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An investigation of patch occupancy and dispersal by third to final instar nymphs of *Brachytrupes megacephalus* Lefèbvre, 1827 (Orthoptera: Gryllidae: Gryllinae) across the sand dune biotope at the Għadira Nature Reserve, Malta

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Abstract

Dispersal patterns of third, fourth and fifth instar nymphs of the stenoecious gryllid, *Brachytrupes megacephalus* (Lefèbvre, 1827), are investigated on the sand dune within the Għadira Nature Reserve, a remnant habitat patch forming part of the core area that supports the largest population of the species in Malta. Field investigations were carried out over a period of 11 weeks during a specific 75 minute time window, when nymphs are known to engage in subaerial activity at the mouth of their respective burrow. Climatic variables are examined in relation to abundance, while dispersal patterns are presented. The study shows that the predominant movement of nymphs across the terrain is northward, mainly to the northwest and the north-northeast. The present contribution also provides a summary of recommendations for conservation of the species, including an interdisciplinary approach to habitat management at multiple spatial scales.

Key words: Central Mediterranean, climatic variables, stenotopic, connectivity, conservation

Introduction

Brachytrupes megacephalus (Lefèbvre, 1827) is a relatively large crepuscular gryllid of Saharo-Mediterranean provenance. It is a species typical of psammophilous biocoenoses and occurs in both coastal and desert environments across parts of the Maghreb, as well as on coastal dunes in Italy and Malta (Chopard, 1943; Massa *et al*., 2012; Cassar, 2019, Cassar *et al*., 2021). The species is also known to occur on friable Quaternary conglomerates (with rebound hammer surface hardness readings ranging between 17.5 and 20 $N.mm^{-2}$), where an established population was discovered within a scree of the Aħrax promontory on the northern coast of Malta (Cassar & Conrad, 2008). This latter finding highlights the species' versatility, notwithstanding its stenoecious nature.

Much has been documented about the species, including its geographic range, distribution and biogeography, its habitat preferences, behavioural ecology and population dynamics, as well as its vulnerability to storm surges and sea-level rise, and its potential as an agricultural pest (Conti *et al*., 2014; Lakhdari *et al*., 2015; Petralia *et al*, 2015; Cassar *et al*., 2019). Cassar *et al*., (2021), provide a thorough overview on the above, in addition to listing disparities in behavioural traits between the different geographical locations within the species' range. This 2021 contribution also includes a comprehensive literature record on the species. However, beyond published findings on breeding, seasonal burrow structure, and adults' dispersal into vacant habitat patches, published observations on the behaviour of nymphs are somewhat limited.

The number of instar (moulting) stages that gryllid species are known to undergo varies appreciably across species (Taniguchi & Tomioka, 2003; Zhemchuzhnikov & Knyazev, 2012; Truman, 2019). In the case of *Brachytrupes* *megacephalus*, it was established that the species undergoes five instar stages (Lakhdari *et al*., 2015). This present work focuses on the dispersal of third, fourth and final instar nymphs during two months of summer (July to September); the latter part of September is when, in the Maltese islands, sub-adults are known to moult into mature adult phase (Cassar, 2019; Cassar *et al*., 2021). The sand dune environment and its immediate surroundings within the Għadira Nature Reserve, which is managed by Birdlife Malta, provided the *area of study* for the observations (Figure 1). The sand dune area falls within the boundaries of the chain-fenced reserve and is spatially relatively limited but the predominance of sand in the soils adjacent to the reserve, notwithstanding active cultivation, tends to complement the dune as far as the cricket is concerned.

Consequently, this provides a more extensive sandy habitat within the immediate landscape matrix onto which the crickets can disperse and thrive. It should be noted that the Għadira sand dune and adjacent sandy soil-dominated terrain support the largest population of *B. megacephalus* in the Maltese islands, even if numbers tend to fluctuate across the years (Cassar *et al*., 2021). A key advantage of the *area of study* is that it is free of stray or feral cats, which are known to hunt crickets at other nearby localities, with Dahlet ix-Xmajjar being a case in point (Cassar *et al*., 2018).

FIGURE 1. Aerial image of the *area of study* and its surrounding terrain (Source: Google Earth—imagery 23/5/2021).

Historical overview of the habitat: The coastal sand dune at Għadira was far more extensive in the past, and is estimated to have extended over around one and a half hectares (≈ 15,000 m^2) less than a century ago, merging, without defined delineation (a function of subsurface hydrological dynamics), with the adjacent saltmarsh environment; this estimation excludes the conversion of sand dune habitat into cultivated plots in historical times, so the dune is expected to have been far larger prior to the expansion of agriculture in antiquity. Indeed, the terrain in the area had been undergoing topographic modification since, at least, the era of the Knights of St John, when salinas (salt-making enclosures) were constructed and operated for some time. The *Saline Vecchie*, as they were referred to, already appear in ancient 17th century maps; one such example is *MELITE INSVLA* of 1664–1665, published by Blaeu atlases (Blaeu, J. Amsterdam—Old Maps online, accessed 26 March 2023).

During the latter half of the previous century, the area continued to undergo various modifications, including some arguably misguided initiatives that were largely incongruent with sand dune biotope conservation. For example, tree-planting activities carried out during the 1970s and 1980s saw the introduction of species alien to the Maltese islands, such as acacia and eucalyptus, or the planting of indigenous species (such as pines) 'out of ecological context'; this led to an alteration of the habitat's dynamics and ecological character. The strategic objective behind tree-planting was to discourage picnicking and camping. However, as the saplings matured and the canopy became more consolidated, dunal species were gradually displaced both physically and through the significant shading created. Moreover, the chemical structure of the dune's sandy soils is expected to have been impacted since pine needles are known to acidify surface substrate to a fair extent, while allelopathic acacias are renowned for preventing understorey vegetation from establishing itself around the trees. As a result, dune flora coverage declined markedly during the years that followed, while formerly mobile sands became more consolidated and compact. Consequent to measures undertaken to prevent illicit breaches by poachers into the reserve in the 1980s, sediment transport dynamics were also impacted through the creation of physical barriers (a shallow ditch, an embankment, and a chain fence), which had a negative influence on foredune mass and coherence. In recent years, however, specific measures have been implemented to improve the dune biotope. Birdlife Malta, under the direction of two of the present authors [MG and DA], is carrying out targeted interventions with a view to improve and extend the habitat for *B. megacephalus*. Aeolian dynamics and dune flora have since begun to re-establish themselves, albeit gradually.

