\pm 5.2\%$ SE) of the locusts were detected alive and 5.0% ($\pm 0.8\%$ SE) dead one week after release. Couloubris showed the highest survival (50.0% $\pm 7.7\%$ SE) and the lowest mean of dead locusts (2.5% $\pm 1.8\%$ SE) (Fig. 1), site differences were however not significant (Table A3). The mean frequencies of crow observations differed significantly between the study sites (ANOVA: $\lambda = -0.12$, $F_{3,88} = 2.76$, $p = 0.047$), with significantly fewer crow observations on Couloubris than on Grosse du Levant (Tukey test: $p = 0.036$, Fig. 1, Table A4).

In total, 78 grazing events (i.e. sheep flock passages documented by the camera trap) and 81 visits of potential predators (i.e. observations of single individuals or groups) were observed on the four study sites. Overall, 58% of the predator observations were made in association with sheep. The difference in number of predator observations between grazed and ungrazed periods was however not significant (χ^2 -Test: $\chi^2 = 2.09$, $df = 1$, $p = 0.148$). Most predator observations were crows (63%) and cattle egrets (25%); other observed potential predators were Eurasian stone-curlew (9%), little bustard (2%) and wild boar (1%) (Table 1). All cattle egret observations were made during grazing and number of cattle egret observations did thus differ significantly between grazed and ungrazed periods (χ^2 -Test: $\chi^2 = 20$, $df = 1$, $p < 0.001$). In contrast, the number of crow observations was similarly high during grazed and ungrazed periods (51% vs. 49%; χ^2 -Test: $\chi^2 = 0.02$, $df = 1$, $p = 0.889$).

In the PCA, 62% of the total variance was explained by the first two principle components (component 1: 44%, component 2: 18%). The first component was mainly explained by sheep number (score: 1.58) and date (-1.42), the second component by grazing frequency (1.18). Grazing, precipitation and presence of cattle egrets and crows were positively correlated (Fig. 2). Environmental fitting revealed a tendency for a correlation of bait survival with both principle components ($p = 0.051$). The vector was negatively correlated with grazing, precipitation, cattle egrets and crow presence.

Based on model ranking of the GLMs (Table A5), survival rate was best explained by the model including either only the variable ‘crow frequency’ (Fig. 3; Hosmer-Lemeshow goodness-of-fit test: $df = 4$, $p = 0.352$) or also including ‘date’. The second-best model (including ‘crow frequency’ and ‘date’) had a delta AICc of 1.7 (i.e. had a similar explanatory value as the best model). Its weight was lower (0.12 compared to 0.29), but the explained deviance slightly higher (18% compared to 14%) compared to the model containing ‘crow frequency’ only.

Grazing peaked in the morning and evening hours, which was also reflected in cattle egret and crow observations (Fig. 4). Hourly numbers of cattle egret and crow observations were both significantly correlated with hourly numbers of grazing observations (linear regressions; crows: $t = 3.09$; $p < 0.009$; cattle egrets: $t = 4.50$, $p < 0.001$). However, the correlation of grazing was stronger with cattle egret presence ($R^2 = 0.61$) than with crow presence ($R^2 = 0.42$, Fig. A3). The sum of cattle egret and crow observations showed an even stronger positive correlation with grazing ($R^2 = 0.71$, $t = 5.66$, $p < 0.001$, Fig. 4). On a seasonal scale, grazing frequency was fluctuating during the study period, but tended to increase until beginning of June and to decrease towards the end of the study period. Daily numbers of cattle egret and crow observations showed a similar pattern (Fig. 4). Number of predator observations per day was highest between 04th and 07th June (5–8 predator observations per day). Linear regressions between daily frequency of grazing and

