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A NEW EXCEPTION TO THE DOMINANCE-DISCOVERY TRADE-OFF RULE IN ANT COMMUNITIES (¹)

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Castracani C., Spotti F.A., Grasso D.A., Fanfani A., Mori A. - A new exception to the dominance-discovery trade-off rule in ant communities.

Interspecific competition is one of the main factor shaping ant community structure. The "dominance-discovery trade-off", an inverse relationship between interference and exploitative competitive ability, is thought to be a fundamental mechanism facilitating coexistence of ants. Despite its widely acceptance in literature, this trade-off appears to be broken in several cases and needs further investigations. Thus, the aim of the present study was to detect the presence/absence of the dominance-discovery trade-off in Mediterranean ant communities. Samplings were conducted inside the Presidential Estate of Castelporziano (Rome, Italy) and seven sampling sites were selected according to their vegetation structure. In each site, baiting was conducted to assess two behavioural indices for each species: the monopolization index and the discovery ability index. Correlation analyses showed no evidence for the existence of a dominance-discovery trade-off. Furthermore, a positive correlation between the two indices was detected in some of the sampling sites. The dominance-discovery trade-off seems therefore to be just one of the possible mechanisms facilitating species coexistence in ant communities.

KEY WORDS: interspecific competition, behavioural dominance, coexistence, ants, Castelporziano Estate.

INTRODUCTION

HÖLLDOBLER and WILSON (1990) defined competition as "the hallmark of ant ecology". Actually, several studies pointed out that interspecific competition is one of the main factor shaping ant community structure (FELLERS, 1987; SAVOLAINEN and VEPSÄLÄINEN, 1988; HERBERS, 1989; ANDERSEN, 1992; SANDERS and GORDON, 2003; PARR *et al.,* 2005). As a consequence, a key issue becomes what allows multiple ant species to coexist in a given habitat (ANDERSEN, 2008; LESSARD *et al.,* 2009). One consolidated hypothesis suggests that an evolutionary trade-off between interference and exploitative competitive ability may facilitate coexistence of ants: this is called "the dominance-discovery trade-off" (FELLERS, 1987). In other words, the ability of a species to discover food resources is inversely related to its ability to defend them. Hence, behaviourally subordinate species, better at discovering food resources, may coexist with behaviourally dominant species that easily monopolise those resources. This trade-off is widely cited in the ant ecology literature and has consequently received general acceptance (SAVOLAINEN and VEPSÄLÄINEN, 1988; PERFECTO, 1994; FEENER, 2000; ADLER *et al.,* 2007; DELSINNE *et al.,* 2007; PARR and GIBB, 2010, 2012; PEARCE-DUVET and FEENER, 2010). On the other hand, several studies document how the dominance-discovery trade-off can be broken by particular biotic factors (DAVIDSON, 1998; HOLWAY, 1999; LEBRUN and FEENER, 2007; ARNAN *et al.,* 2011) or environmental conditions (CERDÀ *et al.,* 1997; BESTELMEYER, 2000; SANTINI *et al.,* 2007; GIBB and PARR, 2010). Thus, the assumption that the trade-off is widespread in ant communities appears actually a hypothesis to be demonstrated and demands further investigations (PARR and GIBB, 2012). According to these requirements, the aim of the present study was to detect the presence/absence of the discovery-dominance trade-off in Mediterranean ant communities.

MATERIALS AND METHODS

Samplings were conducted inside the Presidential Estate of Castelporziano (Rome, Italy), which covers an area of almost 6000 hectares between Rome (S-SW) and the Tyrrhenian cost. Originally used as hunting reserve and farm, this area progressively changed its functions: since 1977 the hunting activity has been prohibited and the cultivated fields offer now a good example of eco-compatible management of agro-ecosystems. Declared Natural Reserve in 1999, the Estate shows a wide range of Mediterranean ecosystems and high levels of biodiversity: it hosts more than 1000 species of plants and more than 2900 species of animals. The area of the Natural Reserve is between 0 and 85 m (a.m.s.l.), with a mean slope of 5% to the sea, and the climate is meso-Mediterranean with a hot and dry period in summer (AA.VV., 2001, 2006).