Currently, the dunal patch characterised by exposed sand (that is, areas within the dune not shaded by the tree canopy) within the precincts of the reserve, measures less than .20 of a hectare (< 2000 m^2). Although the opportunity for foredune development is not presently optimal for aeolian dynamics to occur (mostly due to the aforementioned physical barriers that impede sediment transport processes such as suspension, saltation and surface creep), the dune sequence can best be ascribed to the 'fixed dune' on the basis of morphological expression and associated flora.

Methodology

Fieldwork entailed searching for cricket activity at the burrow entrance, between approximately 05.45 and 07:00 AM (GMT+2), by a group of observers consisting of between four and six individuals. Field observations were conducted each week, for eleven weeks, between July 15th and September 23rd, 2022, during which observers essentially placed a wooden marker with a coloured pennant (mini flag markers) wherever a nymph was spotted at the entrance of its burrow. A different pennant colour was used for each week, while vacant burrow entrances were excluded from weekly counts.

Sightings were logged using a handheld GPS device and the data was saved as GPX files. These were subsequently imported into a GIS environment for visualisation. Markers for each observation period (OP) were organised as separate layers for which heat maps were generated. To ensure consistency across the generated images, all colour bars were normalised. The maps therefore not only show the density distribution but also demonstrate how the number and location of sightings changed over the research period.

Meteorological information was obtained from a weather station located on the coast at Cirkewwa (at a beeline distance of 2.76 km from the *area of study*), which is managed by the Oceanography Malta Research Group within the Department of Geosciences (University of Malta). Data recorded, comprising various parameters (wind speed, gust and direction; air temperature; atmospheric pressure; and humidity), between 03:45 to 05:00 UTC (corresponding to 05:45 to 07:00 local Malta time) were averaged for the duration of the sampling period. Where anomalies in the abundance of individuals were noted, prevailing conditions of previous nights for atmospheric pressure, wind (speed and direction) and precipitation, were also examined, in addition to meteorological data during field observations (presented below).

To investigate potential associations between meteorological parameters and the number of individuals, the data was imported and processed further in IBM SPSS. Bivariate Pearson correlation with a two-tailed significance test was run on all pairs of variables. In addition to count attribute (absolute frequencies), the count interval, i.e., the difference in the number of observations between consecutive survey dates, was included. This allowed an assessment of variations in abundance rather than relying solely on the absolute number of individuals counted.

Results

In analysing spatial distribution within the *area of study* (inclusive of those sectors that are still afforested), the species' habitat preference becomes quite evident. Concentrations of individuals on the open sandy areas of the dune clearly demonstrate the cricket's preference for areas with loose surface sediment, unencumbered by dense vegetation, with only a handful of individuals observed within the afforested zone over the entire eleven weeks of observations (Figure 2).

