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Does interspecific competition drive patterns of habitat use in desert bat communities?

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Abstract Bodies of water are a key foraging habitat for insectivorous bats. Since water is a scarce and limiting resource in arid environments, bodies of open water may have a structuring effect on desert bat communities, resulting in temporal or spatial partitioning of bat activity. Using acoustic monitoring, we studied the spatial and temporal activity patterns of insectivorous bats over desert ponds, and hypothesised that sympatric bat species partition the foraging space above ponds based on interspecific competitive interactions. We used indirect measures of competition (niche overlap and competition coefficients from the regression method) and tested for differences in pond habitat selection and peak activity time over ponds. We examined the effect of changes in the activity of bat species on their potential competitors. We found that interspecific competition affects bat community structure and activity patterns. Competing species partitioned their use of ponds spatially, whereby each species was associated with different pond size and hydroperiod (the number of months a pond holds water) categories, as well as temporally, whereby their activity peaked at different hours of the night. The drying out of temporary ponds increased temporal partitioning over permanent ponds. Differences in the activity of species over ponds in response to the presence or absence of their competitors lend further support to the role of interspecific competition in structuring desert bat communities. We suggest that habitat use and night activity pattern of insectivorous bats in arid environments reflect the trade-offs between selection of preferred pond type or activity time and constraints posed by competitive interactions.

Keywords Resource partitioning · Competitive interactions · Chiroptera · Arid environments · Acoustic monitoring

Introduction

Resource competition is a dominant force structuring ecological communities (e.g. Alexandrou et al. 2011). The characteristic food and water scarcity of arid and semi-arid ecosystems (inclusively referred to here as arid environments) makes interspecific competition an important process structuring desert mammal communities (Polis 1991; Kelt et al. 1999). Since bat activity in arid environments concentrates near bodies of open water (e.g. Korine and Pinshow 2004; Rebelo and Carlos Brito 2006), and water is a scarce and limiting resource in arid environments (Noy-Meir 1973), sympatric bat species may compete for access to this limiting resource.

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Aggregations of large numbers of bats over scarce water sources in arid environments may limit physical access to the water and promote competition for the foraging space above the water surface (Findley 1993). In addition, bat species with separated roosting or foraging habitats, based on difference in their morphology, will overlap in their habitat use when drinking from small desert water sources (Adams and Thibault 2006). The congregation of desert animals around the crucial foraging habitat offered by the riparian communities suggests that fine-grain resource partitioning may take place within these keystone habitats (Williams et al. 2006). Hence, bodies of open water, like permanent and ephemeral desert ponds, may have a structuring effect on desert bat communities, resulting in temporal or spatial partitioning of bat activity.

Spatial partitioning of foraging habitats is recognised as the primary mechanism facilitating the coexistence of sympatric insectivorous bat species (Patterson et al. 2003). For example, Arlettaz (1999) found pronounced spatial segregation of primary foraging habitat between the morphologically similar sympatric bat species, *Myotis myotis* and *M. blythii*, whereby the former forages primarily in woody habitats, while the latter is associated with grassland habitats. Differences in wing morphology (e.g. Kingston et al. 2000), echolocation call structure (Siemers and Schnitzler 2004) and sensory ecology (Siemers and Swift 2006) were shown to contribute to niche differentiation among sympatric bat species.

Although temporal partitioning is regarded as the least common mode of resource partitioning (Schoener 1974), it has been identified in several bat communities. Sympatric insectivorous bats combine partitioning of peak nightly activity time with spatial partitioning of the foraging habitat when temporal foraging patterns overlap, to reduce interspecific competition (Kunz 1973). Moreover, fine-grain temporal partitioning of arrival time to small water holes exists between sympatric *Myotis* bat species in arid environments (Adams and Thibault 2006). However, Saunders and Barclay (1992) and Hickey et al. (1996) failed to find evidence of temporal partitioning among coexisting bat species.

Bats are one of the most diverse and successful groups of desert mammals (Carpenter 1969), yet there is a paucity of studies looking at interspecific competition and differential habitat use by desert bats. We studied the spatial and temporal activity patterns of insectivorous bats over desert ponds, focusing on interactions among the most common species because these species are expected to compete most intensely, and as a result resource partitioning should be more pronounced (Kingston et al. 2000).

