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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.

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Keywords (separated by '-') Resource partitioning - Competitive interactions - Chiroptera - Arid environments - Acoustic monitoring

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

4 Orly Razgour · Carmi Korine · David Saltz

5 Received: 8 July 2010 / Accepted: 5 April 2011  
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**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 environ-  
ments) makes interspecific competition an important pro-  
cess 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.

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

70 Spatial partitioning of foraging habitats is recognised as  
71 the primary mechanism facilitating the coexistence of  
72 sympatric insectivorous bat species (Patterson et al. 2003).  
73 For example, Arlettaz (1999) found pronounced spatial  
74 segregation of primary foraging habitat between the mor-  
75 phologically similar sympatric bat species, *Myotis myotis*  
76 and *M. blythii*, whereby the former forages primarily in  
77 woody habitats, while the latter is associated with grassland  
78 habitats. Differences in wing morphology (e.g. Kingston  
79 et al. 2000), echolocation call structure (Siemers and  
80 Schnitzler 2004) and sensory ecology (Siemers and Swift  
81 2006) were shown to contribute to niche differentiation  
82 among sympatric bat species.

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

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

105 We identified two sets of potentially competing species.  
106 The first, the *Pipistrellus/Hypsugo* group, includes  
107 *Pipistrellus kuhlii*, *Hypsugo bodenheimeri* and *Pipistrellus*

*rupepelli*, three species that are similar morphologically  
108 and in their foraging modes. They are all small (body mass  
109 2.6–6.2 g) and highly manoeuvrable, with relatively low  
110 wing loading and aspect ratio values (Norberg and Rayner  
111 1987). They all forage in background cluttered habitats  
112 (Korine and Pinshow 2004), tend to forage over water  
113 bodies (Razgour et al. 2010) and have similar diets, which  
114 include a high proportion of Diptera and, to a lesser extent,  
115 Lepidoptera (Whitaker et al. 1994; Feldman et al. 2000).  
116 High overlap in diet, when coupled with the characteristic  
117 food limitation of desert ecosystems, indicates that inter-  
118 specific competition for foraging space may be present  
119 (Kronfeld-Schor and Dayan 1999). Hence, these three  
120 species may compete for foraging space above ponds.  
121

122 The second set of potential competitors includes two  
123 morphologically and behaviourally different species,  
124 *P. kuhlii* and the significantly larger *Tadarida teniotis*  
125 (mean body mass 27.2 g), a Lepidoptera specialist (Rydell  
126 and Arlettaz 1994) that forages in open spaces high above  
127 the ground (Whitaker et al. 1994; Korine and Pinshow  
128 2004) owing to its fast, low manoeuvrability flight mode  
129 (Norberg and Rayner 1987). However, both are non-desert  
130 species (Yom-Tov and Kadmon 1998), whose abundance  
131 in the Negev Desert is thought to have increased in the past  
132 century following human settlement and irrigated agricul-  
133 ture (C. Korine, personal observations). As a result of their  
134 non-desert origin, these two species are not well adapted to  
135 conserve water (Marom et al. 2006, for *T. teniotis*), and use  
136 ponds for drinking at a greater frequency than any other  
137 species in the study area (Razgour et al. 2010). Owing to  
138 the unobstructed swoop zone requirements associated with  
139 manoeuvrability restrictions on bats drinking from ponds in  
140 flight (Tuttle et al. 2006), competition between these two  
141 species may be for physical access to the water surface for  
142 the purpose of drinking.

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

## 153 Materials and methods

154 The study was carried out in the Central Negev Highlands,  
155 Israel, an arid region with low precipitation and high inter-  
156 and intra-annual variability (mean precipitation  
157  $93.38 \pm 39.23$  mm/year; Meteorology Unit BIDR 2008).