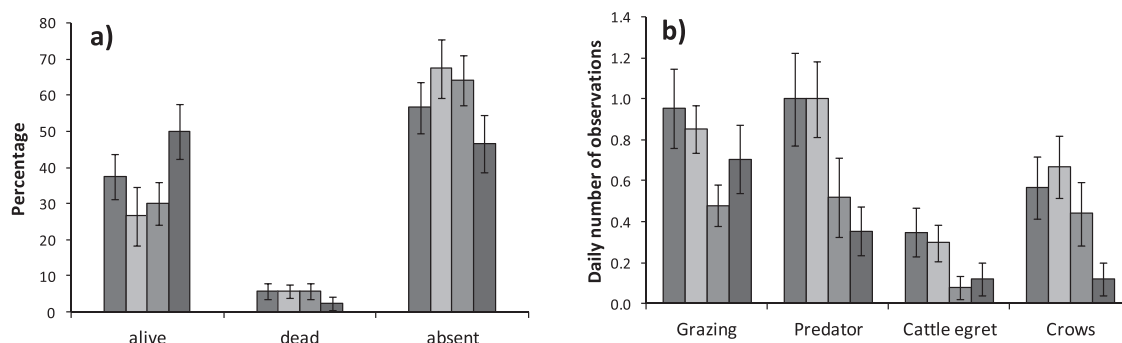


Fig. 1. Comparison of a) the mean percentage of grasshoppers alive, dead and absent after one week after release and b) daily mean frequencies of grazing, predator, cattle egret and crow observations (‘predator’ contains the sum of all observed potential predators), in the reflecting foil experiment (bars from left to right correspond to the study sites: Grosse du Centre, Grosse du Levant, Nouveau carton and Couloubris); error bars are standard errors (SE).

Table 1

Number of observations of potential predators; percentage of observations in sheep presence or without sheep and percentage of total counts per species indicated in brackets.

	Counts during period		Counts
	with sheep presence	without sheep	
Crows	26 (51)	25 (49)	51 (63)
Cattle egret	20 (100)	0 (0)	20 (25)
Stone curlew	1 (14)	6 (86)	7 (9)
Little bustard	0 (0)	2 (100)	2 (2)
Wild boar	0 (0)	1 (100)	1 (1)
Total	47 (58)	34 (42)	81

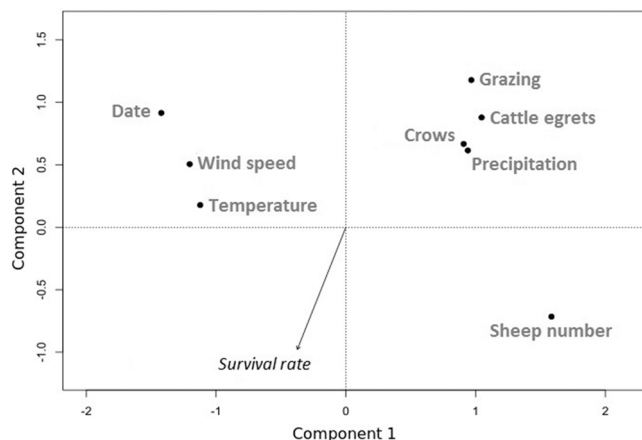


Fig. 2. Plot of the first two components of the principle component analysis (PCA), explaining 62% of the total variance. Variables were daily frequency of crows, cattle egret and grazing observations, daily maximum wind speed, daily maximum temperature and daily precipitation. The arrow indicates the tendency for a correlation ($p = 0.051$) of bait survival rate with the PCA using environmental fitting.

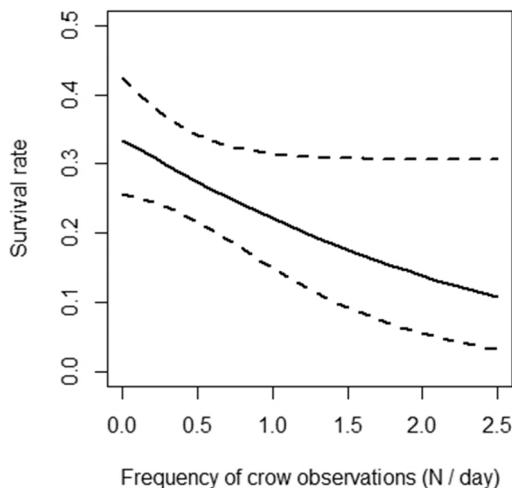


Fig. 3. Model fit of the bait survival rate (solid line) and 95% confidence bands for the optimal GLM model applied on the crow data ($z = -1.88$, $p = 0.060$); note that the graphic shows a back-transformed chart.

predator observations were all significant (crows: $t = 3.77$; $p < 0.001$; cattle egrets: $t = 2.65$, $p = 0.013$; both: $t = 4.24$; $p < 0.001$), but regressions were less strong than for frequency of hourly observations (crows: $R^2 = 0.34$; cattle egrets: $R^2 = 0.20$, Fig. A4; both: $R^2 = 0.39$).

