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The multidimensional behavioural hypervolumes of two interacting species predict their space use and survival

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Individual animals differ consistently in their behaviour, thus impacting a wide variety of ecological outcomes. Recent advances in animal personality research have established the ecological importance of the multidimensional behavioural volume occupied by individuals and by multispecies communities. Here, we examine the degree to which the multidimensional behavioural volume of a group predicts the outcome of both intra- and interspecific interactions. In particular, we test the hypothesis that a population of conspecifics will experience low intraspecific competition when the population occupies a large volume in behavioural space. We further hypothesize that populations of interacting species will exhibit greater interspecific competition when one or both species occupy large volumes in behavioural space. We evaluate these hypotheses by studying groups of katydids (*Scudderia* nymphs) and froghoppers (*Philaenus spumarius*), which compete for food and space on their shared host plant, *Solidago canadensis*. We found that individuals in single-species groups of katydids positioned themselves closer to one another, suggesting reduced competition, when groups occupied a large behavioural volume. When both species were placed together, we found that the survival of froghoppers was greatest when both froghoppers and katydids occupied a small volume in behavioural space, particularly at high froghopper densities. These results suggest that groups that occupy large behavioural volumes can have low intraspecific competition but high interspecific competition. Thus, behavioural hypervolumes appear to have ecological consequences at both the level of the population and the community and may help to predict the intensity of competition both within and across species.

Consistent individual differences in behaviour, known as animal personality, appear to be ubiquitous throughout the animal kingdom (Gosling, 2001; Kralj-Fišer & Schuett, 2014). Animal personality determines aspects of individuals' ecology such as individual variation in social behaviour (Lichtenstein et al., 2016; Wright, Holbrook, & Pruitt, 2014) space use (Pearish, Hostert, & Bell, 2013; Wilson & McLaughlin, 2007) and diet (Wilson, Coleman, Clark, & Biederman, 1993). The personality literature has long argued that a comprehensive understanding of an individual's behaviour requires a multitrait approach (Sih, Bell, & Johnson, 2004; Sih, Cote, Evans, Fogarty, & Pruitt, 2012). Despite this early emphasis on a multitrait approach and the availability of statistical approaches to evaluate multiple behaviours simultaneously, many studies that relate personality to ecological outcomes continue to examine only one trait at a time (Wolf & Weissing, 2012). Here we examine multiple behaviours simultaneously using a recently developed multivariate measure, the behavioural hypervolume (Pruitt, Bolnick, Sih, DiRienzo, & Pinter-Wollman, 2016; Pruitt et al., 2017).

We define a behavioural hypervolume as the volume of an irregular convex polygon in multidimensional behavioural space occupied by an individual, a group, a population or even a community. Multidimensional behavioural space refers to a space in which each dimension represents standardized performance in a different personality test. In other words, behavioural hypervolumes are a metric of behavioural diversity that incorporates three or more personality traits. Behavioural hypervolumes emphasize behavioural extremes, because observations on the boundaries of these shapes in behavioural space dictate their

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hypervolume (Pruitt et al., 2016, 2017). Consequently, individuals in convex polygons that occupy more behavioural space at the group or population level tend to be more behaviourally dissimilar to each other, at least, when one considers the most extreme individuals. This dissimilarity may, in turn, map to individuals' ecological niche, including the degree to which they compete with conspecifics and heterospecifics. There is considerable evidence to suggest that this is true: individual variation in personality often predicts how individuals interact with conspecifics (Kurvers et al., 2009; Laskowski & Bell, 2013) and heterospecifics (Chang, Teo, Norma-Rashid, & Li, 2017; DiRienzo, Pruitt, & Hedrick, 2013; Webster, Ward, & Hart, 2009). Thus, behavioural hypervolumes may impact ecological processes.

For instance, recent work has shown that the behavioural hypervolume of a group can influence the outcome of predator–prey interactions (Pruitt et al., 2017), and the behavioural hypervolume of a mixed-species community can determine their stability (Pruitt et al., 2016). Here we examine whether the behavioural hypervolumes of groups of interacting species can predict the outcome of both intra- and interspecific interactions. We evaluate this possibility by examining two insect species that inhabit and feed on the Canada goldenrod, *Solidago canadensis*. We chose these two species because they are two of the most common insects in old fields, they share a resource and they are found on the same plant parts, especially leaves near the crown, which suggests that they may compete for access to the most preferred regions of their host plant (J. L. L. Lichtenstein & B. McEwen, personal observation). Katydid nymphs from the genus *Scudderia* and the meadow froghopper, *Philaenus spumarius*, both feed on the Canada goldenrod (Weaver & King, 1954). Notably, *Scudderia* nymphs are leaf chewers native to our study site, whereas the froghoppers, *P. spumarius*, are sap-suckers that are wildly successful invaders across the Nearctic. These froghoppers are in some areas the second most abundant herbivore on goldenrods (Root & Cappuccino, 1992) and have more deleterious effects on goldenrod growth and reproduction than other herbivores (Meyer & Root, 1993; Meyer, 1993). Both species reach high densities on goldenrod leaves over large geographical ranges, thus creating ample opportunities for both species to interact with both conspecifics and each other.