158 We compared the bat assemblages over ten natural per- 211  
 159 manent and temporary ponds of different sizes along three 212  
 160 adjacent valleys in the Matsok Ha'Zinim Nature Reserve 213  
 161 (30°51'N, 34°53'E; Supplementary Material 1). 214

162 We used an ultrasonic bat detector (AnaBat II; Titley 215  
 163 Electronics, Australia) to record bat activity over each 216  
 164 pond for one whole night (from dusk to sunrise) every 217  
 165 month between March and November 2007 and between 218  
 166 March and May 2008. We recorded bat activity over 219  
 167 temporary ponds until the ponds dried out (either the end of  
 168 May or July). An AnaBat detector was placed at the longest  
 169 end of each pond, on the ground, up to 1 m away from the  
 170 pond edge, pointing upwards at a 45° angle towards the  
 171 centre of the pond. The detection range of AnaBat detec-  
 172 tors for aerial foraging bats is typically greater than 20 m  
 173 (Collins and Jones 2009). Therefore, a detector would have  
 174 sampled the majority of the airspace above all ponds but  
 175 pond 2 (length 61.5 m), where the detector was placed at  
 176 the edge of the centre of the pond pointing towards the  
 177 widest section, thus covering the maximum airspace  
 178 possible.

179 Since acoustic monitoring does not allow for the iden- 230  
 180 tification of individual bats, we used activity as a surrogate 231  
 181 for density. This approach is common in studies of compe- 232  
 182 tition because of its greater relevance for ecological 233  
 183 interactions and habitat selection (Mitchell et al. 1990). Bat 234  
 184 activity was measured as the number of bat passes in each  
 185 AnaBat recording file, whereby a pass is defined as a  
 186 sequence of bat calls (Fenton 1970). Activity was stand-  
 187 ardised as the number of bat passes per hour of recording.  
 188 We used the ratio of feeding buzzes (increased pulse rep-  
 189 etition rate during the terminal phase of insect capture;  
 190 Griffin et al. 1960) to bat passes as an indicator of the  
 191 importance of the ponds' airspace for foraging.

192 The calls of the studied bat species do not overlap (Dietz 241  
 193 2005; Benda et al. 2008; Supplementary Material, 242  
 194 Appendix 1) and are adequately recorded and distinguished 243  
 195 to the species level using the AnaBat system. Calls with 244  
 196 overlapping frequencies were assigned based on the 245  
 197 remaining calls in the pass; however, a small proportion of 246  
 198 the calls (approximately 1%) could not be adequately 247  
 199 assign to a specific species and were therefore discarded 248  
 200 from further analysis. 249

201 Each sampling night, we measured the maximum length, 250  
 202 width and depth of the ponds, and multiplied these three 251  
 203 variables to calculate an index of maximum pond volume. 252  
 204 We divided the ponds into three size categories based on 253  
 205 maximum pond volume. We further divided the ponds into 254  
 206 three hydroperiod categories: permanent, semi-permanent 255  
 207 (held water until mid-summer), and temporary (held water 256  
 208 until the end of spring). We estimated percent of woody or 257  
 209 herbaceous vegetation cover immediately adjacent to each 258  
 210 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) (Sup-  
 plementary Material, Appendix 2). To test whether tem-  
 perature 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 220

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

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

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

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

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

250 To estimate the presence and intensity of interspecific  
 251 competition and determine competition coefficients from  
 252 the census data, we used the regression method (Crowell  
 253 and Pimm 1976), later modified by Rosenzweig et al.  
 254 (1984) to account for habitat heterogeneity. The method  
 255 uses a regression of the activity density of one species  
 256 against that of its potential competitor at a set of homog-  
 257 enous sites, which differ only in the density of the two  
 258 species. To eliminate the effect of site variability, the

259 residuals of the regression of each species' activity against  
260 its significant habitat variables were used instead of species  
261 activity measures when quantifying the competitive inter-  
262 actions between two species. The slope of the regression  
263 was used as an estimate of the competition coefficient,  $\alpha$ .  
264 The nature of the interaction was determined according to  
265 whether the slope was positive or negative, while the  
266 strength of the competitive interaction was determined by  
267 the steepness of the slope.

