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Patterns in diurnal co-occurrence in an assemblage of hoverflies (Diptera: Syrphidae)

MANUELA D'AMEN[1, 2]*, DANIELE BIRTELE[2], LIVIA ZAPPONI[1, 2] and SÖNKE HARDERSEN[2]

[1] National Research Council, IBAF Department, Monterotondo Scalo, Rome, Italy; e-mails: manuela.damen@ibaf.cnr.it; livia.zapponi@ibaf.cnr.it

[2] Corpo Forestale dello Stato, Centro Nazionale Biodiversità Forestale "Bosco Fontana", Verona, Italy; e-mails: entomologiacfs@libero.it; s.hardersen@gmail.com

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Abstract. In this study we analyzed the inter-specific relationships in assemblages of syrphids at a site in northern Italy in order to determine whether there are patterns in diurnal co-occurrence. We adopted a null model approach and calculated two co-occurrence metrics, the C-score and variance ratio (V-ratio), both for the total catch and of the morning (8:00–13:00) and afternoon (13:00–18:00) catches separately, and for males and females. We recorded discordant species richness, abundance and co-occurrence patterns in the samples collected. Higher species richness and abundance were recorded in the morning, when the assemblage had an aggregated structure, which agrees with previous findings on communities of invertebrate primary consumers. A segregated pattern of co-occurrence was recorded in the afternoon, when fewer species and individuals were collected. The pattern recorded is likely to be caused by a number of factors, such as a greater availability of food in the morning, prevalence of hot and dry conditions in the early afternoon, which are unfavourable for hoverflies, and possibly competition with other pollinators. Our results indicate that restricting community studies to a particular time of day will result in certain species and/or species interactions not being recorded.

INTRODUCTION

Hoverflies have been the focus of many studies because of their role as pollinators and potential as bioindicators (e.g. Stubbs & Falk, 1987; Somaggio, 1999; Branquart & Hemptinne, 2000; Burgio & Somaggio, 2007). The adults feed on pollen, nectar and occasionally honey dew. Thus, hoverflies are adept fliers that interact directly with the vegetation for their dietary requirements (Haslett, 1997). Their larvae have a wide variety of ways of life, feeding on decaying wood, sap flows from trees, fungi, living or rotting plants, dung, muddy water, aphids, ant eggs, larvae and pupae, or other insects (Sommaggio, 1999). Because larvae are much more specialized than adults in their feeding preferences, they often play a key role in determining syrphid distribution (Dziock, 2006). Hoverflies live in a variety of habitats (e.g. grassland, woodlands), where they form diverse and species rich communities (Speight, 1989; Rotheray et al., 2001).

Although many aspects of the biology of hoverflies have been extensively studied (e.g. Goulson & Wright, 1998; Branquart & Hemptinne, 2000; Jauker et al., 2009; Birtele & Hardersen, 2012), one aspect that has received relatively little attention is the interspecific structure of syrphid assemblages. The structure of plant and animal communities is a product of many interacting processes. The mechanisms that lead to nonrandom patterns in multispecies assemblages are a major research focus in ecology, because patterns often reflect the existence of underlying mechanisms that structure community assembly (Weiher & Keddy, 1999; Gotelli, 2000). Time is an important aspect to consider when studying community organization (Baldock et al., 2011). Not all the species inhabiting a certain area co-occur at the same time, thus they do not necessarily interact. Differences in daily activity patterns lead to a succession of pollinator species visiting the flowers of a given plant, thus species belonging to multiple assemblages can feed successively during the course of a day (Baldok et al., 2011) and each one can potentially present a different structure of species interactions. Whether this is the case, has implications for our understanding of the nature of the effect and magnitude of species interactions. Time can be partitioned on both a seasonal and daily scale: considering pollinator species there is widespread evidence for seasonal partitioning of feeding activity (e.g. Sargent & Ackerly, 2008), but most papers on food webs do not provide data on changes in community structure during the day (e.g. Gibson et al., 2006; Nielsen & Bascompte, 2007; Olesen et al., 2008; Petanidou et al., 2008). In particular, the diurnal patterns of species coexistence have not been assessed for hoverflies assemblages.