Seven sampling sites were selected to study the most representative habitats of the Estate (DELLA ROCCA *et al.,*

2001). They are described as follows (for further details, see CASTRACANI *et al.*, 2010; SPOTTI *et al.,* 2010):

1. Cultivated Field (CF) - Fields cultivated with lucerne (*Medicago sativa*)
2. Dry Grassland (DG) - Dry pasture lands (*Dasypyrum villosum* and *Vulpia ligustica*)
3. Wet Grassland (WG) - Wet pasture lands (Molinio-Arrhenatheretea group plants)
4. Pine-wood (PW) - Reforestations with umbrella pines (*Pinus pinea*)
5. Pure Ilex Grove (PIG) - High scrub and Mediterranean wood (*Quercus ilex*)
6. Mixed Oak Wood (MOW) - Tyrrhenian deciduous oak wood (*Quercus cerris*, *Quercus frainetto*, *Carpinus orientalis*)
7. Mediterranean Scrub (MS) - Acidophilous Mediterranean woods and bushes (*Erica arborea*, *Quercus suber* and, subordinately, *Quercus ilex*).

The first three sites (CF, DG, WG) are characterized by the presence of low vegetation, whereas the other four sites (PW, PIG, MOW, MS) are arboreal habitats (high vegetation sites).

Sampling took place during July 2007. In every site, three parallel 100-m linear transects were set up: each one consisting of 10 traps with 10-m spacing. The first transect was composed of pitfall traps: the experimental protocol and the results from this data collection are shown in SPOTTI *et al.* (2010). The other two transects consisted of two types of food baits: cookie + honey (10 baits) or tuna + oil (10 baits). All resources were placed on graph paper squares (7x7 cm) with scotch-tape on the lower side to prevent liquid leakage under the bait. This kind of baits are commonly used in studies on ant community ecology to simulate naturally occurring, patchy, large food resources for which ants frequently compete (FELLERS, 1987; ANDERSEN, 1992; CERDÀ *et al.,* 1997; AGOSTI *et al.,* 2000; PARR *et al.,* 2005; FEENER *et al.,* 2008; LESSARD *et al.,* 2009; STUBLE *et al.,* 2012). Each bait was observed at 5, 15, 30 and 60 minutes after the beginning of the experiment. For each species, the number of individuals feeding on the resource was recorded. Ants at baits were identified directly in the field or collected for further identification using the dichotomous keys of HÖLLDOBLER and WILSON (1990) and BOLTON (1994). For some specimens identification at species level was achieved with the collaboration of Dr. Fabrizio Rigato (Natural History Museum of Milan, Italy). All specimens are preserved in the Laboratory of Myrmecology, Department of Life Sciences, University of Parma, Italy. In order to cover a wider range of foraging activity, baiting was run in early morning and replicated in late afternoon. A total of 280 baits were placed (10 baits x 2 types of food x 2 periods of the day x 7 site types).

For each species, data from baits enabled to calculate two behavioural indices: the Monopolisation Index (MI) and the Discovery Ability Index (DAI) (SANTINI *et al.,* 2007).

MI is the ratio between the number of monopolised baits and occurrence, that is the number of visited baits. A bait was considered monopolised by a species when, after 60 min, one of these three conditions occurred:

– the species was the only one at the bait and it occurred with at least 5 individuals (SANTINI *et al.*, 2007);
– there were two species at the bait and one was present with twice as many ants as the other one;
– there were two species at the bait and the non-monopolising one occurred with less than 5 individuals.

DAI is the ratio of discovered baits (i.e. the baits where a species is first to arrive) and occurrence.