We identified two sets of potentially competing species. The first, the *Pipistrellus/Hypsugo* group, includes *Pipistrellus kuhlii, Hypsugo bodenheimeri* and *Pipistrellus rueppelli*, three species that are similar morphologically and in their foraging modes. They are all small (body mass 2.6–6.2 g) and highly manoeuvrable, with relatively low wing loading and aspect ratio values (Norberg and Rayner 1987). They all forage in background cluttered habitats (Korine and Pinshow 2004), tend to forage over water bodies (Razgour et al. 2010) and have similar diets, which include a high proportion of Diptera and, to a lesser extent, Lepidoptera (Whitaker et al. 1994; Feldman et al. 2000). High overlap in diet, when coupled with the characteristic food limitation of desert ecosystems, indicates that interspecific competition for foraging space may be present (Kronfeld-Schor and Dayan 1999). Hence, these three species may compete for foraging space above ponds.

The second set of potential competitors includes two morphologically and behaviourally different species, *P. kuhlii* and the significantly larger *Tadarida teniotis* (mean body mass 27.2 g), a Lepidoptera specialist (Rydell and Arlettaz 1994) that forages in open spaces high above the ground (Whitaker et al. 1994; Korine and Pinshow 2004) owing to its fast, low manoeuvrability flight mode (Norberg and Rayner 1987). However, both are non-desert species (Yom-Tov and Kadmon 1998), whose abundance in the Negev Desert is thought to have increased in the past century following human settlement and irrigated agriculture (C. Korine, personal observations). As a result of their non-desert origin, these two species are not well adapted to conserve water (Marom et al. 2006, for *T. teniotis*), and use ponds for drinking at a greater frequency than any other species in the study area (Razgour et al. 2010). Owing to the unobstructed swoop zone requirements associated with manoeuvrability restrictions on bats drinking from ponds in flight (Tuttle et al. 2006), competition between these two species may be for physical access to the water surface for the purpose of drinking.

We hypothesised that bat species partition the foraging space above ponds based on interspecific competitive interactions. Therefore, we predicted that: (1) competing bat species will be associated with different ponds and pond size or hydroperiod categories (spatial habitat partitioning); (2) when using the same pond, the activity of competing species will peak at different times of the night (temporal partitioning); and (3) changes in the activity of bat species will affect the habitat use and night activity pattern of their competitors.

Materials and methods

The study was carried out in the Central Negev Highlands, Israel, an arid region with low precipitation and high inter- and intra-annual variability (mean precipitation 93.38 ± 39.23 mm/year; Meteorology Unit BIDR 2008).

We compared the bat assemblages over ten natural permanent and temporary ponds of different sizes along three adjacent valleys in the Matsok Ha'Zinim Nature Reserve (30°51′N, 34°53′E; Supplementary Material 1).

We used an ultrasonic bat detector (AnaBat II; Titley Electronics, Australia) to record bat activity over each pond for one whole night (from dusk to sunrise) every month between March and November 2007 and between March and May 2008. We recorded bat activity over temporary ponds until the ponds dried out (either the end of May or July). An AnaBat detector was placed at the longest end of each pond, on the ground, up to 1 m away from the pond edge, pointing upwards at a 45° angle towards the centre of the pond. The detection range of AnaBat detectors for aerial foraging bats is typically greater than 20 m (Collins and Jones 2009). Therefore, a detector would have sampled the majority of the airspace above all ponds but pond 2 (length 61.5 m), where the detector was placed at the edge of the centre of the pond pointing towards the widest section, thus covering the maximum airspace possible.

Since acoustic monitoring does not allow for the identification of individual bats, we used activity as a surrogate for density. This approach is common in studies of competition because of its greater relevance for ecological interactions and habitat selection (Mitchell et al. 1990). Bat activity was measured as the number of bat passes in each AnaBat recording file, whereby a pass is defined as a sequence of bat calls (Fenton 1970). Activity was standardised as the number of bat passes per hour of recording. We used the ratio of feeding buzzes (increased pulse repetition rate during the terminal phase of insect capture; Griffin et al. 1960) to bat passes as an indicator of the importance of the ponds' airspace for foraging.

The calls of the studied bat species do not overlap (Dietz 2005; Benda et al. 2008; Supplementary Material, Appendix 1) and are adequately recorded and distinguished to the species level using the AnaBat system. Calls with overlapping frequencies were assigned based on the remaining calls in the pass; however, a small proportion of the calls (approximately 1%) could not be adequately assign to a specific species and were therefore discarded from further analysis.