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

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

287 To test whether competing bat species partition their  
288 nightly use of ponds temporally, we compared the peak  
289 activity time and night activity pattern of the different  
290 species over pond 10 during April 2007, when all species  
291 were present and active throughout the night, and in August  
292 2007, when *P. kuhlii* and *T. teniotis* were present in the  
293 study area. Pond 10 concentrates high levels of activity of  
294 all competing species, perhaps due to its isolation (Sup-  
295 plementary Material 1), and is relatively short (15.8 m),  
296 and therefore may limit the amount of individuals that can  
297 use it simultaneously. To test the effect of seasonality, we  
298 compared the arrival time of *P. kuhlii* and *T. teniotis* to  
299 pond 10 between spring, when temporary ponds were  
300 present and bats could employ spatial partitioning, and  
301 summer, when the pond was isolated.

302 Because bats cannot be efficiently excluded from their  
303 foraging habitat, nor can their density be easily manipu-  
304 lated under field conditions, we used natural changes in the  
305 activity of species following seasonal movements away  
306 from the study area, as a surrogate for removal experi-  
307 ments. *P. rueppelli* and *H. bodenheimeri* were only present  
308 in the study area at high activity levels between March and  
309 April 2007 and between November 2007 and April 2008.

310 Therefore, we were able to determine the effect of their  
311 presence on their potential competitor, *P. kuhlii*, by com-  
312 paring its activity over three permanent ponds before and  
313 after the arrival of the two migrant species, using Wilco-  
314 xon's matched pairs test. We used chi square test to  
315 determine whether in the absence of its competitors,  
316 *P. kuhlii* still selected the same ponds and pond types.  
317 Finally, we used Kolmogorov–Smirnov tests to compare  
318 the distribution of *P. kuhlii*'s night activity over pond 10  
319 between spring of 2007, when *P. rueppelli* and *H. boden-*  
320 *heimeri* were present and summer of 2007, when they were  
321 absent from the study area. Statistical analyses were per-  
322 formed with STATISTICA 7 (StatSoft) and SPSS (v.15).  
323 We considered results to be significant at  $P < 0.05$ .

## 324 Results

### 325 Species competitive interactions

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

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

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

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



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

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

X<sub>1</sub> pond length (m), X<sub>2</sub> square root pond volume (m<sup>3</sup>), X<sub>3</sub> arcsin percent of vegetation cover around the pond, X<sub>4</sub> distance to nearest cliff (m), and X<sub>5</sub> distance to nearest permanent water source (m)

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

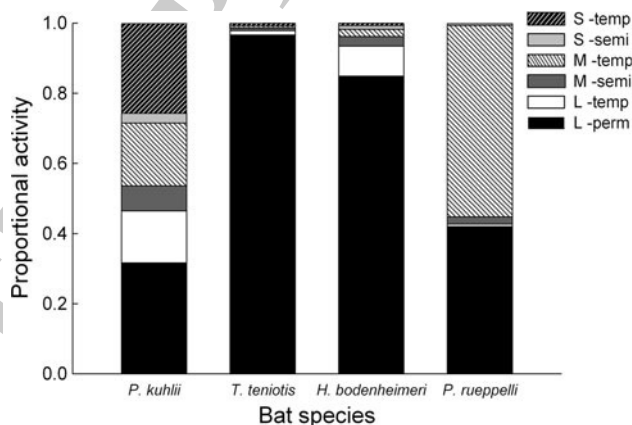
|                               | <i>Pipistrellus kuhlii</i> | <i>Tadarida teniotis</i> | <i>Hypsugo bodenheimeri</i> | <i>Pipistrellus rueppelli</i> |
|-------------------------------|----------------------------|--------------------------|-----------------------------|-------------------------------|
| <i>Pipistrellus kuhlii</i>    |                            | -0.95                    | -0.12                       | -0.52                         |
| <i>Tadarida teniotis</i>      | -0.36                      |                          | 0.08                        | 0.38                          |
| <i>Hypsugo bodenheimeri</i>   | -2.9                       | 4.9                      |                             | 3.1                           |
| <i>Pipistrellus rueppelli</i> | -0.91                      | 1.8                      | 0.23                        |                               |