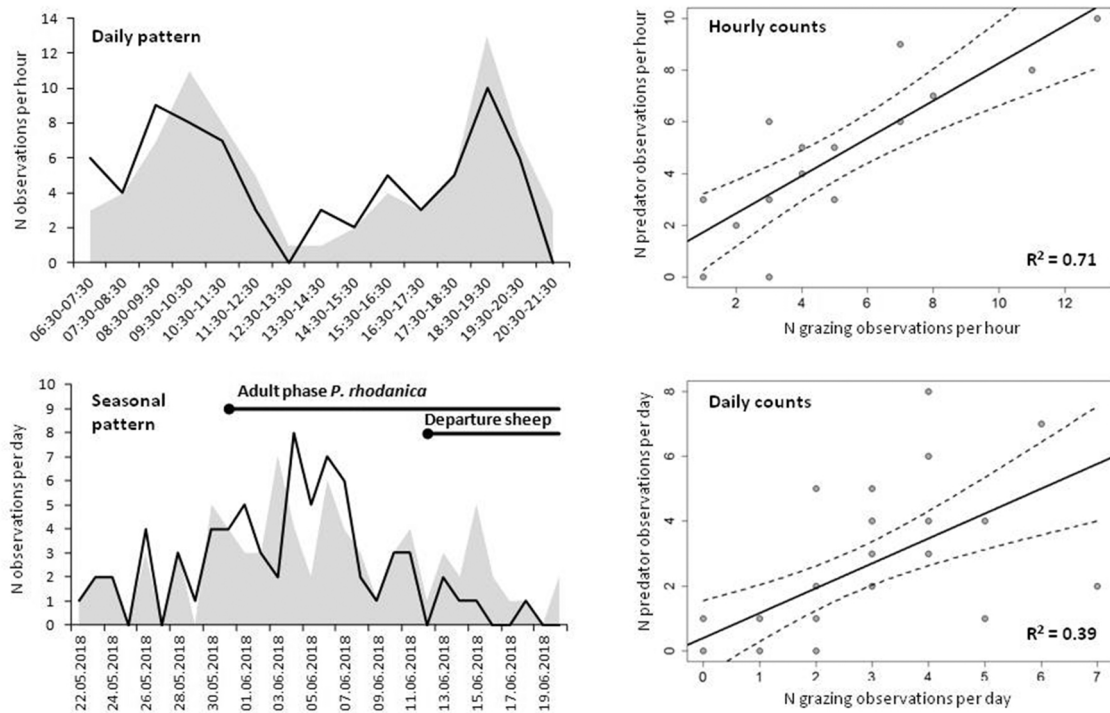


Fig. 4. Left: Daily and seasonal variation in frequency of grazing (grey area) and crow + cattle egrets visits (black line); Right: positive correlation between these variables (linear regressions with 95% confidence intervals; for hourly counts: $R^2 = 0.71$, $t_{1,13} = 5.66$, $p < 0.001$; for daily counts: $R^2 = 0.39$, $t_{1,28} = 4.24$, $p < 0.001$); the line “Adult phase *P. rhodanica*” illustrates the period of presence of adult Crau plain grasshoppers, the line “Departure of sheep” represents the period when sheep number was reduced by $\geq 25\%$ (compared to the beginning of the study period) because of transhumance.

4. Discussion

4.1. Synanthropic avian predation as potential threat

Our results give some first indications of the role of predation for the Crau Plain Grasshopper. The results from the camera trap experiment suggest that, in the Crau steppe, birds are the main predators of flightless grasshoppers, as we mainly observed predation by crow species, particularly rooks. In the second experiment (the reflecting foil experiment), cattle egrets and crows were observed most often as potential predators and the results further showed that their presence was positively related to grazing activity. Finally, even though the survival analysis did not show a strong significant effect of predation, it is in accordance with the results of the camera trap experiment as bait survival turned out to be negatively affected by crow presence.

The three corvid species that were observed during the study period, i.e. rooks, western jackdaws and carrion crows, have different species attributes regarding habitat use and feeding behavior. Carrion crows are ubiquitous and opportunistic for food and nesting sites, occupying a wide range of open and semi-open habitats (Deceuninck, 2015). Food type varies over the year, but as an omnivorous species, carrion crows are also feeding on invertebrates (Jollet, 1984). Jackdaws have a preference for short grass swards which are typically derived from heavy sheep grazing. Such environments are often frequented in mixed flocks with rooks for feeding on soil and surface invertebrates, but the species also exploits the invertebrate fauna of dung (Fuller, 1996). Jackdaws are more insectivorous compared with other corvids, feeding particularly on small insects, spiders and mollusks during the reproduction period (Burn and Madge, 1999). Rooks are mainly vegetarian (seeds, fruits etc.), but insects and earth worms are principally consumed during the reproduction period (Olioso and Grolleau, 2015). Feeding behavior of crows might be critical for the Crau plain grasshopper, as reproduction periods with increased consumption of insects (rooks: March to July, jackdaws: April to July, carrion crows: March to June) are largely overlapping with the presence of the grasshopper (Nymphs: April to July, Adults: June to July). In our study, we observed that crow frequency increased during the early adult phase of the Crau plain grasshopper (i.e. the early reproduction period), suggesting that crows may potentially impact its population. Contrary to jackdaws and carrion crows, rooks colonized the study area only in 2003/2004 (Olioso and Grolleau, 2015), i.e. relatively recently and were not present before the extreme population decline of the Crau plain grasshopper that occurred during the last two decades. Considering the high predation rate by rooks in the camera trap experiment, it is therefore possible that the progressive arrival of rooks was a key trigger for the population decline of the Crau plain grasshopper.