Each sampling night, we measured the maximum length, width and depth of the ponds, and multiplied these three variables to calculate an index of maximum pond volume. We divided the ponds into three size categories based on maximum pond volume. We further divided the ponds into three hydroperiod categories: permanent, semi-permanent (held water until mid-summer), and temporary (held water until the end of spring). We estimated percent of woody or herbaceous vegetation cover immediately adjacent to each pond (a measure of habitat clutter) following Korine and Pinshow (2004), and used ArcGIS (v.9.2, ESRI) to measure the distance between each pond and the nearest permanent pond (a measure of pond isolation) and cliff (a measure of pond accessibility and degree of habitat openness) (Supplementary Material, Appendix 2). To test whether temperature affects temporal patterns of bat activity, we measured the hourly night ambient temperature using iButtons® that were tied to the vegetation near each pond at approximately 0.5 m above the ground.

Data analysis

Although empirical methods are currently recognised as the more direct and reliable means of measuring competition (e.g. Abramsky et al. 1990), experimental manipulation may be impractical when studying animals like bats, which are capable of flight and long distance dispersal, and are difficult to study employing traditional ecological methods (Findley 1993). Hence, indirect measures may be more relevant for quantifying the presence and extent of competition in studies of bat communities.

We used Pianka's (1973) measure of niche overlap to quantify the extent of pond use overlap between these two sets of potential competitors. This is a measure of symmetric competition that quantifies the proportion of the resource used in common (O_{jk}), such that:

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where P_{ij} is the proportion that resource i is of the total resources used by species j; P_{ik} is the proportion that resource i is of the total resources used by species k; and n is the total number of resource states (the ten studied ponds).

To determine whether the extent of niche overlap is greater or less than would be expected by chance, we used the software EcoSim (v.7; Gotelli and Entsminger 2001) to generate 1,000 simulated matrices of randomised levels of activity (using Randomisation Algorithm 3) of the four species over the ten ponds and compare observed and randomly simulated extents of niche overlap. Bonferroni corrections were applied to retain the significance value at $P < 0.05$, resulting in significance level set at $P < 0.017$.

To estimate the presence and intensity of interspecific competition and determine competition coefficients from the census data, we used the regression method (Crowell and Pimm 1976), later modified by Rosenzweig et al. (1984) to account for habitat heterogeneity. The method uses a regression of the activity density of one species against that of its potential competitor at a set of homogenous sites, which differ only in the density of the two species. To eliminate the effect of site variability, the residuals of the regression of each species' activity against its significant habitat variables were used instead of species activity measures when quantifying the competitive interactions between two species. The slope of the regression was used as an estimate of the competition coefficient, α. The nature of the interaction was determined according to whether the slope was positive or negative, while the strength of the competitive interaction was determined by the steepness of the slope.

To avoid pseudo-replications due to repeated measures of ponds we only included in the regression analysis one measure of each pond, when it was at its maximum size ($n = 10$; Appendix 2). We performed backward stepwise multiple regressions on the activity of the four species against five pond microhabitat variables (measures of pond size—pond length and pond volume; measures of pond accessibility—percent of vegetation cover around the pond and distance to nearest cliff; and measure of isolation—distance of pond to nearest permanent pond). The number of months the pond held water, a measure of hydroperiod, was omitted from the analysis due to its strong correlation with pond volume ($R^2 = 0.7$, $F_{1,\ 8} = 19.6$, $P = 0.002$).

To measure resource partitioning in spring, when all ponds were present, we used chi square tests to compare the mean proportional activity of the four species over each pond, and tested for significant associations between potentially competing species and ponds, as well as pond size and pond hydroperiod categories.

To test whether competing bat species partition their nightly use of ponds temporally, we compared the peak activity time and night activity pattern of the different species over pond 10 during April 2007, when all species were present and active throughout the night, and in August 2007, when *P. kuhlii* and *T. teniotis* were present in the study area. Pond 10 concentrates high levels of activity of all competing species, perhaps due to its isolation (Supplementary Material 1), and is relatively short (15.8 m), and therefore may limit the amount of individuals that can use it simultaneously. To test the effect of seasonality, we compared the arrival time of *P. kuhlii* and *T. teniotis* to pond 10 between spring, when temporary ponds were present and bats could employ spatial partitioning, and summer, when the pond was isolated.