The influence of food, time of day and their interactions on species occurrence was tested through a two-way independent ANOVA. Food and time of day were included as fixed factors. To test the existence of competition trade-offs, a Spearman's rank correlation coefficient (rho) was used to test pairwise correlations between the behavioural indices. All analysis were carried out using R version 3.0.2 (CRAN project software).

RESULTS

Baiting permitted to collect 20413 specimens belonging to 3 subfamilies, 14 genera and 23 species (Table 1). In the whole study area, two-way independent ANOVA on occurrence for each species underlined no significant effect for food, time of day nor their interactions (Table 1). Acquiring this result allowed considering the four transects placed in each site as four replicas of the same environment. Therefore, in order to evaluate the existence of a dominance-discovery trade-off in ant communities of Castelporziano, data from all transects of one site were pooled to calculate behavioural indices values for each species. Correlation tests between MI and DAI were not significant considering the whole community (Spearman rank correlation, $r_s = 0.369$, $p = 0.083$). According to high and low vegetation classification, the trade-off was still absent in the first group ($r_s = 0.222$, $p = 0.446$), whereas analyses showed a positive significant correlation for the community of low vegetation sites ($r_s = 0.676$, $p = 0.016$) (Fig. I, 1). In particular, MI and DAI were significantly correlated in WG ($r_s = 1$, $p = 0.040$) (Fig. I, 2) but not in CF ($r_s = 0$, $p = 1$) and in DG ($r_s = -0.389$, $p = 0.611$). Correlation tests for the remaining sites were not significant (PW: $r_s = -0.272$, $p = 0.728$; PIG: $r_s = -0.308$, $p = 0.552$; MOW: $r_s = 0.144$, $p = 0.786$; MS: no monopolising species). Nevertheless, the comparison between behavioural indices of the same species in different sites underlined some interesting differences. *Messor minor* changed indices values from DG to CF (DG: DAI = 0.45, MI = 0.6; CF: DAI = 0, MI = 1) as well as *Tetramorium caespitum* (DG: DAI = 0.5, MI = 0.5; CF: DAI = 1, MI = 1). Moreover, *Plagiolepis pygmaea* showed a reversal in indices values from PW to PIG (PW: DAI = 1, MI = 0; PIG: DAI = 0, MI = 1).

DISCUSSION

According to baiting data, there was no evidence for the existence of a dominance-discovery trade-off in the studied Mediterranean ant communities. On the contrary, a positive correlation between discovery ability (DAI) and monopolisation (MI) was detected in some of the environments chosen for the analyses. Therefore, we agree with PARR and GIBB (2012) suggesting that the dominance-discovery trade-off does not always play a major role in structuring ant assemblages. It is likely that multiple mechanisms contribute to facilitate species coexistence (ANDERSEN, 2008). For example, other trade-offs, such as between thermal tolerance and competitive ability, are likely to play a role in some habitats (CERDÀ *et al.,* 1998, 2013; BESTELMEYER, 2000; WIESCHER *et al.,* 2011). Partitioning the activity space and time is another way that ants use to avoid or reduce competition within their

Table 1 - Species Check list and Two-way independent ANOVA on species occurrence at baits. Food and time of day were included as fixed factors. No significant effect was detected for the factors nor their interactions.