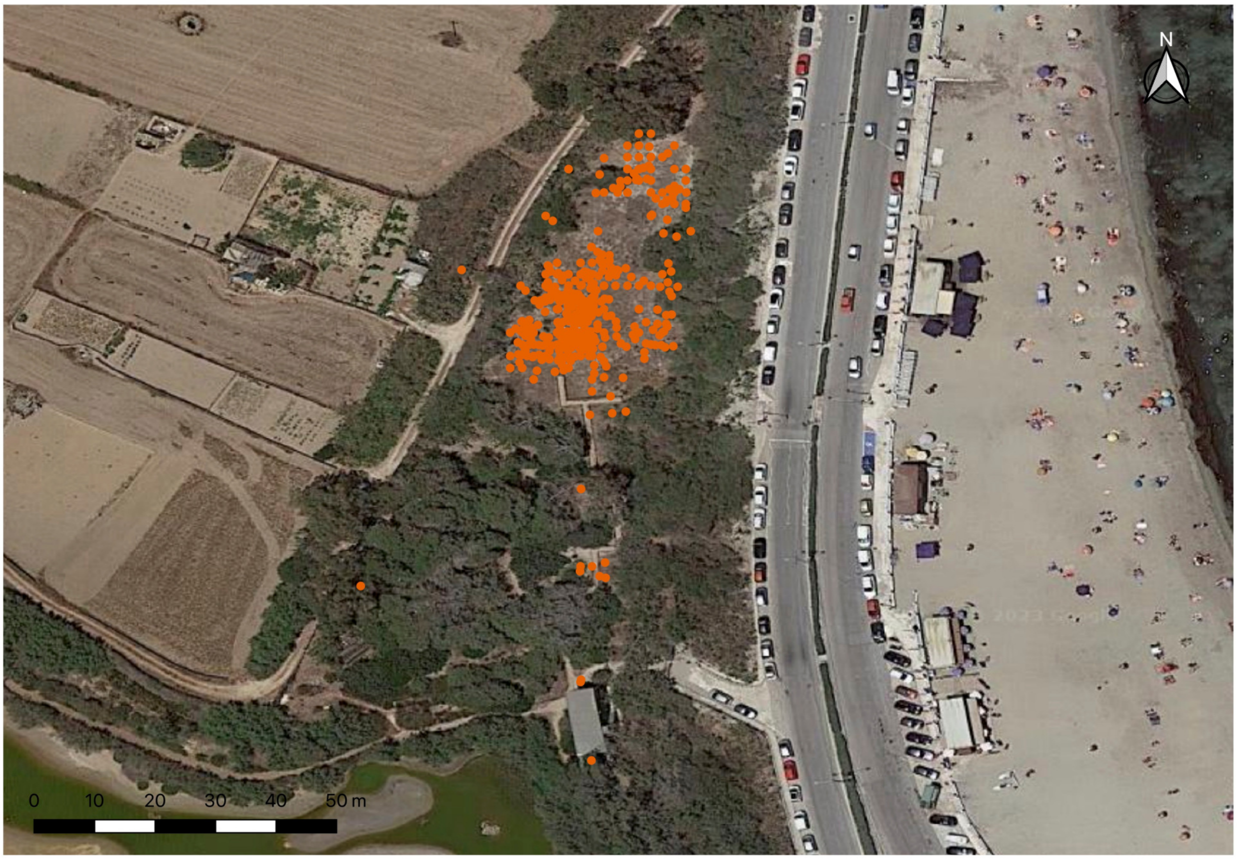

FIGURE 2. The high concentration of individuals on the sand dune biotope patch devoid of trees demonstrates a preference for such habitat conditions (each orange dot represents a single sighting record).

As outlined in the Methodology, data for each weekly observation period (OP 1–11) of individual nymphs at the mouth of their respective burrow, between 15th July and 23rd September 2022, was organised as a separate layer. Heat maps were generated for the first ten observation periods (weeks 1–10). OP11 (23rd September) was omitted in view of the fact that only a single specimen was recorded (this observation was nonetheless included in Figures 2 and 3).

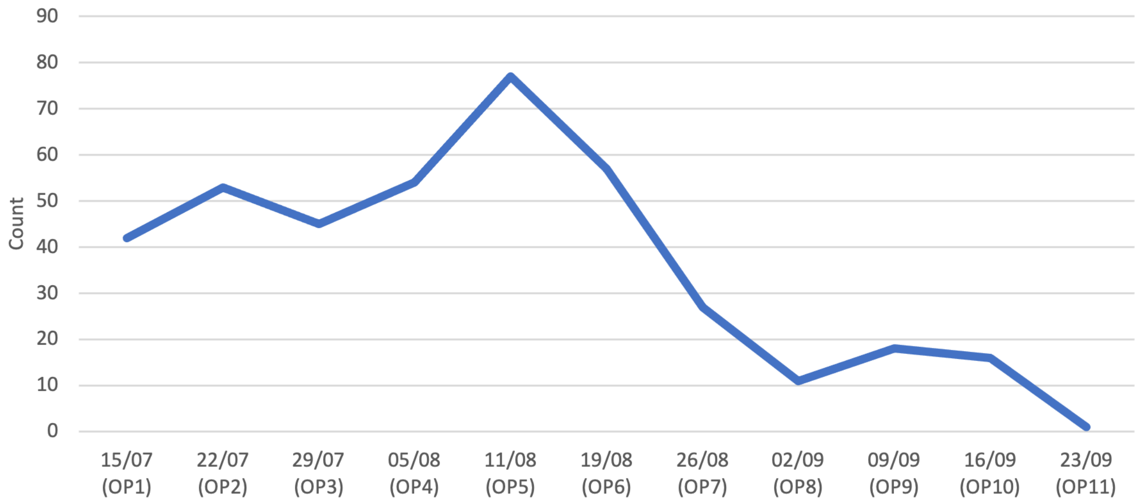

FIGURE 3. Abundance across the eleven weeks of field observations on the *area of study* and its immediate surroundings.

In terms of abundance (Figure 3), the highest number of individuals was registered on 11 August (OP5), when a total of 77 individuals was recorded. Overall, numbers of nymphs recorded tended to increase from week to week between OP1 (15.VII) and OP5 (11.VIII), with a slight dip being registered during OP3 (29.VII). Subsequent to the OP5 peak, abundance began to decline; individuals that had been steadily moving towards the northern boundaries of the reserve were presumably dispersing onto adjacent terrain. Another somewhat significant dip was registered between OP6 (19.VIII), when 57 individuals were recorded, and OP7 (26.VIII) when 27 individuals were recorded. In terms of trend, another anomaly was noted during OP8 (02.IX), when numbers decreased to 11 individuals and then rose to 18 the following week (09.IX).

The heat maps show spatial distribution and density across the *area of study* and its immediate surroundings; in comparing data of weekly sightings, the general direction of dispersal that can be discerned is, overall, northerly (Figure 4). Although minor exceptions did occur, the vast majority of individuals diffused towards the north-northeast (NNE) and the northwest (NW), in the direction of terrain harbouring well drained sandy soils and manifestly away from the saline marshland and afforested areas, where soil moisture and compaction are evidently higher in view of the hydrodynamic processes at play in proximity of the wetland. A key consideration that ought to be factored in is *(i)* the unspecified rate of mortality among nymphs (e.g., through natural predation by skinks, micro-mammals, etc.), and *(ii)* the number of sub-adults that actually remain on the sand dune within the reserve after they reach adult phase, as dispersal eases pressures posed by density within the niche.

Climatic conditions prevalent during field observation periods were examined for any potential correlation with nymph abundance (Figures 5–7). From the onset, it should be noted that the *area of study* during observation periods (inclusive of the twelve hours prior to each OP) did not experience any significant decline in atmospheric pressure. The barometric range across the different observation periods varied from *shallow low* to *standard* (normal at sea-level), specifically from 1007.8 to 1013.2 hPa (*or* mBar).