To fill this gap, the main aim of this paper was to analyze the daily temporal dynamics of species co-occurrences in hoverflies inhabiting a hay meadow in northern Italy. In particular, using temporally structured sampling we examined a syrphid assemblage for non-random patterns in species co-occurrence, as previously found in other pollinator assemblages (e.g. Baldock et al.,

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* Present and corresponding address: Corpo Forestale dello Stato, Centro Nazionale Biodiversità Forestale "Bosco Fontana", Strada Mantova 29, 46045, Marmirolo – Mantova, Italy

Fig. 1. Location of the study site in Italy (a), picture of the Bosco Fontana reserve where this study was carried out (b) and diagram indicating the positioning of the pan traps (c).

2011). In particular, we hypothesized differences in the patterns of diurnal species co-occurrences due to the interplay of factors related to the availability of floral resources (e.g., daily timing of flower opening) and species biology (e.g. thermal physiology, sexual interactions and nesting cycles) (Willmer, 1988; Stone et al., 1999; Willmer & Stone, 2004) In addition, we tested for gender differences in patterns of species assemblages. Distinct patterns in the inter-specific relations between genders can be expected due to differences in their reproductive biology and dietary requirements. In fact, females depend more on sources of floral pollen as they need to obtain the amino acids necessary for egg production and therefore spend more time feeding than males (Gilbert, 1985; Haslett, 1989).

MATERIAL AND METHODS

Syrphids were sampled using yellow pan traps i.e. circular plastic bowls 12,5 cm in diameter and 4 cm deep, positioned at height of 50 cm and filled with water and with a few drops of soap to reduce surface tension. A grid of 40 traps (45 × 35 m) was placed in a hay meadow (33 ha) in the Bosco Fontana nature reserve, Po Valley, northern Italy (Coordinates: 637337, 5006236 WGS84, UTM 32N) (Fig. 1). From 1.vi. to 6.vi.2012 syrphids were collected twice a day; the time frames were: 8:00–13:00 (morning) and 13:00–18:00 (afternoon). All syrphids were identified to species.

To investigate patterns of species coexistence in the hoverfly assemblage, we adopted a null model approach (Gotelli & Graves, 1996). Data were organized in a presence-absence (1-0) matrix (McCoy & Heck, 1987), where each row represents a single pan trap and each column a hoverfly species. The use of presence/absence matrices allows lower uncertainty than abundance data to measure occurrence, and does not mask non-random community patterns (see Haukisalmi & Henttonen, 1993). We used two indices: the C-score (Stone & Roberts, 1990) and variance ratio (V-ratio) (Schluter, 1984). Briefly, the C-score indicates the degree of species co-occurrence and is calculated as the average number of checkerboard units that are found for each pair of species. For an assemblage that is competitively structured, the C-score should be significantly larger than expected by chance (Gotelli, 2000). The V-ratio is the ratio between the variance in species richness and the sum of the variance in species occurrence. When the value of the ratio equals 1 species are distributed independently. If it is smaller or greater than 1 then it indicates a negative or positive covariance between species pairs, respectively. Refer to Gotelli (2000) for the statistical properties of these indices.

First, we tested whether a different community structure can be recognized in the species sampled at different times during the day. In other words we compared co-occurence patterns in the morning and afternoon samples of hoverflies. To do this, we analyzed whether the mean C-score index in the assemblages in the different time frames [observed index (O)] was larger or smaller than expected by chance (E). Following Lehsten & Harmand (2006) we used 3×10^4 random Monte Carlo permutations to compare mean index from null matrices obtained by reshuffling the region labels among the different sites with the observed index. Afterwards, we constructed a presence/absence matrix of hoverfly species for each temporal sample and calculated the metrics described above (both pooling and separating male and females specimens). Again, for each matrix we contrasted the observed index with that simulated using 3×10^4 iterations. We used fixed-equiprobable (*fe*) simulation algo-

TABLE 1. Number of individuals collected.