Species	Factor	d.f.	F	P
Aphaenogaster subterranea (Latreille 1798)	Food	1, 24	2.0833	0.1613
	Time slot	1, 24	0.0000	1.0000
	Interaction	1, 24	0.0000	1.0000
Camponotus lateralis (Olivier 1792)	Food	1, 24	1.0000	0.3273
	Time slot	1, 24	1.0000	0.3273
	Interaction	1, 24	1.0000	0.3273
Camponotus vagus (Scopoli 1763)	Food	1, 24	0.3333	0.5691
	Time slot	1, 24	0.3333	0.5691
	Interaction	1, 24	0.3333	0.5691
Crematogaster scutellaris (Olivier 1792)	Food	1, 24	1.7363	0.2000
	Time slot	1, 24	0.5034	0.4848
	Interaction	1, 24	0.8322	0.3707
Formica cunicularia Latreille 1798	Food	1, 24	0.2658	0.6109
	Time slot	1, 24	0.4394	0.5137
	Interaction	1, 24	0.0488	0.8270
Lasius lasioides (Emery 1869)	Food	1, 24	1.0000	0.3273
	Time slot	1, 24	1.0000	0.3273
	Interaction	1, 24	1.0000	0.3273
Lasius paralienus Seifert 1992	Food	1, 24	0.1935	0.6639
	Time slot	1, 24	0.0000	1.0000
	Interaction	1, 24	0.7742	0.3876
Messor capitatus (Latreille 1798)	Food	1, 24	2.0769	0.1625
	Time slot	1, 24	2.0769	0.1625
	Interaction	1, 24	2.0769	0.1625
Messor minor (André 1883)	Food	1, 24	0.1200	0.7320
	Time slot	1, 24	0.1200	0.7320
	Interaction	1, 24	0.0000	1.0000
Messor wasmanni Krausse 1910	Food	1, 24	0.2222	0.6416
	Time slot	1, 24	0.2222	0.6416
	Interaction	1, 24	0.0000	1.0000
Monomorium monomorium Bolton 1987	Food	1, 24	0.0681	0.7963
	Time slot	1, 24	0.2207	0.6427
	Interaction	1, 24	0.0245	0.8769
Myrmica scabrinodis (Nylander 1846)	Food	1, 24	0.7826	0.3851
	Time slot	1, 24	0.0870	0.7706
	Interaction	1, 24	0.0000	1.0000