357 Spatial patterns of habitat use

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

379 Temporal patterns of pond use

380 Patterns of activity over pond 10, a large permanent pond  
 381 differed between the three *Pipistrellus/Hypsugo* species  
 382 (chi square  $\chi^2 = 875.6$ ,  $df = 18$ ,  $P < 0.001$ ; Fig. 2),  
 383 whereby the peak in their activity did not overlap and each  
 384 species was associated with a different section of the night.  
 385 *H. bodenheimeri* displayed a bimodal pattern of night  
 386 activity, preferring the first (standardised chi square

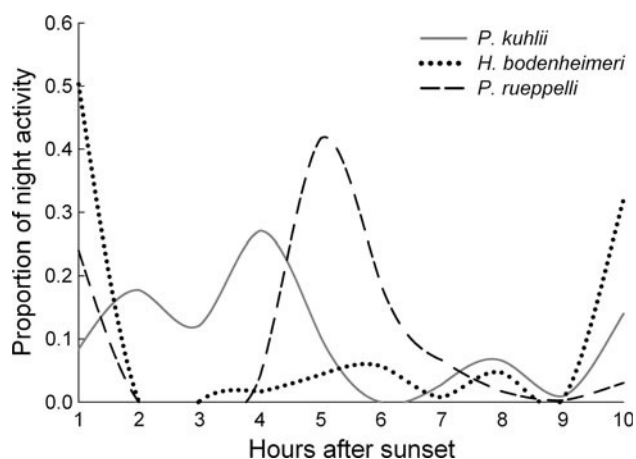


**Fig. 1** Total number of passes per hour of *Pipistrellus kuhlii*, *Tadarida teniotis*, *Hypsugo bodenheimeri* and *P. rueppelli* over different pond size and hydroperiod categories (L large, M medium, S small, perm permanent, semi semi-permanent, temp temporary) in the spring of 2007 at the Negev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

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  $P > 0.05$ ).