Species	Morning		Afternoon	
	m	f	m	f
Chalcosyrphus nemorum		1		
Chrysotoxum cautum		1		
Episyrphus balteatus	68	66	27	20
Eristalis arbustorum	43	37	3	
Eristalis tenax	9	21	5	
Eristalinus aeneus	32	31	2	6
Eristalinus sepulchralis	3			
Eumerus sp.		1		
Eumerus ornatus	1			
Eupeodes corollae	9	6		
Eupeodes lapponicus		1		
Ferdinandea cuprea	3	2		1
Melanostoma mellinum		1		
Merodon constans		5		2
Myathropa florea		1		
Paragus pecchiolii			1	1
Scaeva selenitica		1		
Sphaerophoria scripta	2	3	2	1
Syrphus vitripennis	1	5	1	

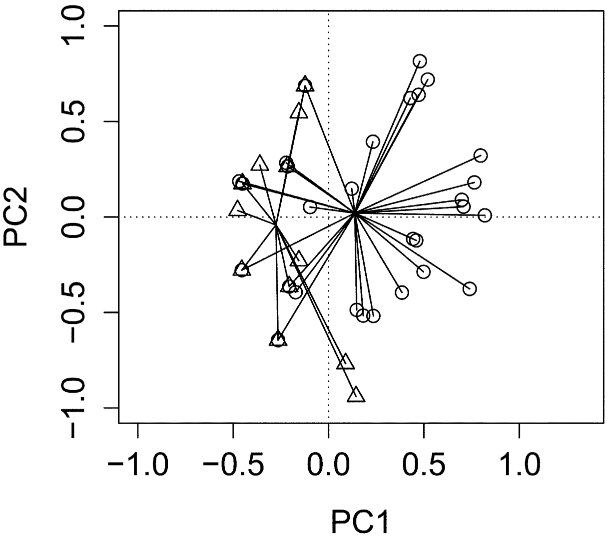

Fig. 2. Results of the principal component analysis (PCA) of the morning (circles) and afternoon (triangles) samples. The results for the empty traps were not included in the analyses.

rithm, which is appropriate for this kind of data (Gotelli & Entsminger, 2001). The variance ratio (V-ratio) index was calculated both including and excluding the results for the empty pan traps. All analyses were carried out using EcoSim 7.0 software (Gotelli & Entsminger, 2001). Significance values were considered after Bonferroni correction, here $P = 0.00416$ (the critical P value divided by the number of individual tests; Legendre & Fortin, 1989).

RESULTS

A total of 19 species of hoverfly were collected (Table 1). All but one species were collected during the morning (354 individuals). Nine species were collected in the afternoon, eight of which were caught also in the morning (72 individuals) (Table 1). There were no significant differences in relative abundances of the sexes in the two time frames ($\chi^2 = 1.74$, $P_{(O<E)} = 0.53$, Monte Carlo χ^2 test). Morning and afternoon assemblages clearly segregate in ordination space (Fig. 2). The comparison of co-occurrence patterns confirmed a significant difference between the morning and afternoon assemblages, the overall mean C-score of the observed dataset (11.99) was larger than the simulated mean C-scores (7.01) ($P_{(O>E)} = 0.00019$).

The indices of co-occurrence that we calculated for the assemblages collected indicated that species did not co-occur randomly in the morning and afternoon samples. However, the results of the analyses of the two samples were very different. The C- and V-scores indicated that the morning assemblage had an aggregated structure (Table 2, Figs 3–5). Considering gender, the aggregated structure is evident only for females based on both indices, while for males the pattern did not differ from random. The analysis of the afternoon sample indicated a different pattern, with the C-score indicating significant segregation in the whole assemblage of species (Table 1, Fig. 3). This was evident for both males and females when the presence/absence patterns were analyzed separately. The results, based on the variance test (V-score), were significant for a competitive structure in the afternoon sample only for females (Table 2, Fig. 5).

DISCUSSION

Our results indicate that the structure of hoverflies assemblages in the morning and afternoon in the study area differed significantly. We recorded discordant species richness, abundance and co-occurrence patterns in the two time frames of insect collection. High activity levels (i.e. more species and individuals caught) were recorded in the morning, which is in accordance with the results of Gilbert (1985). The differences can be explained in terms of the temporal variation in floral resources and physiological limits of the species, which determine when during the day the flower-pollinator interactions occur. During the morning, more flowers open and pollen and nectar are more abundant, while the amount of nectar secreted per flower tends to decrease towards evening (e.g. Ford, 1979; Pleasants & Chaplin, 1983). The greater availability of food in the morning is

TABLE 2. Summary of the null model analyses of the pattern in diurnal co-occurrences of hoverflies based on all the hoverflies caught and separately for both sexes using *fe* null model algorithms for C-score. O < E = number of samples for which the observed value of the index was significantly less than expected by chance; O > E = number of samples for which the observed value of the index was significantly greater than expected by chance. Significant values are in bold. Numbers of hoverflies are in parentheses. Acronyms in alphabetical order: E = expected; *fe* = fixed-equiprobable algorithm; O = observed; WI = with empty sites; WO = without empty sites.