Here, we ask whether behavioural hypervolumes shape how each species interacts with conspecifics (intraspecific interaction) and with other species (interspecific interaction). Specifically, we evaluated two predictions. First, we predicted that single-species groups of katydids with greater behavioural hypervolumes would cluster together in space more than groups with small behavioural hypervolumes. We reasoned that individuals in single-species groups occupying larger hypervolumes differ from each other more in their niches, thus reducing intraspecific competition. This is based on the assertion that personality traits relate to the ecological niche that individuals occupy, such as differences among individuals in diet (Wilson et al., 1993) and space use (Pearish et al., 2013; Wilson & McLaughlin, 2007).

Second, we predicted that greater behavioural hypervolumes in katydids, froghoppers, or both, would decrease the survival of froghoppers due to interspecific competition. There is considerable evidence showing that individuals' personality scores relate to the strategies that animals use when interacting with other species (Belgrad & Griffen, 2016; Chang et al., 2017; DiRienzo et al., 2013; Webster et al., 2009). Therefore, we reasoned that behaviourally diverse groups would contain a greater diversity of these interaction strategies, thus causing them to interact with other species more frequently and intensely. Addressing these hypotheses will allow us to further evaluate the ecological consequences of behavioural hypervolumes and potentially extend the ecological niche concept to behavioural or personality ‘niches’.

METHODS

Collection Site and Study Organisms

We performed our experiments at the Donald S. Wood Field Laboratory (DSW) of the Pymatuning Laboratory of Ecology in June, July, and August 2016. The DSW is located in northwest Pennsylvania (41°34′09.6″N, 80°27′51.4″W). The property is composed of mixed forest and semiannually mowed old field. The old field portion is dominated by the goldenrod species *Solidago canadensis*, *Solidago grandiflora* and *Solidago rugosa*, in order of relative abundance. At our collection site, these species tend to form dense monospecific stands comprising hundreds or thousands of stems with a few lone stems scattered around (J. L. L. Lichtenstein & B. McEwen, personal observation). We collected roughly 1000 froghoppers, *P. spumarius* (Aphrophoridae), and approximately 400 third- to seventh-instar katydid nymphs from the genus *Scudderia* (Tettigoniidae) from a 40 × 60 m section of the old field via sweep netting. *Philaenus spumarius* are an invasive insect native to the Palearctic that has spread over the entire Nearctic and feeds on hundreds of plant species, including *S. canadensis* (Weaver & King, 1954). At an average length of 6 mm, froghoppers are much smaller than katydid nymphs but they are the longest and fastest-jumping insect species relative to body size yet measured, surpassing even fleas (Burrows, 2003). They reach densities of more than 15 individuals per host plant at our site (J. L. L. Lichtenstein & B. McEwen, personal observation). Katydid nymphs of the two species that occur at our site (*Scudderia curvicauda* and *Scudderia furcata*) are indistinguishable as nymphs and preferentially inhabit moist and poorly drained old field areas (Cantrall, 1943). We found both of these insects frequently in *S. canadensis* stands and observed them feeding on *S. canadensis* leaves in the laboratory and in situ. After we captured the insects, we kept each individual in a 50 ml tube (12 cm tall, 3 cm diameter) with an *S. canadensis* leaf. Aside from the insects we used for our personality repeatability trials described below, we did not keep insects in tubes for more than 24 h.

Behavioural Assays

To acquire behavioural hypervolumes, we ran our insects through three behavioural tests: (1) perch height (i.e. habitat use), (2) activity level and (3) boldness. We performed these tests in the same sequence for each individual before returning them to their home containers, with 2 h between tests of different behaviours. To assess the repeatability of these traits, we performed each behavioural assay on each individual once per day for four consecutive days on 13 froghoppers and 12 katydid nymphs. After establishing the repeatability of these behaviours, we concluded that our behavioural assays quantified temporally consistent personality traits in these species. This allowed us to run individuals in each behavioural assay only once for the mesocosm and space use studies (described below).

Perch height

To quantify an individual's perch height, we measured the height at which an individual perched in a novel 50 ml storage tube containing a single leaf of their host plant. We made sure that each tube had a leaf of a similar size (6–7 cm length). This species spends much of their time on goldenrod leaves, particularly near the crown of the plant. Therefore, we measured the specific location on leaves where they might spend most of their time. The trial was initiated by setting an individual at the bottom of a clean tube and then gently placing a leaf so that it extended up the side of the tube, with the stem facing downward. We then permitted the