Because bats cannot be efficiently excluded from their foraging habitat, nor can their density be easily manipulated under field conditions, we used natural changes in the activity of species following seasonal movements away from the study area, as a surrogate for removal experiments. *P. rueppelli* and *H. bodenheimeri* were only present in the study area at high activity levels between March and April 2007 and between November 2007 and April 2008. Therefore, we were able to determine the effect of their presence on their potential competitor, *P. kuhlii,* by comparing its activity over three permanent ponds before and after the arrival of the two migrant species, using Wilcoxon's matched pairs test. We used chi square test to determine whether in the absence of its competitors, *P. kuhlii* still selected the same ponds and pond types. Finally, we used Kolmogorov–Smirnov tests to compare the distribution of *P. kuhlii*'s night activity over pond 10 between spring of 2007, when *P. rueppelli* and *H. bodenheimeri* were present and summer of 2007, when they were absent from the study area. Statistical analyses were performed with STATISTICA 7 (StatSoft) and SPSS (v.15). We considered results to be significant at $P < 0.05$.

Results

Species competitive interactions

High ratios of feeding buzzes to bat passes in the spring, when all competitors were present in the study area (*P. kuhlii*: 9.9 ± 4.5%; *H. bodenheimeri*: 15.3 ± 6.5%; and *P. rueppelli*: 16.5 ± 9%; Appendix 1), confirmed that the three *Pipistrellus*/*Hypsugo* species used all ponds for foraging.

The extent of overlap in pond use was greater than expected by chance between *P. kuhlii* and *T. teniotis* (Pianka's Measure of Niche Overlap: $O_{ij} = 0.74$, $P = 0.015$). However, niche overlap was not significantly different from random among the second group of competitors (*P. kuhlii* and *H. bodenheimeri*: $O_{jk} = 0.63$; *P. kuhlii* and *P. rueppelli*: $O_{jk} = 0.46$; and *H. bodenheimeri* and *P. rueppelli*: $O_{jk} = 0.46$).

Multiple regression of species activity over ponds against the five microhabitat variables revealed that the activity of all species increased with pond volume, and for *P. kuhlii* activity also decreased with pond length and increased with distance to the cliff (Table 1).

Once habitat heterogeneity was accounted for by regressing the activity of each species against its respective significant habitat variables, both sets of potentially competing species showed negative competitive interactions (Table 2). *H. bodenheimeri* exerted a particularly strong negative effect on *P. kuhlii* ($\alpha = -2.9$), while *P. kuhlii* negatively affected all its competitors, especially *T. teniotis* ($\alpha = -0.95$). In contrast, species that were not identified as potential competitors showed a positive or negligible effect on each other. Despite being identified as potential competitors, *H. bodenheimeri* had a strong positive effect on *P. rueppelli* (Table 2).

Table 1 Multiple regression of bat species against the five pond habitat variables

Species	Regression equation	R^2	F (*df*)	P
P. kuhlii	$Y = 1.28 - 0.5X_1 + 1.35X_2 + 0.12X_4$	0.85	11.5 (3, 6)	0.007
T. teniotis	$Y = -0.5 + 0.12X_2$	0.82	36.2 (1, 8)	<0.001
H. bodenheimeri	$Y = 0.46 + 0.16X_2$	0.78	28.7 (1, 8)	<0.001
P. rueppelli	$Y = -2.4 + 0.52X_2$	0.73	21.7 (1, 8)	0.002

X_1 pond length (m), X_2 square root pond volume (m^3), X_3 arcsin percent of vegetation cover around the pond, X_4 distance to nearest cliff (m), and X_5 distance to nearest permanent water source (m)

Table 2 The competitive effect (the slope of the regression: α) of species down the rows on species along the columns, based on the regression of their residuals

	Pipistrellus kuhlii	*Tadarida teniotis*	*Hypsugo bodenheimeri*	*Pipistrellus rueppelli*
Pipistrellus kuhlii		−0.95	−0.12	−0.52
Tadarida teniotis	−0.36		0.08	0.38
Hypsugo bodenheimeri	−2.9	4.9		3.1
Pipistrellus rueppelli	−0.91	1.8	0.23	

Spatial patterns of habitat use

The four potential competitors differed in their use of the different ponds (chi square: $\chi^2 = 365.1$, $df = 27$, $P < 0.001$), and pond types ($\chi^2 = 298.5$, $df = 15$, $P < 0.001$, Fig. 1). The individual standardised residuals of chi square show that pond size or hydroperiod categories preferred by one species are generally avoided by at least one of its potential competitors. *P. kuhlii* was most strongly associated with small temporary ponds (standardised residuals: $\chi = 7.3$) and avoided large permanent ponds ($\chi = -4.4$). *P. rueppelli*, on the other hand, preferred medium temporary ponds ($\chi = 8.4$), but avoided small ($\chi = -3.7$) and large ($\chi = -3.1$) temporary ponds. *T. teniotis* and *H. bodenheimeri* displayed similar patterns of pond type selection, as they were both associated with large permanent ponds ($\chi = 4.7$ and $\chi = 4.3$, respectively) and avoided medium ($\chi = -4$ and $\chi = -4.7$) and small ($\chi = -2.4$ and $\chi = -3.1$) temporary ponds. However, patterns of specific pond selection show that despite their common pond type preference the two species were associated with different ponds (*T. teniotis* with pond 10 and *H. bodenheimeri* with pond 2).