		Morning			Afternoon		
		tot (140)	f (108)	m (84)	tot (30)	f (14)	m (19)
fe	C-score	10.830	9.992	12.667	10.333	14.000	5.400
	p (O < E)	**>0.001**	**>0.001**	0.115	0.991	0.999	0.964
	p (O > E)	1.000	1.000	0.890	**>0.001**	**>0.001**	**>0.001**
	V-ratio	1.95417	1.91419	1.32604	0.72222	0.22222	0.44737
WI	*p* (O < E)	0.99993	0.99973	0.95533	0.5363	0.01093	0.04697
	p (O > E)	**>0.001**	**>0.001**	0.08613	0.4637	0.98907	0.98497
WO	*p* (O < E)	0.99993	0.99993	0.93463	0.2382	**>0.001**	0.3397
	p (O > E)	**>0.001**	**>0.001**	0.06537	0.766	0.99973	0.68953

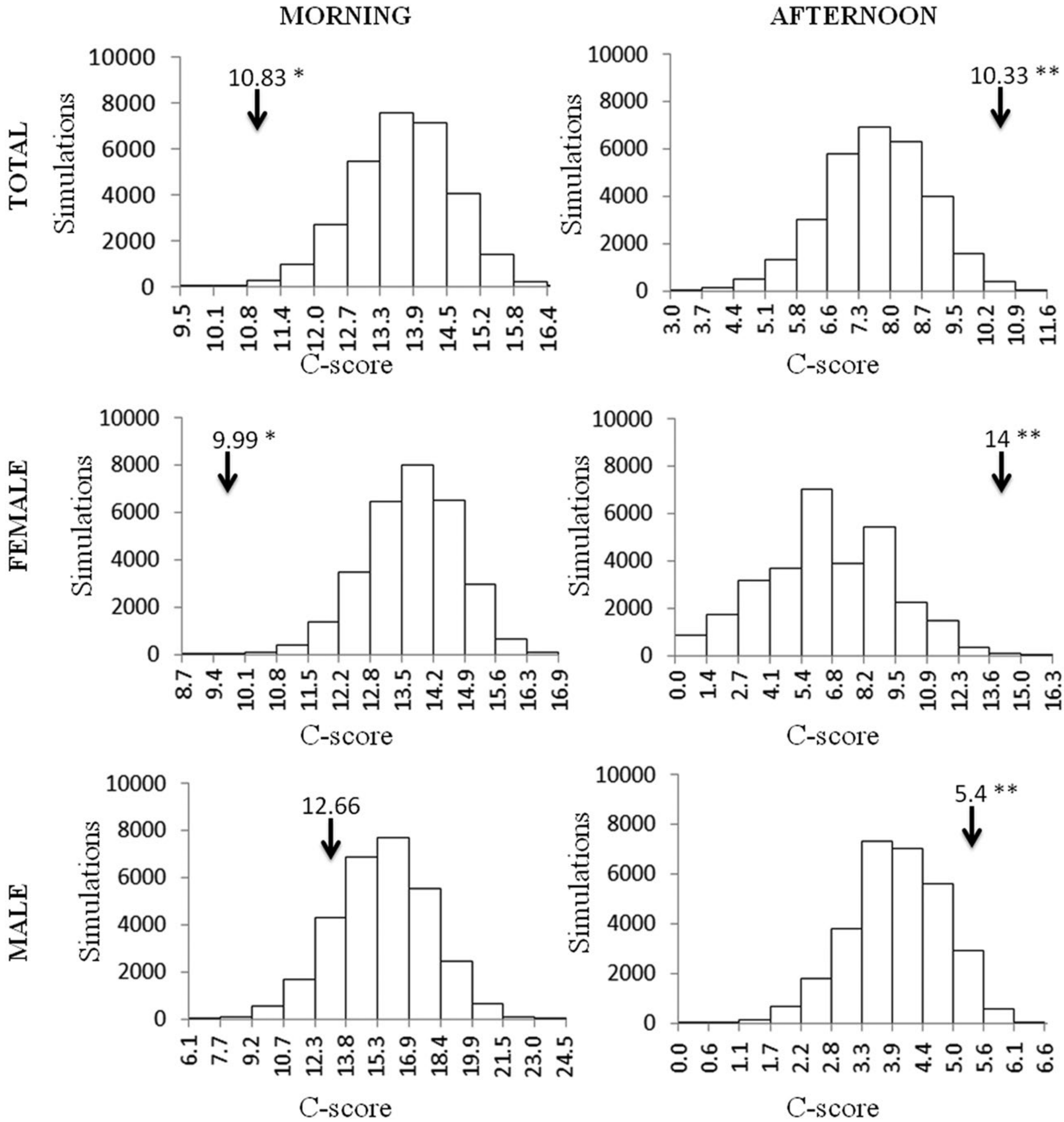

Fig. 3. Histograms of the distribution of C-score indices recorded in the simulated communities. The arrow indicates the observed C-score index. Asterisks indicate an observed C-score significantly less than (one asterisk) or greater than (two asterisks) expected by chance.

one likely cause of the higher species richness and absence of species segregation recorded in the morning. A lack of species competition in hoverfly communities was observed in an urban habitat by Gilbert & Owen (1990).

We detected a significant aggregation of hoverfly species, a pattern previously recorded in communities of invertebrate primary consumers (e.g. Bell et al., 2010). Many pollinators have physiological limits that influence their interactions with flowers. In hoverflies their reproductive behaviour may play an important role in determining the observed pattern in timing, as aphidophagous syrphids lay eggs preferentially in the early afternoon (Peschken, 1965), which constrains the feeding activity of females to other times of the day. Also limitations imposed by thermal physiology and water balance may have an important role in determining the observed daily patterns of species richness and abundance, as in hymenoptera (Willmer, 1988). Very hot and dry conditions, similar to those measured at our study site in late morning/early afternoon (values not shown for brevity), adversely affect hoverfly activity (Gilbert, 1985) and thus there are likely to be fewer species (and individuals) active in the afternoon. These climatic conditions also