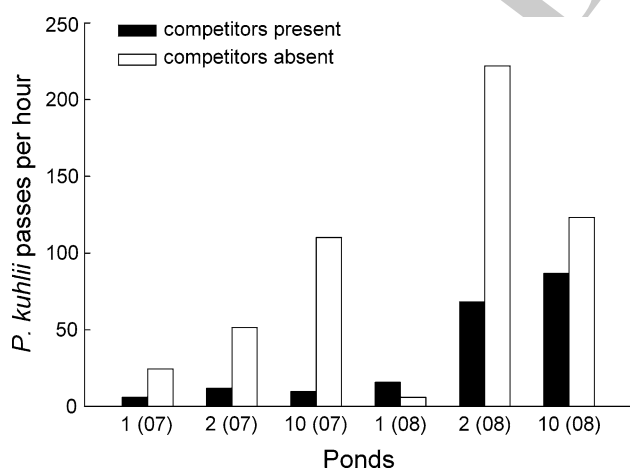
Author Proof



**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

#### 400 Effect of seasonal changes in species composition

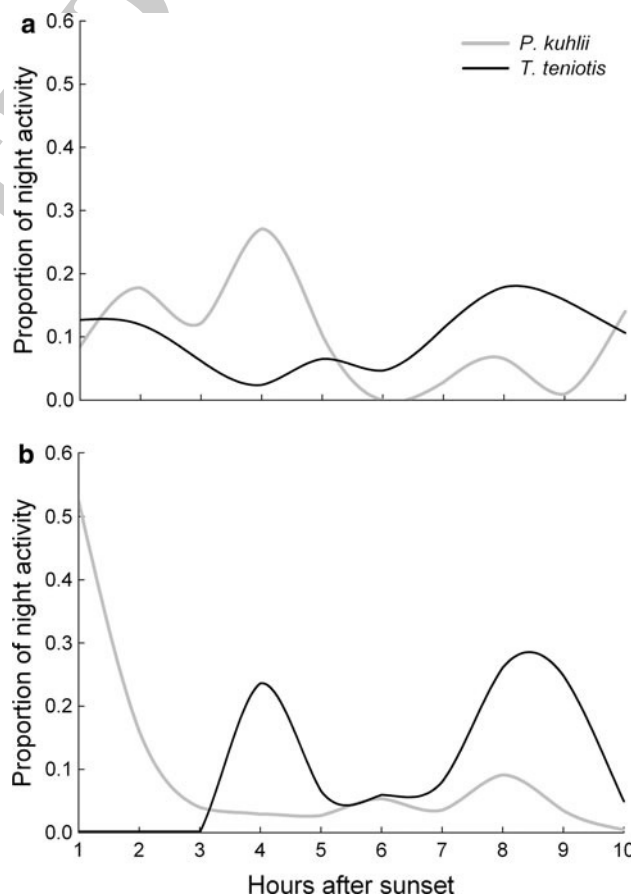
401 The activity of *P. kuhlii* over the three permanent ponds was  
 402 higher during the months when *P. rueppelli* and *H. boden-*  
 403 *heimeri* were absent from the study area (June–September  
 404 2007 and May 2008) than when they were present (April  
 405 2007, October 2007 and April 2008) (Wilcoxon matched  
 406 pairs test  $Z = 1.99$ ,  $df = 6$ ,  $P = 0.046$ ; Fig. 3). During the  
 407 months when *P. rueppelli* and *H. bodenheimeri* were absent  
 408 from the study area, but temporary ponds were still present,  
 409 *P. kuhlii* was not associated with any pond, pond size or pond  
 410 permanence categories (all standardised residuals were not  
 411 significant). It only avoided pond 2 ( $\chi = -3.9$ ), a pond  
 412 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  
 413 ponds within the first hour after dusk. However, in spring,  
 414 when *P. rueppelli* and *H. bodenheimeri* were present in the  
 415 study area, the activity of *P. kuhlii* over pond 10, a pond used  
 416 by all species, was lower and spread more evenly throughout  
 417 the night than in summer, when it peaked at the beginning of  
 418 the night, with 725 passes in the first hour after sunset, and  
 419 was low for the remainder of the night. The distribution of  
 420 nightly activity of *P. kuhlii* differed significantly between  
 421 spring and summer (Kolmogorov–Smirnov test: max nega-  
 422 tive difference =  $-0.9$ ,  $P < 0.001$ ).  
 423

*T. teniotis*, on the other hand, arrived to pond 10 sig-  
 424 nificantly later once adjacent temporary ponds dried out  
 425 (one-way ANOVA, log transformed:  $F_{1,12} = 30.95$ ,  
 426  $P = 0.0001$ ). In spring 2007, when temporary ponds were  
 427 present, it arrived on average less than half an hour after  
 428 *P. kuhlii*, while in summer it arrived on average more than  
 429 4 h after its potential competitor. Consequently, differ-  
 430 ences in the night activity patterns of the two species were  
 431 more pronounced during summer (summer:  $\chi^2 = 873.5$ ;  
 432 spring:  $\chi^2 = 164.4$ ; Fig. 4).  
 433



**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

434 **Discussion**

435 The community composition of desert bats is highly  
 436 dynamic and constantly changing because of the need to  
 437 congregate around few available water sources, many of  
 438 which are temporary and vary in size throughout the sea-  
 439 son. While spatial partitioning of pond and pond type use  
 440 in our study took place in spring, the desiccation of tem-  
 441 porary ponds in summer reduced the scope for spatial  
 442 partitioning and increased temporal partitioning of night  
 443 activity among species that remained in the area. Chesson  
 444 (2000) suggested that such seasonal changes in the size and  
 445 availability of temporary ponds may provide the temporal  
 446 variation in environmental conditions necessary for the  
 447 coexistence of species with similar ecologies but different  
 448 responses to the varying environment.