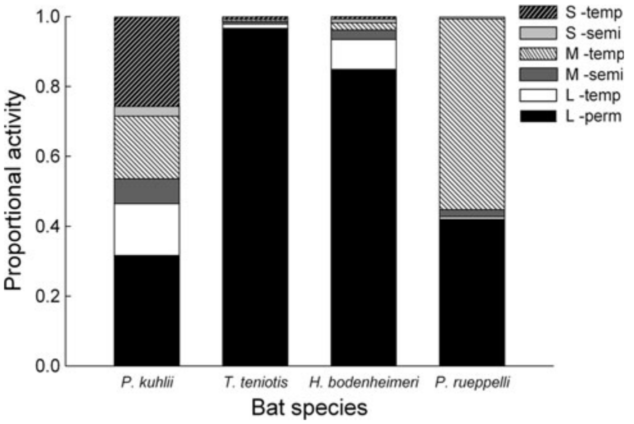

Fig. 1 Total number of passes per hour of *Pipistrellus kuhlii*, *Tadarida teniotis, Hypsugo bodenheimeri* and *P. rueppelli* over different pond size and hydroperiod categories (*L* large, *M* medium, *S* small, *perm* permanent, *semi* semi-permanent, *temp* temporary) in the spring of 2007 at the Negev Desert

Temporal patterns of pond use

Patterns of activity over pond 10, a large permanent pond differed between the three *Pipistrellus/Hypsugo* species (chi square $\chi^2 = 875.6$, $df = 18$, $P < 0.001$; Fig. 2), whereby the peak in their activity did not overlap and each species was associated with a different section of the night. *H. bodenheimeri* displayed a bimodal pattern of night activity, preferring the first (standardised chi square residuals $\chi = 5.2$) and last hours of the night ($\chi = 6.1$). In contrast, the activity of *P. kuhlii* and *P. rueppelli* was unimodal. *P. kuhlii* was associated with the 2nd–4th hours of the night ($\chi = 12.9$, $\chi = 10.2$ and $\chi = 10.5$), while *P. rueppelli* with the 5th and 6th hours of the night ($\chi = 11.6$ and $\chi = 5.8$).

Differences in night activity pattern were also identified between the second set of competitors ($\chi^2 = 164.4$, $df = 9$, $P < 0.001$), whereby the proportional nightly activity of *P. kuhlii* peaked when the activity of *T. teniotis* was at its lowest and vice versa. The hourly night activity of all species was not correlated with the hourly night ambient temperatures (all correlations $P > 0.05$).

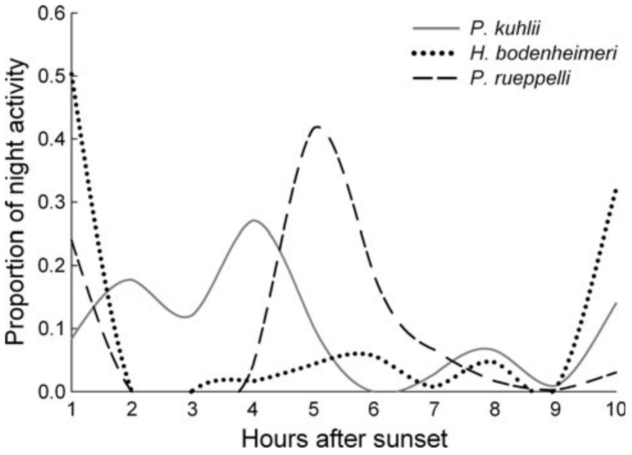

Fig. 2 Differences in peak activity time of *Pipistrellus kuhlii*, *Hypsugo bodenheimeri* and *P. rueppelli* over pond 10 in the spring of 2007 at the Negev Desert

Effect of seasonal changes in species composition

The activity of *P. kuhlii* over the three permanent ponds was higher during the months when *P. rueppelli* and *H. bodenheimeri* were absent from the study area (June–September 2007 and May 2008) than when they were present (April 2007, October 2007 and April 2008) (Wilcoxon matched pairs test $Z = 1.99$, $df = 6$, $P = 0.046$; Fig. 3). During the months when *P. rueppelli* and *H. bodenheimeri* were absent from the study area, but temporary ponds were still present, *P. kuhlii* was not associated with any pond, pond size or pond permanence categories (all standardised residuals were not significant). It only avoided pond 2 ($\chi = -3.9$), a pond strongly preferred by *T. teniotis* in summer ($\chi = 9.9$).