While low temperatures are known to influence stridulatory activity during the mating season in spring (Cassar, 2019; Cassar *et al*., 2021), air temperatures during nymph dispersal observations (15th July–16th September), which fluctuated between 25.5° C and 29.3° C (Figure 5), are not expected to have unduly influenced subaerial activity. Although air temperature is a critical variable, adult crickets have been observed outside their burrows in spring (stridulating in the case of males and scurrying across the terrain in the case of females) at ambient air temperatures of between 16° C and 21° C; on at least one occasion at Għadira, stridulatory activity continued, albeit limited, when ground level air temperatures fell to 14° C (Cassar, 2019). Given that the lowest recorded temperature during field observations for the present contribution was 25.5° C (OP1—15th July), ground air temperature, considered in isolation, does not appear to have had any significant impact on nymphs' subaerial dispersal. However, as demonstrated and further discussed below, the influence of climate could in reality be somewhat complex because of the interdependence of different climatic variables.

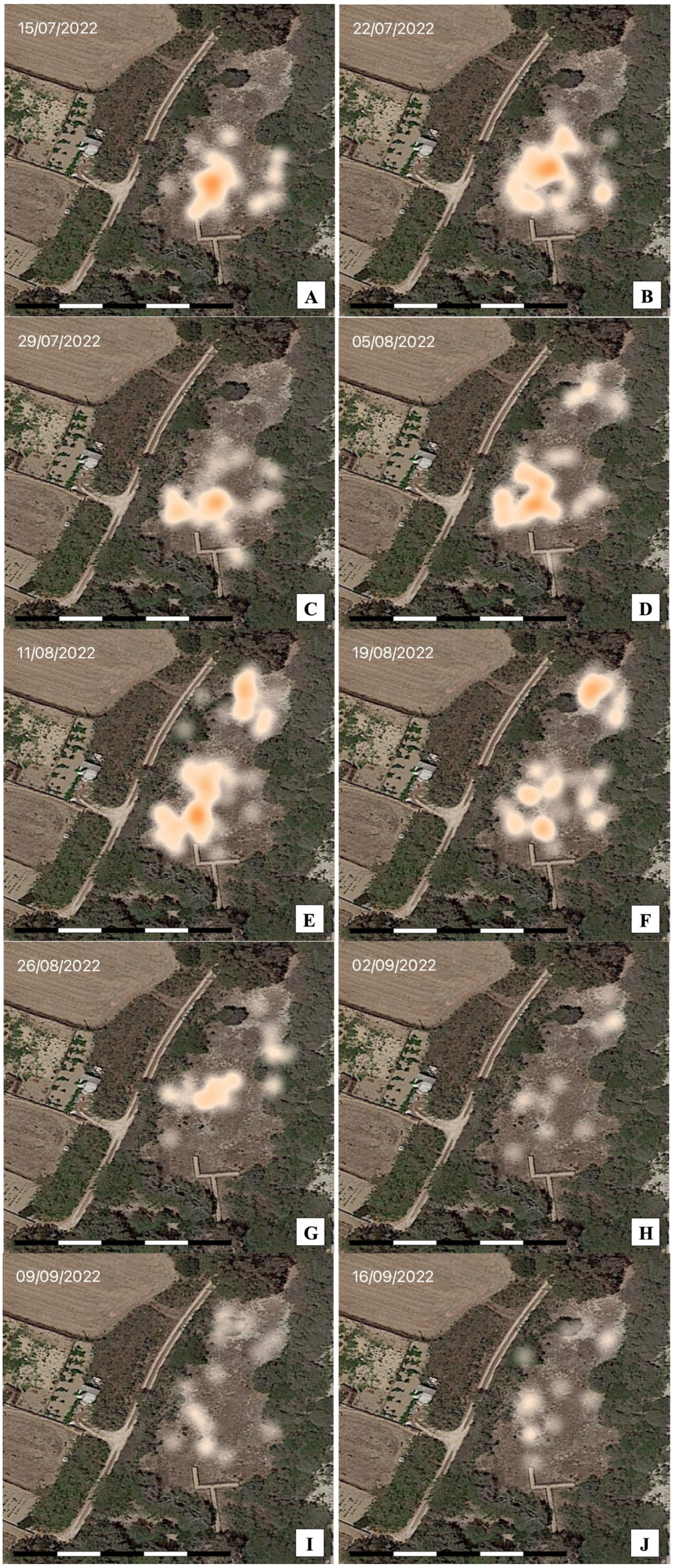

FIGURE 4 (A–J). Heat maps based on weekly observation data of *Brachytrupes megacephalus* third, fourth and fifth instar nymphs at their respective burrow entrance—*area of study*: sand dune, Għadira Nature Reserve.