## 449 The role of interspecific competition

450 Interspecific competition is an important mechanism  
 451 structuring ecological communities by determining the  
 452 number and type of coexisting species and by affecting  
 453 patterns of habitat use (Schoener 1983). Interspecific  
 454 competition drives morphological differentiation and  
 455 influences the phenotypic structure of insectivorous bat  
 456 communities (Kingston et al. 2000; Schoeman and Jacobs  
 457 2008). The role of competition in structuring bat commu-  
 458 nities may be particularly pronounced in arid environments  
 459 due to the characteristics resource limitation of these eco-  
 460 systems (Noy-Meir 1973; Findley 1993). Indeed, our study  
 461 shows that in the Negev Desert interspecific competition  
 462 appears to influence the structure of insectivorous bat  
 463 assemblages over ponds. Measures of niche overlap show  
 464 no significant overlap in the use of ponds among the  
 465 *Pipistrellus/Hypsugo* group of competitors, while the  
 466 regression method identified potential negative competitive  
 467 interactions between most studied species. Lack of nega-  
 468 tive competitive interactions among potential competitors,  
 469 however, is not necessarily due to an absence of competi-  
 470 tion but could also be the result of habitat segregation in  
 471 response to past interspecific competitive interactions (“the  
 472 ghost of competition past”) (Rosenzweig 1981).

473 Measures of niche overlap cannot be used to estimate  
 474 the intensity of competition; however, they can be used to  
 475 describe the potential for competition if resources are in  
 476 short supply (Abrams 1980). Since the availability of water  
 477 and in particular natural larger water bodies is limited in  
 478 desert environments (Noy-Meir 1973), lack of significant  
 479 niche overlap implies the presence of interspecific com-  
 480 petition. Competition, in our study, appears to be for access  
 481 to the water surface, either for drinking or foraging.  
 482 Feeding buzz activity ratios calculated in our study are  
 483 comparable to those used by previous studies to indicate

the presence of feeding activity (e.g. Vaughan et al. 1997: 484  
 8%; Walsh and Harris 1996: 20%), thus lending further 485  
 support to the use of desert ponds as foraging sites by 486  
*Pipistrellus/Hypsugo* species. 487

Although we were unable to manipulate bat densities or 488  
 carry out exclusion experiments to test our predictions, 489  
 changes in the night activity patterns and pond habitat use 490  
 of *P. kuhlii* in response to natural seasonal changes in the 491  
 activity of *H. bodenheimeri* and *P. rueppelli* may be 492  
 regarded as equivalent to a shift in patterns of habitat use 493  
 following experimental removal of competitors, and 494  
 therefore indicate the presence of ongoing interspecific 495  
 competition (Abramsky et al. 2005). Because *P. kuhlii* is 496  
 not restricted in its habitat use to natural ponds or habitats 497  
 (Korine and Pinshow 2004), it may leave ponds favoured 498  
 by its migrating competitors, once they arrive at the area in 499  
 autumn and spring, to forage instead around adjacent 500  
 human settlements. 501

## 502 Spatial resource partitioning

The *Pipistrellus/Hypsugo* group was strongly associated 503  
 with different pond size and hydroperiod categories, 504  
 despite their similar morphology (Norberg and Rayner 505  
 1987) and foraging mode (Feldman et al. 2000; Korine and 506  
 Pinshow 2004). Differential preferences, combined with a 507  
 general tendency to avoid ponds associated with competi- 508  
 tors, indicate that interspecific competition affects pond 509  
 habitat use by insectivorous bats in arid environments. 510