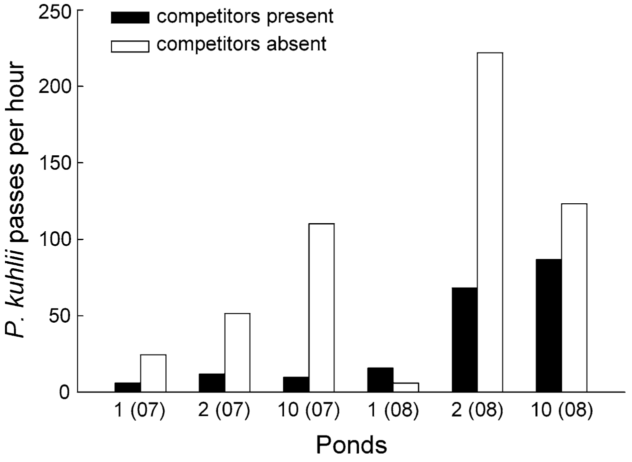

Fig. 3 Differences in the activity of *Pipistrellus kuhlii* over three permanent ponds (ponds *1*, *2* and *10*) between months when its competitors *Hypsugo bodenheimeri* and *P. rueppelli* were present versus absent from the study area, during the two sampling years 2007 (*07*) and 2008 (*08*)

Throughout the sampling period, *P. kuhlii* arrived to all ponds within the first hour after dusk. However, in spring, when *P. rueppelli* and *H. bodenheimeri* were present in the study area, the activity of *P. kuhlii* over pond 10, a pond used by all species, was lower and spread more evenly throughout the night than in summer, when it peaked at the beginning of the night, with 725 passes in the first hour after sunset, and was low for the remainder of the night. The distribution of nightly activity of *P. kuhlii* differed significantly between spring and summer (Kolmogorov–Smirnov test: max negative difference = −0.9, $P < 0.001$).

T. teniotis, on the other hand, arrived to pond 10 significantly later once adjacent temporary ponds dried out (one-way ANOVA, log transformed: $F_{1,12} = 30.95$, $P = 0.0001$). In spring 2007, when temporary ponds were present, it arrived on average less than half an hour after *P. kuhlii,* while in summer it arrived on average more than 4 h after its potential competitor. Consequently, differences in the night activity patterns of the two species were more pronounced during summer (summer: $\chi^2 = 873.5$; spring: $\chi^2 = 164.4$; Fig. 4).

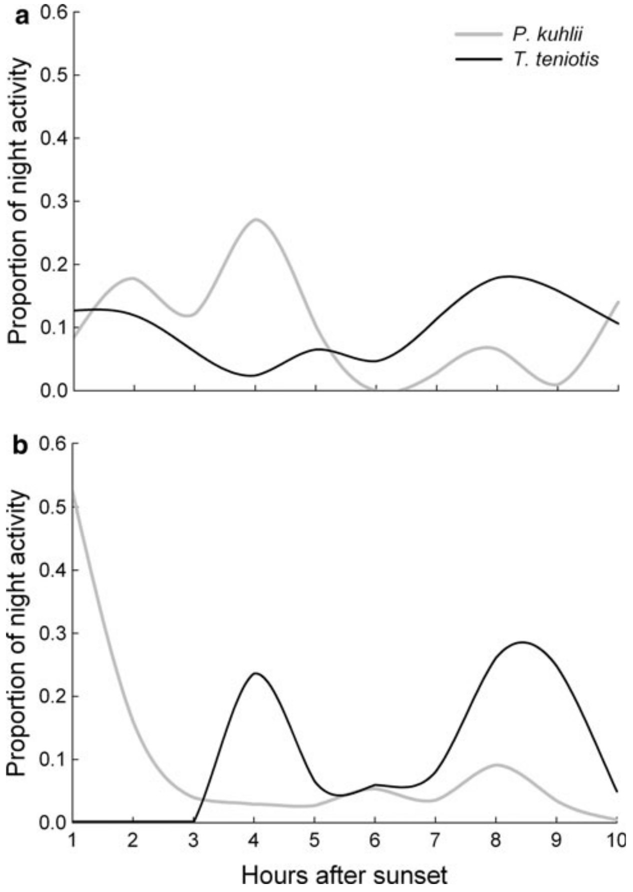

Fig. 4 Comparison of the nocturnal distribution of activity of *Pipistrellus kuhlii* and *Tadarida teniotis* over pond 10 during the spring of 2007 (**a**) and the summer of 2007 (**b**) in the Negev Desert