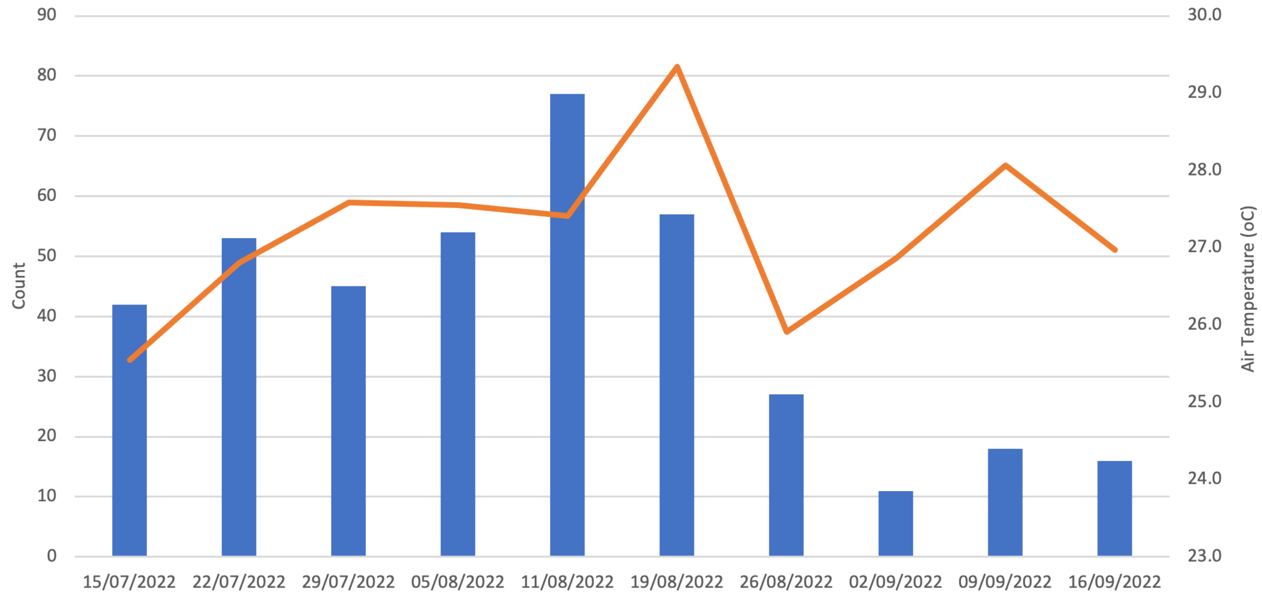

FIGURE 5. Air temperature for observation periods 1–10; the highest nymph count was that of 77 individuals (OP5) and the lowest was that of 11 individuals (OP8).

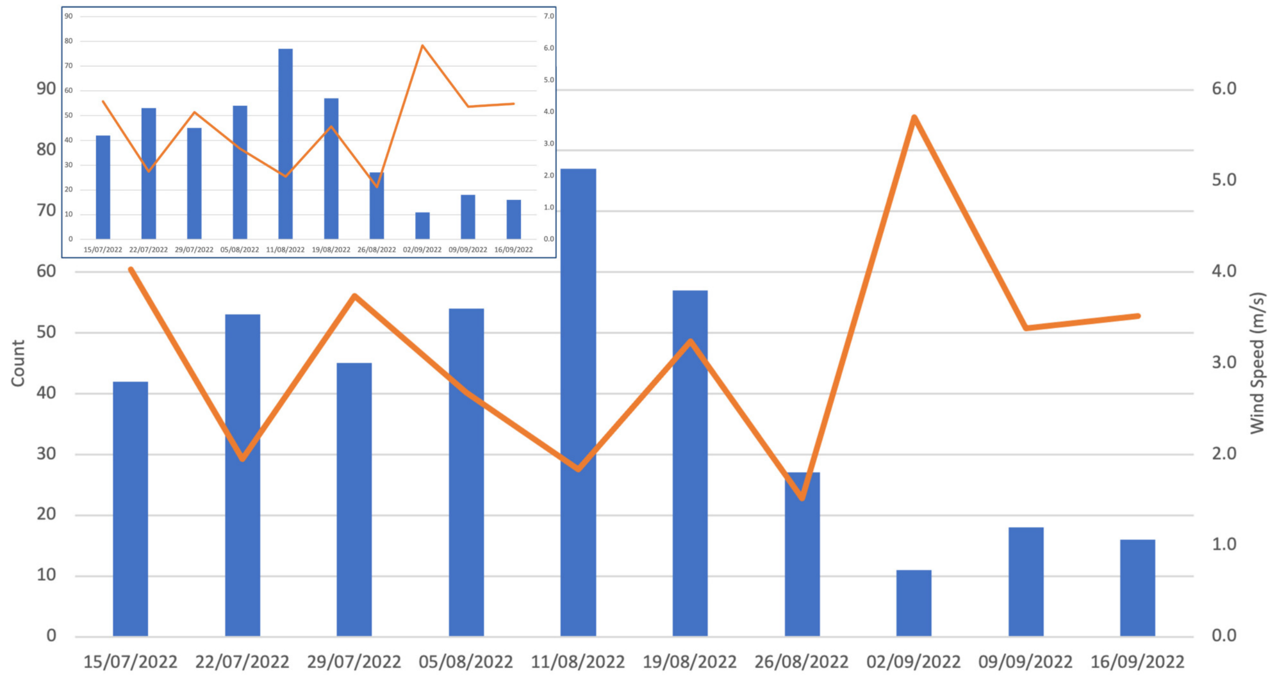

FIGURE 6. Sustained wind speed (main chart) and accompanying wind gusts (inset) are practically aligned, which indicates a quasi-constant wind during observation periods.

Wind is another important climatic variable. The Għadira Nature Reserve lies on a graben nestled between the elevated karstland at Biskra on its southern flank and a horst, known as Marfa Ridge, to its north. The resulting topographic relief provides a degree of shelter from winds blowing directly from the north and from the south. However, in view of the graben's alignment, the sand dune remains exposed to north-easterlies, westerlies, and the prevailing northwest, while less so to other directional winds (Figure 1).