| Species	Factor	d.f.	F	P
Pheidole pallidula (Nylander 1849)	Food	1, 24	0.1412	0.7104
	Time slot	1, 24	0.5647	0.4597
	Interaction	1, 24	0.0000	1.0000
Plagiolepis pygmaea (Latreille 1798)	Food	1, 24	0.3429	0.5637
	Time slot	1, 24	0.3429	0.5637
	Interaction	1, 24	0.3429	0.5637
Solenopsis fugax (Latreille 1798)	Food	1, 24	0.6667	0.4222
	Time slot	1, 24	0.6667	0.4222
	Interaction	1, 24	0.0000	1.0000
Tapinoma subboreale Seifert 2012	Food	1, 24	0.0105	0.9191
	Time slot	1, 24	0.8526	0.3650
	Interaction	1, 24	0.0947	0.7609
Tapinoma erraticum (Latreille 1798)	Food	1, 24	1.0000	0.3273
	Time slot	1, 24	1.0000	0.3273
	Interaction	1, 24	1.0000	0.3273
Temnothorax alienus Schulz, Heinze & Pusch, 2007	Food	1, 24	0.0000	1.0000
	Time slot	1, 24	0.0000	1.0000
	Interaction	1, 24	0.0000	1.0000
Temnothorax nylanderi (Foerster, 1850)	Food	1, 24	1.0000	0.3273
	Time slot	1, 24	1.0000	0.3273
	Interaction	1, 24	1.0000	0.3273
Temnothorax parvulus (Schenck, 1852)	Food	1, 24	0.5647	0.4597
	Time slot	1, 24	2.2588	0.1459
	Interaction	1, 24	0.5647	0.4597
Temnothorax unifasciatus (Latreille, 1798)	Food	1, 24	0.9494	0.3396
	Time slot	1, 24	0.9494	0.3396
	Interaction	1, 24	0.3418	0.5643
Tetramorium caespitum (Linnaeus, 1758)	Food	1, 24	0.2182	0.6446
	Time slot	1, 24	0.0000	1.0000
	Interaction	1, 24	0.8727	0.3595
Tetramorium moravicum Novák & Sadil, 1941	Food	1, 24	0.4000	0.5331
	Time slot	1, 24	1.6000	0.2180
	Interaction	1, 24	0.4000	0.5331
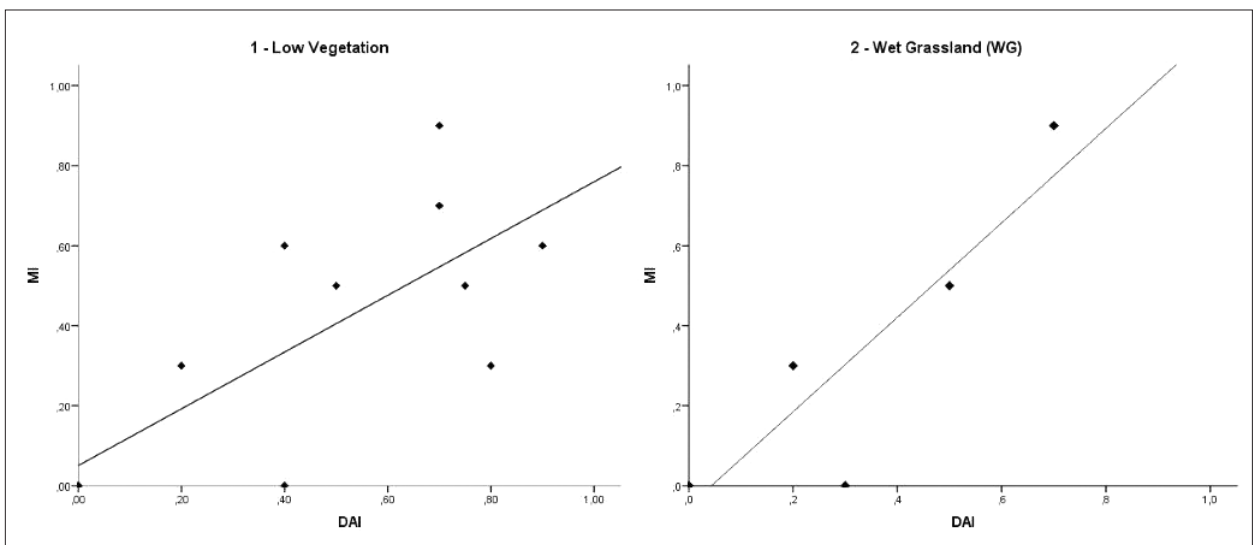
Fig. I - Correlation analyses between the behavioural indices MI and DAI. In pooled low vegetation sites (1) and in WG (2), a positive significant correlation was detected. (1): $r_s = 0.676$, $p = 0.016$. (2): $r_s = 0.832$, $p = 0.040$.

community (CROS *et al.,* 1997; ALBRECHT and GOTELLI, 2001; MOONEY and TILLBERG, 2005; SOLIDA *et al.,* 2011, 2014).

Moreover, habitat complexity and vegetative structure are among the main factors affecting community dynamics (CERDÀ *et al.,* 2013). For example, the increased heterogeneity and rugosity of structurally complex habitats may reduce the chance of species interactions, thus facilitating coexistence (PARR and GIBB, 2012). It was likely the case of Wet Grassland (WG), according to the results we found in our previous study with pitfall traps (SPOTTI *et al.,* 2010) and the present one with baits. Maybe the higher level of complexity and diversification of this habitat supported a variegated ant assemblage, as we found with pitfall trapping, even if there were species extremely dominant from a behavioural point of view.

In addition, the present results highlighted a trend of some species behaviour to be affected by the site type. Actually, we recorded a change in monopolisation and discovery ability of the same species in different sites. These differences could not be detected considering only data on numerical dominance, but they add important pieces of information on community dynamics. Further investigations are needed to understand what are the main factors that may influence this aspect, such as vegetative structure or competitive interactions. We conclude that an integrated approach considering numerical and behavioural data is a useful tool to analyse ant community coexistence mechanisms more in details.

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