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Social context, but not individual personality, alters immigrant viability in a spider with mixed social structure

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Immigrant viability is a major determinant of the realized rate of gene flow across populations. For social organisms, the social context in which immigrants disperse across contrasting environments may have important implications for their viability post dispersal. Here, we use social spiders whose individual personalities as well as group personality compositions vary across sites to test whether the strength of selection against immigrants (i.e. mortality rates) differs depending on whether spiders are transplanted (1) as individuals and remain alone, (2) join pre-existing colonies at their new non-native environment, or (3) move with their native group. We also tested for an effect of individual personality on survival. We found that social context, and not individual personality, affects individual survival in foreign environments with contrasting resource levels. Individuals that were transplanted with their native groups suffered higher mortality rates compared to individuals transplanted as singletons, regardless of whether or not they were assimilated into native colonies. Moving as individuals could thus provide an avenue for ongoing gene flow among populations from different resource environments. We found no depressed performance of control colonies that were transplanted across sites with resource levels similar to each colony's site of origin. These results are at odds with the intuition that dispersing as a group should generally enhance the viability of immigrants, at least in social species. We propose that these results could be explained by a mismatch in the ideal group compositions (personality compositions) favoured in different environments, despite a lack of selection on individual personality traits. These results provide a first glimpse into the relative roles of individual personality and social context in mediating gene flow among populations from divergent environments.

Ecology has often considered individual variation in animal behaviour within populations to be noise around an adaptive mean, or to be due to human sampling or observational error (Wilson, 1998). However, the past two decades have seen a surge in empirical evidence that such interindividual variation in behaviour represents an ecologically and evolutionarily significant behavioural phenomenon, often dubbed 'animal personality' (Gosling, 2001; Ingley & Johnson, 2014; Réale, Dingemanse, Kazem, & Wright, 2010; Sih, Bell, & Johnson, 2004; Wolf & Weissing, 2012). The field of animal personality describes interindividual behavioural tendencies that are consistent through time (either short or long term) and across various ecological contexts (e.g. mating, feeding, or interspecific interactions), which has been a pattern of interest to psychologists for decades (Gosling, 2001; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih et al., 2004). Animal personalities, like their human analogues, are often heritable (Réale et al., 2007; Wolf & Weissing, 2012), although environmental factors can also have notable effects on personality (Dingemanse et al., 2009). Interestingly, different personality axes (e.g. 'boldness' or 'aggressiveness'; also known as 'behavioural types') often covary predictably across a variety of species. This recognition has led to the emergence of a body of literature that addresses the ecological and evolutionary causes and consequences of this variation (Réale et al., 2007; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Sih et al., 2004; Wolf & Weissing, 2012).

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Because animal personality variation is often linked with individual fitness in a site-specific manner (Dall, Houston, & McNamara, 2004; Dingemanse & Réale, 2005; Smith & Blumstein, 2008), it has the potential to contribute to the speciation process by limiting realized gene flow (i.e. dispersal and subsequent reproduction) across environments (Ingley & Johnson, 2014). Local adaptation has long been a central topic in ecology and evolution because adaptive, specialized traits can allow species to expand into new environments, which in turn can help promote diversification (Coyne & Orr, 2004; Funk, 1998; Rundle & Nosil, 2005; Sandoval & Nosil, 2005; Schluter, 2000). Populations that occur in different selective regimes often become locally adapted to their native environment, sometimes resulting in phenotypic trade-offs (i.e. negative correlations among beneficial traits) in one or more ecologically relevant, fitness-determining traits (Agrawal, Conner, & Rasmann, 2010; Ingley & Johnson, 2016a, 2016b; Joshi & Thompson, 1995; Schluter, 2000; Via, Bouck, & Skillman, 2000). These trade-offs may then lead to the emergence of closely related populations that differ substantially in one or more traits. Where divergent traits are locally adaptive, but maladaptive in non-native selective regimes, movement of individuals among populations, and consequently realized gene flow, can be restricted by selection (Coyne & Orr, 2004; Dobzhansky, 1937; Mayr, 1942, 1963; Nosil, 2012; Nosil, Vines, & Funk, 2005).