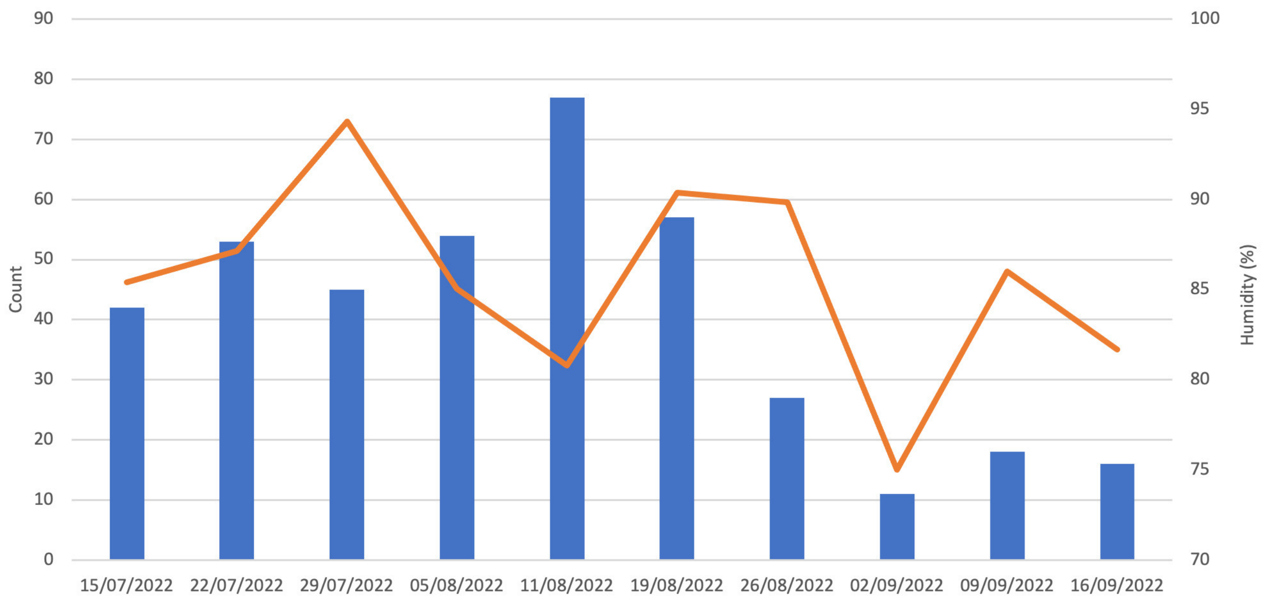

FIGURE 7. Humidity chart across observation periods with a range varying from 75% to 94%. Notwithstanding the high level of humidity registered on some days, no precipitation was recorded during or immediately prior to field sessions.

During periods of observation (Figure 6), the wind blew from the west at 6 kts during OP1 (15.VII), the northeast at > 5 kts during OP3 (29.VII) and from the northwest at > 10 kts during OP8 (02.IX). Being the first field observation for the present study, OP1 is being regarded as a baseline observation. During the subsequent OP3 and OP6, numbers appeared to dip, especially during the latter (OP6), when wind speed and wind gusts reached 5.7 and 6.1 m/s, respectively. The cooling effect by wind-chill resulting from these northern winds at daybreak were also considered; however, temperatures never reached the effective threshold of 10° C within which real-feel temperatures could have had an impact. During other observation periods, the wind was either insignificant in terms of speed or else it blew from directions from which the sand dune was sheltered by topography.

Humidity levels were always relatively high during field observation sessions, with readings varying from 75% (OP8) to 94% (OP3); nine of the ten observation periods registered humidity levels > 80% (Figure 7). However, no precipitation was registered during any of the field sessions or within twelve hours prior. In the absence of any rains and in combination with the typically dry, hot summer weather, surface sediments within the dune were predictably dry.

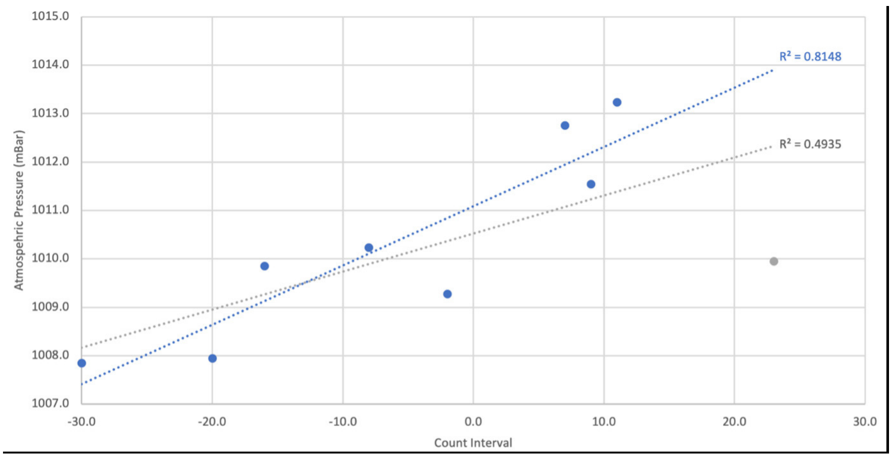

FIGURE 8. Correlation between atmospheric pressure and the count interval (difference in the count between successive, weekly observation periods) with trendlines for all points (grey) and when not considering the only outlier (blue).

The correlation matrix (TABLE 1) revealed a significant and meaningful association (at the 0.05 level) between the count interval and atmospheric pressure (Figure 8). This strong relationship only deviated on the 11th of August (OP5), when a notable presence of individuals was recorded despite relatively stable atmospheric pressure; specifically, a total of 77 individuals (23 more individuals than the count on OP4) were observed. The coefficient of determination (R^2) for the dataset was calculated as 0.4935, indicating a moderate level of explanatory power. Upon removing this outlier, R^2 improved to 0.8148. This suggests that atmospheric pressure, along with other associated meteorological parameters, potentially influences the subaerial presence of *Brachytrupes megacephalus*; however, further research is necessary to confirm this correlation.

TABLE 1. Matrix summarising the bivariate Pearson correlation values (top row) and the corresponding p-values (bottom row) for all the variables evaluated. Values in bold show statistically significant correlations.