Discussion

The community composition of desert bats is highly dynamic and constantly changing because of the need to congregate around few available water sources, many of which are temporary and vary in size throughout the season. While spatial partitioning of pond and pond type use in our study took place in spring, the desiccation of temporary ponds in summer reduced the scope for spatial partitioning and increased temporal partitioning of night activity among species that remained in the area. Chesson (2000) suggested that such seasonal changes in the size and availability of temporary ponds may provide the temporal variation in environmental conditions necessary for the coexistence of species with similar ecologies but different responses to the varying environment.

The role of interspecific competition

Interspecific competition is an important mechanism structuring ecological communities by determining the number and type of coexisting species and by affecting patterns of habitat use (Schoener 1983). Interspecific competition drives morphological differentiation and influences the phenotypic structure of insectivorous bat communities (Kingston et al. 2000; Schoeman and Jacobs 2008). The role of competition in structuring bat communities may be particularly pronounced in arid environments due to the characteristics resource limitation of these ecosystems (Noy-Meir 1973; Findley 1993). Indeed, our study shows that in the Negev Desert interspecific competition appears to influence the structure of insectivorous bat assemblages over ponds. Measures of niche overlap show no significant overlap in the use of ponds among the *Pipistrellus/Hypsugo* group of competitors, while the regression method identified potential negative competitive interactions between most studied species. Lack of negative competitive interactions among potential competitors, however, is not necessarily due to an absence of competition but could also be the result of habitat segregation in response to past interspecific competitive interactions (“the ghost of competition past”) (Rosenzweig 1981).

Measures of niche overlap cannot be used to estimate the intensity of competition; however, they can be used to describe the potential for competition if resources are in short supply (Abrams 1980). Since the availability of water and in particular natural larger water bodies is limited in desert environments (Noy-Meir 1973), lack of significant niche overlap implies the presence of interspecific competition. Competition, in our study, appears to be for access to the water surface, either for drinking or foraging. Feeding buzz activity ratios calculated in our study are comparable to those used by previous studies to indicate the presence of feeding activity (e.g. Vaughan et al. 1997: 8%; Walsh and Harris 1996: 20%), thus lending further support to the use of desert ponds as foraging sites by *Pipistrellus/Hypsugo* species.

Although we were unable to manipulate bat densities or carry out exclusion experiments to test our predictions, changes in the night activity patterns and pond habitat use of *P. kuhlii* in response to natural seasonal changes in the activity of *H. bodenheimeri* and *P. rueppelli* may be regarded as equivalent to a shift in patterns of habitat use following experimental removal of competitors, and therefore indicate the presence of ongoing interspecific competition (Abramsky et al. 2005). Because *P. kuhlii* is not restricted in its habitat use to natural ponds or habitats (Korine and Pinshow 2004), it may leave ponds favoured by its migrating competitors, once they arrive at the area in autumn and spring, to forage instead around adjacent human settlements.

Spatial resource partitioning

The *Pipistrellus/Hypsugo* group was strongly associated with different pond size and hydroperiod categories, despite their similar morphology (Norberg and Rayner 1987) and foraging mode (Feldman et al. 2000; Korine and Pinshow 2004). Differential preferences, combined with a general tendency to avoid ponds associated with competitors, indicate that interspecific competition affects pond habitat use by insectivorous bats in arid environments.

T. teniotis, the species with the highest frequency of drinking in the study area (Razgour et al. 2010) and lowest manoeuvrability (Norberg and Rayner 1987), was not surprisingly associated with large permanent ponds. Because the abundance of Diptera tend to increase with pond size (Bazzanti et al. 2006), we would expect that all species in the *Pipistrellus/Hypsugo* group will also be associated with larger ponds. However, only *H. bodenheimeri*, the most manoeuvrable of the three species (Norberg and Rayner 1987), was associated with large ponds.