In the camera trap experiment, cattle egrets were not observed as grasshopper predators, but in the PCA, survival rate was

negatively correlated with the inter-correlated parameters grazing activity, precipitation, and cattle egret and crow presence. Considering the strong expected correlation of cattle egret presence with grazing activity, its predation effect might be rather local and temporary, i.e. meaningful only in case of a local grazing event. In contrast, crows were also frequently observed foraging independently of sheep grazing, making them a kind of omnipresent predator, which might potentially explain their considerable effect on bait survival.

During our camera trap experiment, we observed predation by lesser kestrel only once, even though the species is a known predator of grasshoppers (Pilard, 2011) and has benefited from a reinforcement program that led to a strong population increase in recent decades. A local study of the diet of this species over 12 years (Pilard and Tatin, 2013) found that the Crau plain grasshopper represents only a minor fraction of their prey ($< 0.1\%$). Our observation suggests that lesser kestrel exerts only low predation pressure to the Crau plain grasshopper – at least at the current lesser kestrel and grasshopper densities. One explanation could be that the well camouflaged and immobile grasshopper is not easily detectable during hunting in flight. Our results further suggest that predation pressure by other native species, such as Eurasian stone-curlew, little bustard or ocellated lizard, might also be negligible compared with crows.

Overall, the impact of birds hunting in groups on the ground and often in sheep flock presence (cattle egrets and crows) was more important than the impact of species hunting individually and in flight (lesser kestrel). Foraging in groups and associated with livestock is an efficient foraging strategy (Dinsmore, 1973) that was probably not common in the Crau steppe before the increase of cattle egret and crows. The Crau plain grasshopper might be particularly vulnerable to this new foraging strategy due to its strong habitat specialization, low mobility and narrow distribution. Hunting in groups and in association with sheep probably induces escape jumps by the elusive grasshopper and thus increases the detection rate, which may override its anti-predator strategy based on camouflage and inconspicuous behavior. The lack of adequate predator defense for this kind of predator behavior is very likely a consequence of 'prey inexperience' (see David et al., 2017).

The dimension of crow and cattle egret predation associated with grazing may be underestimated and consequently mostly neglected in conservation planning. However, the clear peak of crow and cattle egret presence at the beginning of the adult phase of the Crau plain grasshopper (see Fig. 4) needs to be considered in future reserve management. This is particularly relevant, as the Crau plain grasshopper might be a highly attractive prey species, because of its large body size and its remarkable weight, as well as its early presence in the season. It is one of the first grasshopper species becoming adult, during a period when few other large insect species are available. The arrival of two avian predators in its habitat exerting increased predation pressure during the early reproduction period does, therefore, represent a plausible threat to the Crau plain grasshopper and, even if not trivial to counteract, should be integrated in the conservation program of the species.

4.2. Conservation management implications

It has recently been shown that intensive grazing represents a threat to the Crau Plain Grasshopper, even though the mechanisms were poorly understood (Bröder et al., 2019). Seasonal exclusion from grazing has led to an increase in population size of the Crau Plain Grasshopper at the Peau de Meau site (Bröder et al., 2020). We here show that grazing frequency is correlated to the presence of crows and cattle egrets. It is likely that adaptation of grazing practice to weather conditions might indirectly regulate the presence of omnivorous species associated to sheep flocks (e.g. no grazing during hot or rainy periods of the day). Such practices might explain why precipitation was positively correlated with grazing frequency, cattle egret and crow presence in the PCA. At a seasonal scale, increasing temperature during the study period might cause the initial increase of grazing frequency. Subsequent decrease in grazing frequency might, however, be related to progressive departure of sheep due to transhumance. It might be difficult to adjust a grazing practice that is largely based on adaptation to weather conditions and vegetation availability. However, potentially, there are also other factors, such as sheep density and flock movement, which might be relevant in terms of grazing frequency. Reliable information on factors determining the variation in grazing frequency is necessary to develop adequate grazing management strategies considering the interest of both, conservation and pastoralism. Therefore, we strongly recommend investigating grazing practice and variation in the Crau steppe in more detail with the objective to better understand spatio-temporal variation in grazing practices and to identify the underlying factors leading to these practices (see also Vidaller et al., 2022).