	Count	Count Interval	Wind Speed (m/s)	Wind Gust (m/s)	Wind Direction (° N)	Air Temp (° C)	Atm Pressure (mBar)	Humidity (%)	Heat Index
Count	1.000	0.479 (0.192)	-0.549 (0.101)	-0.618 (0.057)	-0.098 (0788)	0.268 (0.455)	0.058 (0.873)	0.280 (0.434)	0.300 (0.399)
Count Interval	0.479 (0.192)	1.000	-0.271 (0.480)	-0.237 (0.538)	0.088 (0.823)	0.101 (0.796)	**0.702 (0.035)**	-0.267 (0.480)	0.063 (0.873)
Wind Speed (m/s)	-0.549 (0.101)	-0.271 (0.480)	1.000	**0.988 (< 0.001)**	0.280 (0.433)	0.031 (0.932)	0.020 (0.955)	-0.410 (0.239)	0.048 (0.896)
Wind Gust (m/s)	-0.618 (0.057)	-0.237 (0.538)	**0.988 (< 0.001)**	1.000	0.253 (0.481)	0.064 (0.860)	0.045 (0.902)	-0.417 (0.231)	0.071 (0.845)
Wind Direction (° N)	-0.098 (0.788)	0.088 (0.823)	0.280 (0.433)	0.253 (0.481)	1.000	-0.106 (0.770)	0.386 (0.271)	-0.475 (0.166)	-0.162 (0.654)
Air Temp (° C)	0.268 (0.455)	0.101 (0.796)	0.031 (0.932)	0.064 (0.860)	-0.106 (0.770)	1.000	-0.143 (0.693)	0.214 (0.553)	**0.976 (<0.001)**
Atm Pressure (mBar)	0.058 (0.873)	**0.702 (0.035)**	0.020 (0.955)	0.045 (0.902)	0.386 (0.271)	-0.143 (0.693)	1.000	-0.078 (0.831)	-0.107 (0.769)
Humidity (%)	0.280 (0.434)	-0.267 (0.480)	-0.410 (0.239)	-0.417 (0.231)	-0.475 (0.166)	0.214 (0.553)	-0.078 (0.831)	1.000	0.359 (0.309)
Heat Index	0.300 (0.399)	0.063 (0.873)	0.048 (0.896)	0.071 (0.845)	-0.162 (0.654)	**0.976 (<0.001)**	-0.107 (0.769)	0.359 (0.309)	1.000

Discussion

A key factor upon which spatial distribution depends is typically competition. Accordingly, the capacity of *B. megacephalus* to disperse across suitable habitat is crucial. This is particularly the case as nymphs undergo hemimetabolous development, requiring more resources as they progress through successive immature phases. Space becomes even more critical once the mature adult phase is reached, not only in terms of competition for food resources required by a larger organism, but also in view of reproductive competition.

This stenoecious species' complex competition-related behaviour across different seasons has been thoroughly demonstrated by disparities in tunnel development (layout, depth, and spatial density) during and outside its breeding season, in spring and mid-summer to early autumn, respectively. Variances in ambient conditions, notably air temperatures but more importantly ground moisture, also have an influence on burrowing activity, including the shape, size, and angle of repose of the subaerial mound formed by the excavating organism (Cassar, 2019, Cassar *et al*., 2021). Evidence of disparities in patch occupancy between spring and early autumn of 2018 was demonstrated by field observations carried out over a specific *area of study*, adjacent to the Għadira Nature Reserve, measuring just over 80 m^2. During the peak of the breeding season (mid-April), the total number of in-situ stridulating males

(Figure 9) did not exceed nine individuals (this excludes female individuals that were attracted from adjoining habitat patches), while the total number of sub-adult (fifth instar) individuals of both sexes recorded on the exact study plot in early autumn was that of 59. Soon after this observation, the number declined appreciably as sub-adults underwent the final phase of hemimetabolous metamorphosis and adult forms gradually dispersed across adjacent habitat (*Cassar/Conrad: field notes, 2018*; Cassar *et al*., 2021).

It is not entirely clear why third, fourth, and final instar nymphs exit their burrows at dawn more readily than first and second instar individuals. While published observations on populations in south-eastern Algeria have indicated that all five nymphal phases tend to appear on the surface at dawn within the hyper-arid desert environment of Oued Righ near Touggourt (Lakhdari *et al*., 2015), it seems that early instar nymphs in Malta tend to venture outside their tunnel complex far less frequently. At first light, nymphs have been observed pushing small quantities of loose sand out of the tunnel. However, it has also been noted that they subsequently lie practically motionless, unless disturbed, at the mouth of the burrow for a length of time. Since there is no means of appraising the degree of competition for resources, patch quality and habitat extent from their subterranean burrows, it is postulated that the reason for such behaviour is patch occupancy, that is, to gauge density of other individuals in proximity of their respective burrow. Further research is necessary to confirm this.

The results obtained demonstrate a relatively well-defined trend in the northward movement of nymphs. Habitat quality and competition are assumed the primary drivers of patch-occupancy dynamics at play, as nymphs undergo metamorphosis and develop into larger instars. As the need for more space and resources increases, nymphs would gradually begin to radiate towards the spatially open terrain characterised by sandy soils, consequentially triggering a shift of the individuals' habitat niche centre.

FIGURE 9. A stridulating male at the mouth of its burrow. The wide mouth of the burrow serves as an 'acoustic chamber' for amplification (Photo: J.J. Borg).

The coastal dune at Ghadira is totally encircled by a major thoroughfare to the east, active cultivation on its northern and western flanks, and the saline marshland to the south. The only possibility for expansion of the dune biotope is within itself, through the gradual and strategic elimination of some of the trees, which lead to fragmentation of the cricket's habitat. A reduction in extent of the canopy and the shade it casts will effectively lead to the potential recovery of open sandy substrate, thus paving the way for future ecological restoration. Such a measure will afford *B. megacephalus* additional habitat, while also reducing physical barriers and facilitating better connectivity with surrounding habitat patches beyond the reserve precincts.