*T. teniotis*, the species with the highest frequency of 511  
 drinking in the study area (Razgour et al. 2010) and lowest 512  
 manoeuvrability (Norberg and Rayner 1987), was not 513  
 surprisingly associated with large permanent ponds. 514  
 Because the abundance of Diptera tend to increase with 515  
 pond size (Bazzanti et al. 2006), we would expect that all 516  
 species in the *Pipistrellus/Hypsugo* group will also be 517  
 associated with larger ponds. However, only *H. boden- 518*  
*heimeri*, the most manoeuvrable of the three species 519  
 (Norberg and Rayner 1987), was associated with large 520  
 ponds. 521

We suggest that in spring *P. kuhlii* is associated with 522  
 small ponds, despite their lower insect abundance, to avoid 523  
 competition with *T. teniotis* and *H. bodenheimeri* for 524  
 drinking or foraging space above large ponds and with 525  
*P. rueppelli* for foraging space above medium ponds. 526  
 Similarly, sympatric cryptic *Pipistrellus* species in the UK 527  
 partition their foraging habitat to the extent that *P. pipi- 528*  
*strellus* actively avoids riparian habitats, which are pre- 529  
 ferred by *P. pygmaeus*, despite their greater insect resource 530  
 value (Nicholls and Racey 2006). 531

Although the diversity of Dipterans increases with pond 532  
 area and hydroperiod (Bazzanti et al. 2006), some species 533  
 may be found exclusively in lower volume, shorter-lived 534

535 ponds to avoid predation (Dodson 1987). Consequently, the  
536 association of *P. kuhlii* with small temporary ponds may be  
537 the result of preference for prey taxa restricted to these  
538 ponds. However, the fact that in the absence of its compet-  
539 itors, in summer, *P. kuhlii* did not display the same  
540 pattern of habitat selection suggests that extensive use of  
541 small temporary ponds is more of a response to interspe-  
542 cific competition for foraging space than a by-product of  
543 prey preference. Hence, habitat selection of specific pond  
544 types may be a mechanism of coexistence, via habitat  
545 partitioning, in desert bat communities.

#### 546 Temporal resource partitioning

547 During the non-reproductive season (Kuenzi and Morrison  
548 2003), the night activity of temperate insectivorous bats has  
549 two peaks, corresponding to the dusk and pre-dawn peaks  
550 in insect activity (Kunz and Brock 1975; Anthony et al.  
551 1981; Fukui et al. 2006; Gotelli and Entsminger 2001).  
552 Shifts from these patterns suggest possible competitive  
553 displacement.

554 In the Negev Desert, as in North America (Kunz 1973;  
555 Adams and Thibault 2006), sympatric insectivorous bat  
556 species differ in their nightly pattern of activity, indicating  
557 niche separation. Although the *Pipistrellus/Hypsugo* spe-  
558 cies primarily feed on Diptera (Feldman et al. 2000), only  
559 the activity of *H. bodenheimeri* corresponded to the dawn  
560 and dusk peaks in Diptera activity (e.g. Rydell et al. 1996).  
561 In contrast, the night activity pattern of *P. kuhlii* and *P.*  
562 *rueppelli* in spring may be influenced by the activity of  
563 their competitors. Only in ponds avoided by their compet-  
564 itors, or when their competitors were absent from the  
565 study area, did the activity of *P. kuhlii* and *P. rueppelli*  
566 concentrate at the beginning of the night, thus corre-  
567 sponding to the expected dawn peak in Diptera activity.  
568 Shifts in peak activity time towards more profitable for-  
569 aging periods following the experimental removal of  
570 competitors was used to demonstrate how interspecific  
571 competition shapes desert gerbil communities (Ziv et al.  
572 1993).

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

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

#### 595 Conclusions

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

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

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627

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