Grazing has also a direct effect on vegetation structure, which is a key factor in determining the usage by foraging birds (Atkinson et al., 2004). We have shown before that sites where the Crau plain grasshopper survived have a higher vegetation cover than sites where the species went extinct (Bröder et al., 2019). Maintaining a habitat with a heterogeneous vegetation might thus be fundamental to reduce prey accessibility to omnivorous birds and to create shelter for insects and other invertebrates. Monitoring of habitat structure and adaptive grazing management should consequently be a priority in Crau plain grasshopper conservation planning.

One possible management action to reduce grazing pressure and to avoid impact of predators associated with livestock is non-permanent fencing or straight omission of grazing in specific areas. Temporal and local grazing exclusion in areas of interest during presence of the target species is likely to be sufficiently effective (Bröder et al., 2019). In our case, such management may mostly reduce predation by cattle egrets, as these were stronger associated with sheep presence than crows. Potentially, it might be possible that predators (particularly crows) become attracted to fenced or omitted areas, if prey density increases in response to the management measure. An associated monitoring of the target species is, therefore, crucial to identify emerging population decreases and to adapt the management respectively (Bröder et al., 2020).

Explicit management of corvids is difficult because of their wide and abundant distribution (Boarman, 2003). Reducing corvid predation on threatened and endangered species is "a complex issue with no simple solution" and management has to be developed in adaptation to the individual context (Liebezeit and George, 2002). However, a couple of management approaches exist, such as reduction of anthropogenic sources of food and water or removal of nest and perch sites (Colwell et al., 2009; Liebezeit and George,

2002). In context of the Crau plain grasshopper, it would be crucial to obtain good data on crow habitat use (e.g. by using GPS tracking systems to study spatial crow behavior) and factors determining their seasonal variation of abundance in the Crau steppe.

5. Conclusions

We here show that our two prey-focusing methods for studying the effects of predation could provide valuable information on predator-related mortality in insects. Even though the statistic relationship between grasshopper survival and predator presence was weak, the strong intercorrelations between grazing and grasshopper mortality on the one hand and between predator presence and grazing on the other hand, suggest that predators might indeed deserve some stronger consideration for conserving insects at the brink of extinction. Generally, there are only a very few studies on the predation effects of birds on insects (e.g. Bael et al., 2008) and most of them are either focusing on pest management (e.g. Jones et al., 2005) or target exclusively larval stages (e.g. Drozdova et al., 2013). Increased predation pressure caused by synanthropic insectivorous birds may however represent a plausible threat - particularly to microendemic, immobile or highly specialized species. The case of the Crau plain grasshopper shows that the simple protection of a habitat does not save a species from extinction and that threat identification is a basic but essential step to adapt conservation management adequately. Our experimental approach to quantify predation risk from the preys' perspective should therefore encourage researchers with interest on predation effects on insects to carry out similar studies. Moreover, the influence of grazing on the presence of avian predators deserves more attention in the context of insect conservation. So far, the interaction of grazing, birds and insects was mainly investigated from a bird conservation perspective, aiming to preserve insects as food source (e.g. Atkinson et al., 2004; Dennis et al., 2007). This approach is of course valuable, as insects, and particularly grasshoppers, represent a primary food source for many threatened bird species. Our study shows, however, that it is also worth to switch the focus and consider the preys' perspective, if we want to reveal the subtle interactions in grazed ecosystems with the aim to preserve global biodiversity.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Prof. Dr. Axel Hochkirch reports equipment, drugs, or supplies and travel were provided by Mohamed bin Zayed Species Conservation Fund. Dr. Linda Broeder reports financial support and travel were provided by Studienstiftung des deutschen Volkes. Dr. Laurent Tatin reports administrative support and equipment, drugs, or supplies were provided by Coussouls de Crau national nature reserve. Dr. Laurent Tatin reports administrative support was provided by Direction regionale environnement PACA. Dr. Laurent Tatin reports a relationship with National Geographic Society that includes: funding grants. Dr. Laurent Tatin reports a relationship with Department of Bouches-du-Rhône that includes: funding grants. Dr. Laurent Tatin reports a relationship with Direction regionale environnement PACA that includes: funding grants.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02485](https://doi.org/10.1016/j.gecco.2023.e02485).

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