Conclusions

Brachytrupes megacephalus is protected under the EU Habitats Directive—92/43/EEC (consolidated 2007), Annex II and Annex IV—and the Bern Convention—Annex 1 Res. 6 (1998): designation of Areas of Special Conservation Interest (ASCIs). The IUCN status for Europe/EU lists the species as Vulnerable. Its protection is thus critical and an obligation. To achieve such a goal, conservation planning and associated actions need to be formulated and implemented at multiple spatial scales.

The need to ensure that dune dynamics prevail is a major priority, not only for the species but for the entire biotope, given that successful conservation measures depend on broad-scale and long-term efforts. While it may seem inconceivable to remove the barriers (placed to ensure that no illicit breaches into the reserve for poaching purposes take place), or the dense shrubbery (strategically planted perimeter trees) in view of the major thoroughfare that abuts the reserve, some measures need to be taken to allow aeolian dynamics to prevail. Some form of wind channels can be considered to permit a natural flow of sand grains from the beach sector onto the dune within the reserve. This will not only nourish the sand dune biotope with fresh sediment, but also create appropriate conditions for mobile sands to generate foredune mass.

The importance of maintaining linkages with surrounding terrain cannot be overstated. As indicated above, the Għadira sand dune supports the largest concentration of *B. megacephalus* in the Maltese islands, with a population that is, however, seemingly unconnected with the metapopulation on the Aħrax promontory, where as many as twelve subpopulations are known to occur (Cassar *et al*., 2018; Cassar, 2019, Cassar *et al*., 2021). It is therefore critical that ecological connectivity is prioritised by the responsible entities, coupled with efforts in ecological restoration of the sand dune by way of increasing the area of exposed sandy substrate to allow indigenous dune flora to proliferate. Physical linkages with adjacent terrain, including agricultural areas where soils are predominately sandy, need to be actively pursued.

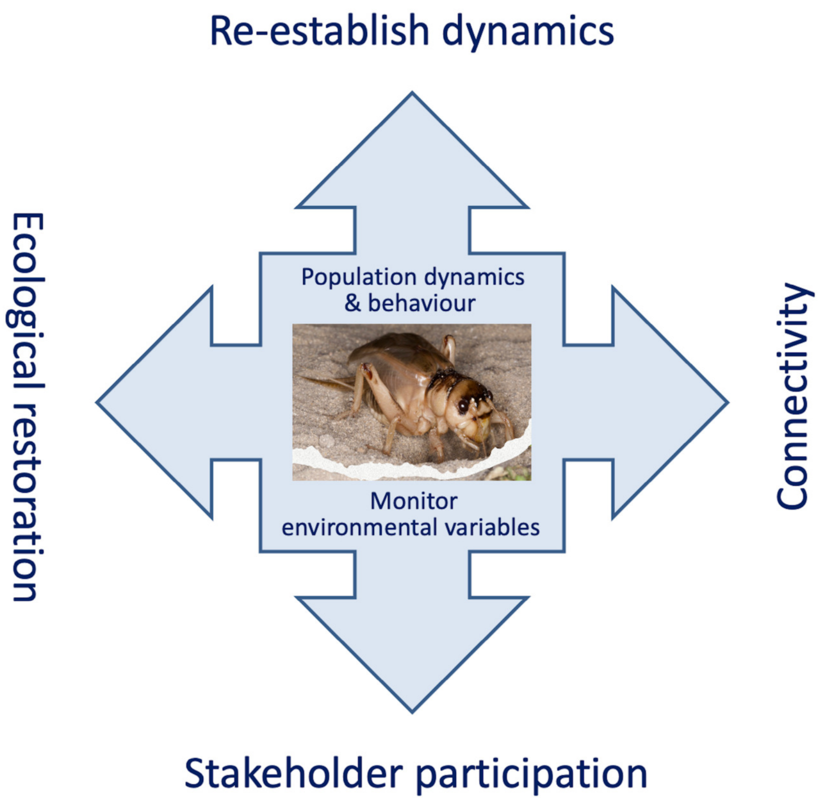

FIGURE 10. A multifaceted approach for the conservation of *Brachytrupes megacephalus* (Photo inset: J.J. Borg).

On this latter point, discussions with local stakeholders, namely members of the farming community, also need to be considered. Although, in the Maltese islands, the species is not regarded as a major agricultural pest, it is nonetheless still known to cause minor damage to some crops (Cassar *et al*., 2021). Engaging with farmers in the area, especially those landowners around the reserve, would seem pertinent. Finally, an established long-term monitoring initiative should be set up, with a view to observe trends, in respect to population numbers, behaviour and distribution over time.

In summary, the potential for the successful conservation of *B. megacephalus* within spatially restricted habitat patches, such as those within the Għadira Nature Reserve, lies in a multifaceted approach (Figure 10). First, habitat accessibility needs to be ensured, both in terms of geomorphology and associated vegetation. If aeolian dynamics can be re-established by way of resuming sediment transport processes, stenoecious dune vegetation will gradually regenerate itself (naturally or aided by techniques in restoration ecology, or both), resulting in a more extensive habitat patch. Second, the creation and maintenance of ecological corridors will further facilitate dispersal onto adjoining patches, which would minimise the level of vulnerability and any risk of isolation due to habitat fragmentation, and the effect of population bottlenecks; this will necessitate a planned strategic reduction in tree cover to allow less consolidated sands to expand. Third, where the potential of any conflict with stakeholders exists, due to competing land-uses and incompatible interests, appropriate measures in conflict resolution and management will need to be employed, possibly through participatory methods for decision-making. Such involvement has the potential of ensuring a better cooperation towards a common goal, as a result of which conservation efforts stand to benefit. Finally, while the afore-mentioned environmental management measures are being implemented, field studies involving population dynamics and behaviour, as well as the monitoring of climatic and other environmental variables in relation to the species, need to be undertaken on an on-going basis.

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