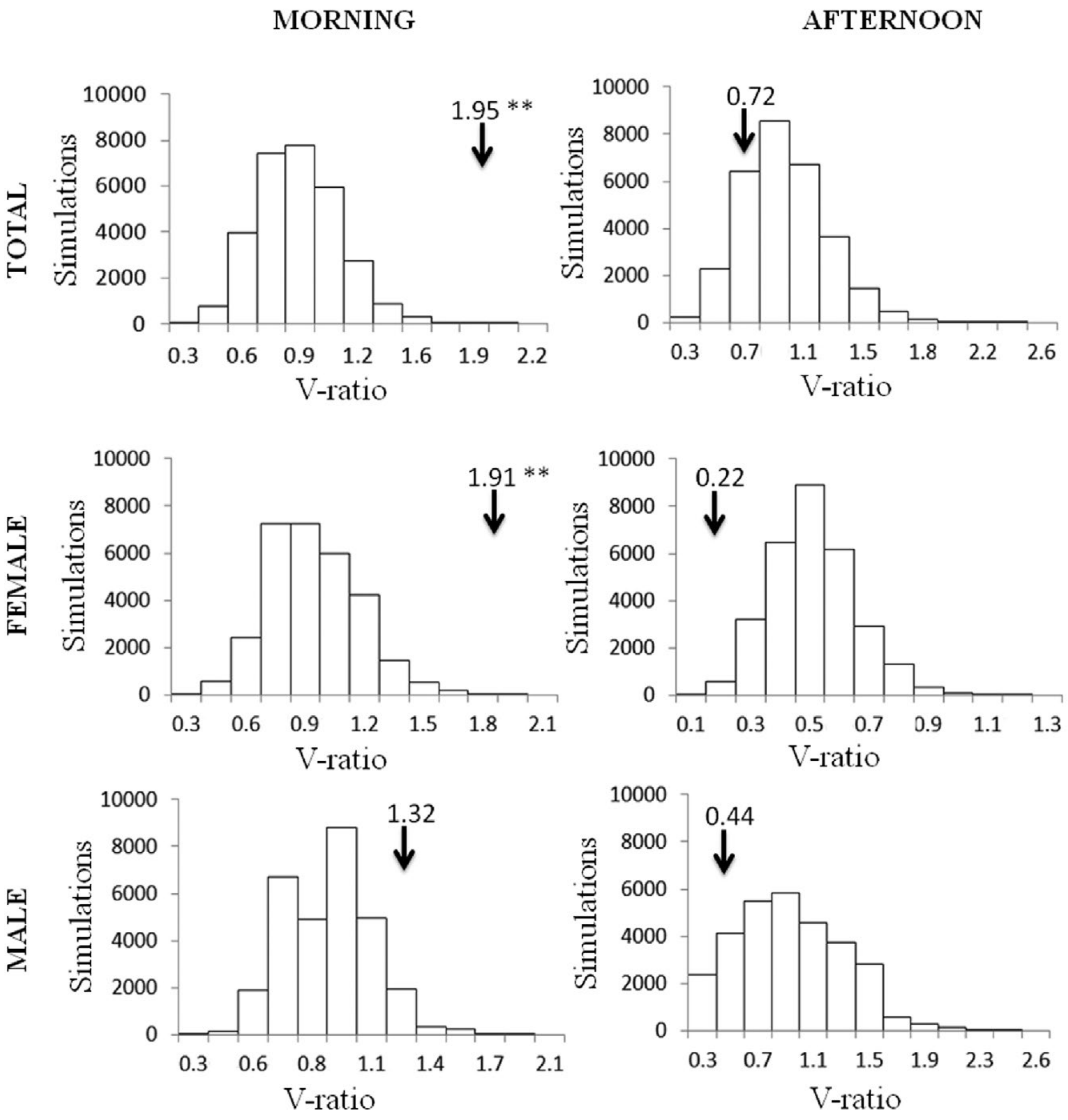

Fig. 4. Histograms summarizing the distribution of the V-ratio indices predicted for the simulated communities calculated including the results for the empty pan traps. The arrow indicates the observed V-ratio. Asterisk indicate an observed V-ratio significantly less than (one asterisk) or greater than (two asterisks) expected by chance (See Table 2 for *p* values).

influence nectar availability, as its production decreases. In addition, increased evaporation leads to a further reduction in volume (Edge et al., 2011). As a consequence, we hypothesize that the species active in the afternoon display negative co-occurrence due to interspecific competition for the limited resources. This is particularly the case for females as they are more dependent on pollen for egg maturation (Irvin et al., 1999). In addition, it is also the reason why females are more often found at the flower-rich ground level of forests than males (Birtele & Hardersen, 2012).

Potential biases in our results may arise from the sampling efficiency of the collecting method, as all trap types show a certain bias. However, this bias is similar for all traps and pan traps are commonly used in studies of hoverflies (e.g. Laubertie et al., 2006; Campbell & Hanula, 2007; Vrdoljak & Samways, 2012). In addition, it is often difficult to generalise from the results of regional projects, as they may depend on the particular geographical location or climate of the region. Our findings are supported by many studies which show that different pollinator taxa in a given community are active at different times of the day in order to avoid competition