We suggest that in spring *P. kuhlii* is associated with small ponds, despite their lower insect abundance, to avoid competition with *T. teniotis* and *H. bodenheimeri* for drinking or foraging space above large ponds and with *P. rueppelli* for foraging space above medium ponds. Similarly, sympatric cryptic *Pipistrellus* species in the UK partition their foraging habitat to the extent that *P. pipistrellus* actively avoids riparian habitats, which are preferred by *P. pygmaeus*, despite their greater insect resource value (Nicholls and Racey 2006).

Although the diversity of Dipterans increases with pond area and hydroperiod (Bazzanti et al. 2006), some species may be found exclusively in lower volume, shorter-lived ponds to avoid predation (Dodson 1987). Consequently, the association of *P. kuhlii* with small temporary ponds may be the result of preference for prey taxa restricted to these ponds. However, the fact that in the absence of its competitors, in summer, *P. kuhlii* did not display the same pattern of habitat selection suggests that extensive use of small temporary ponds is more of a response to interspecific competition for foraging space than a by-product of prey preference. Hence, habitat selection of specific pond types may be a mechanism of coexistence, via habitat partitioning, in desert bat communities.

Temporal resource partitioning

During the non-reproductive season (Kuenzi and Morrison 2003), the night activity of temperate insectivorous bats has two peaks, corresponding to the dusk and pre-dawn peaks in insect activity (Kunz and Brock 1975; Anthony et al. 1981; Fukui et al. 2006; Gotelli and Entsminger 2001). Shifts from these patterns suggest possible competitive displacement.

In the Negev Desert, as in North America (Kunz 1973; Adams and Thibault 2006), sympatric insectivorous bat species differ in their nightly pattern of activity, indicating niche separation. Although the *Pipistrellus/Hypsugo* species primarily feed on Diptera (Feldman et al. 2000), only the activity of *H. bodenheimeri* corresponded to the dawn and dusk peaks in Diptera activity (e.g. Rydell et al. 1996). In contrast, the night activity pattern of *P. kuhlii* and *P. rueppelli* in spring may be influenced by the activity of their competitors. Only in ponds avoided by their competitors, or when their competitors were absent from the study area, did the activity of *P. kuhlii* and *P. rueppelli* concentrate at the beginning of the night, thus corresponding to the expected dawn peak in Diptera activity. Shifts in peak activity time towards more profitable foraging periods following the experimental removal of competitors was used to demonstrate how interspecific competition shapes desert gerbil communities (Ziv et al. 1993).

Although differences in the arrival time of bat species to ponds can be influenced by distances to day roosts (Kunz and Lumsden 2003), differences in the arrival time of *T. teniotis* to a permanent pond in response to changes in the activity pattern of competitors (*P. kuhlii*) suggest that interspecific competition, rather than distance to roosts, determines the night activity pattern of this species over desert ponds. Correspondingly, Adams and Thibault (2006) identified shifts in arrival time of *Myotis* species to small desert water holes in response to the abundance of competitors despite similar mean roost emergence times and similar distances of roost sites to water holes.

Competing bat species arriving to desert ponds to drink may use temporal partitioning of arrival time to avoid overcrowding and prevent collisions when approaching the water surface to drink (Adams and Simmons 2002). The arrival time of *T. teniotis* to a much longer permanent pond (Pond 2; ~60 m length) remained the same in spring and summer, presumably because the more than fourfold greater pond length and more open habitat would have allowed for spatial partitioning of the pond surface and consequently simultaneous drinking by several bats.

Conclusions

Spatial and temporal patterns of pond habitat-use by desert-dwelling insectivorous bats may reflect the trade-offs between selection of preferred pond type or activity time and the constraints posed by competitive interactions. Our results show that interspecific competition plays an important role in structuring desert bat assemblages and that bat species shift their pond habitat selection and night activity patterns in response to changes in the presence and activity density of their competitors.

Since sympatric bat species partition their use of ponds based on pond size, small temporary desert ponds offer an important foraging habitats for competitors displaced from larger ponds. The increased presence of *P. kuhlii* around desert ponds is of concern. Other *Pipistrellus* species whose populations expanded in response to anthropogenic habitat alteration were cited as possible contributors to the decline of more specialist bat species (Arlettaz et al. 2000). Given that interspecific competition can contribute to the decline of species that are sensitive to human habitat modification, it is particularly important to study the effects of the increase in the abundance of non-desert bat species such as *P. kuhlii* on their desert competitors.

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