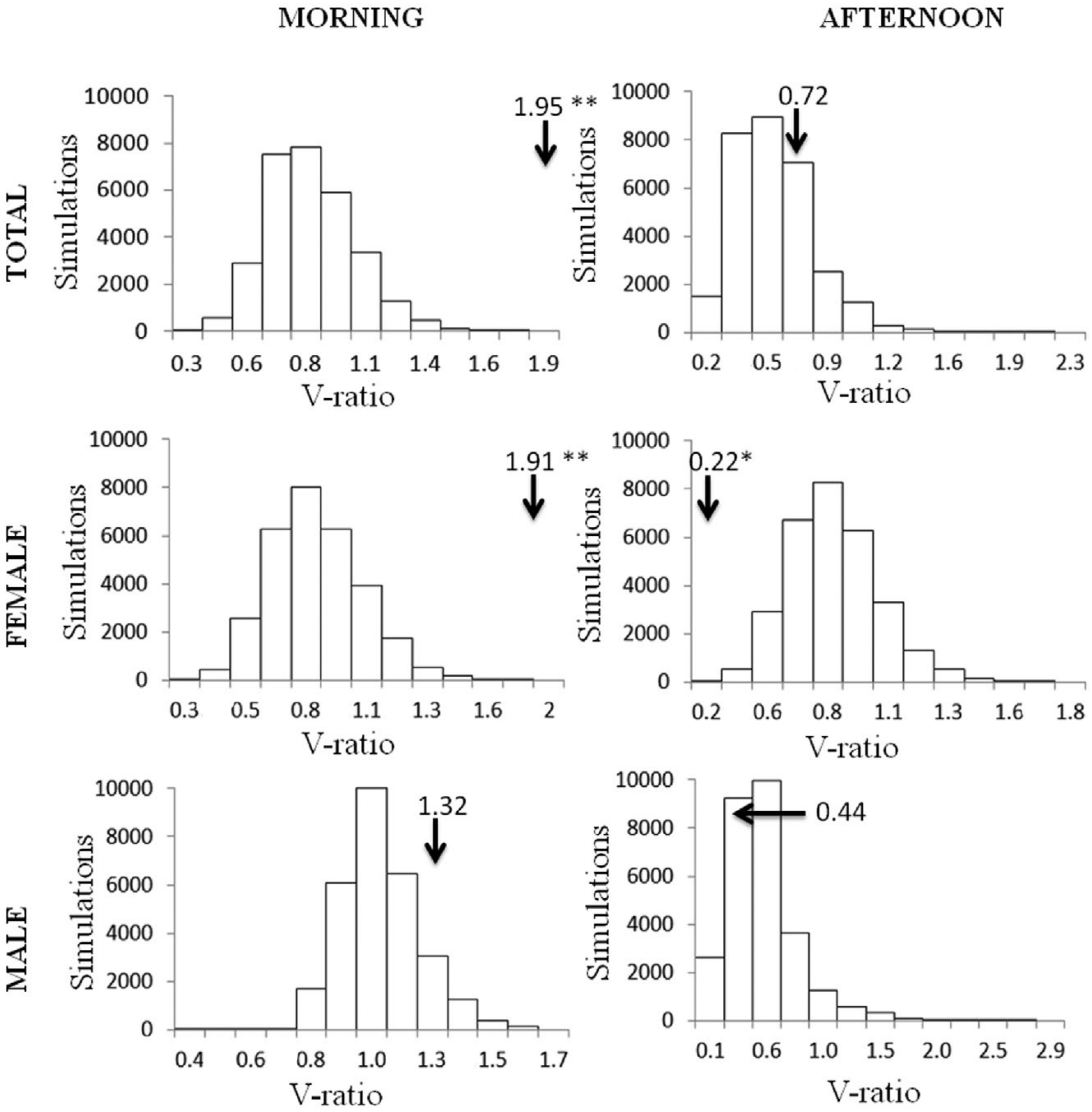

Fig. 5. Histograms summarizing the distribution of V-ratio indices predicted for simulated communities calculated excluding the results for the empty pan traps. The arrow indicates the observed V-ratio. Asterisk indicates an observed V-ratio significantly less than (one asterisk) or greater than (two asterisks) expected by chance (See Table 2 for *p* values).

(e.g. Willmer & Stone, 2004). As we studied only hoverflies, we cannot exclude the effect of competition with other pollinator taxa in determining the recorded changes in community structure. There is thus the potential for further investigations of the diurnal activities of hoverflies at other sites, and eventually the inclusion of other pollinator groups.

From a methodological point of view our findings suggest that time of day is important when interpreting hoverfly data. On the one hand, we showed that morning is the best time to collect hoverflies, which is well supported by the large literature on the ecology of this group (Gilbert, 1985). On the other hand, our study implies that restricting observations to a particular time of day would result in failure to detect certain species. In addition, by focusing on short intervals of time it would be impossible to analyze changes in species interactions throughout a day.

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