Social organisms add an additional layer of complexity to the study of local adaptation and its consequences for realized gene flow and population connectivity. This is because local adaptation can occur both in individual phenotypes (Riechert, 1993; Storfer & Sih, 1998) and in the collective traits of groups (Gordon, 2013; Pruitt & Goodnight, 2014). Thus, whether realized gene flow is reduced or maintained among populations of social organisms could rely on patterns of local adaptation and divergent selection on both tiers of phenotypes. For example, realized gene flow among populations could be maintained if divergent selective regimes act on maladapted collective traits but not on individual traits, such that individuals that disperse alone could potentially escape the consequences of group selection and successfully join, survive and reproduce in existing groups. Thus, in social organisms, the social context in which an individual disperses (i.e. whether an individual disperses as a singleton, joins a pre-existing group, or moves with its natal group), beyond only the trait expressed in the individual, could have profound consequences for immigrant success in a novel environment. To date, tests of the role of social context versus individual traits are lacking.

Recent work on the social spider *Anelosimus studiosus* (Araneae, Theridiidae) suggests that it is well suited for evaluating the effects of individual personality and social context on patterns of gene flow across populations. Populations across Appalachia in eastern North America repeatedly occur in divergent ‘resource environments’ (which include differences in the amount of resources, social parasites and disease outbreaks, despite very similar forest structure), with populations near dams having higher resource availability, more social parasites and more disease outbreaks than populations situated away from dams but still close to rivers (Pruitt, 2012, 2013). These populations have been found to have site-specific ratios of docile to aggressive individuals (Pruitt & Goodnight, 2014), and these ratios affect colony success (Pruitt, 2012, 2013). High-resource environments favour an increasingly aggressive colony composition as they increase in size, while the opposite is favoured in low-resource environments. Furthermore, naturally occurring colonies exhibit personality mixtures that promote colony survival at their site of origin (Pruitt & Goodnight, 2014). These personality traits (as well as group trait mixtures) are highly repeatable and heritable (Pruitt & Goodnight, 2014). Thus, individual personality traits, the personality mixture of a colony, or both, potentially play an important role in the fitness of immigrants as they move from one resource environment to another. Here we critically evaluate (1) whether an individual immigrant's personality, its social context (i.e. dispersing as a singleton, joining a pre-existing group, or moving with its natal group), or both determine its viability in a divergent environment; and (2) whether realized gene flow (i.e. dispersal and subsequent reproduction) across populations of *A. studiosus* is lower than the migration rate, particularly given the available evidence for strong selection on and apparent local adaption in groups' compositions (Pruitt & Goodnight, 2014).

We present findings here from a reciprocal transplant experiment in which we simulate immigration of *A. studiosus* from one resource environment to an opposing resource environment in three social contexts, all of which occur in nature: movement outside a colony as singleton individuals; movement as intact foreign colonies (e.g. rafting colonies after storms); and movement as singleton individuals into native colonies. These treatments mimic dispersal conditions observed in *A. studiosus* and other species of subsocial or social spiders: long-distance dispersal as singletons (Powers & Aviles, 2003), many of which remain as singletons post dispersal (Jones, Pruitt, & Riechert, 2010); group budding/bridging behaviour (in which an entire colony disperses, often assisted by birds/bats, or storms; Lubin & Robinson, 1982); and individuals joining resident groups (Lubin, Birkhofer, Berger-Tal, & Bilde, 2009). Our results are significant because they provide a first glimpse into the relative role of individual traits and social context in shaping patterns of gene flow across populations of social animals.

METHODS

Reciprocal Transplant Experiment

Colony collection and laboratory maintenance

Anelosimus studiosus colonies containing recently matured females were collected at four field sites in May 2015: Melton Hill, Tennessee (high resource), IC King, Tennessee (low resource), Chilhowee, Tennessee (high resource), Cheoah, Virginia (low resource; see Pruitt & Goodnight, 2014, for site details). For all sites we focused on recently matured females because both aggressive and docile phenotypes (see below) are less aggressive as juveniles (Riechert & Jones, 2008), but more aggressive when gravid or guarding eggcases (Watts, Ross, & Jones, 2015); using only recently matured females allowed us to avoid potentially confounding effects of age and reproductive state on behavioural measures. We determined age by carefully monitoring populations' phenology to ensure we conducted behavioural assays at the moment that individual differences were most pronounced, and when we could hold most other variables constant. Once collected, colonies were transported to a laboratory at the University of Tennessee Knoxville and dissected by hand. The number of resident females was counted and their personality was determined using an interindividual distance test (described below). Females were then deployed into the field in one of three social conditions (described below). All spiders included in the study were held in the laboratory for no longer than 48–72 h prior to being deployed into the field.

Interindividual distance test

To determine females' personality types, two individually marked females of unknown personality type were placed in a clear, square plastic container. Females were then given 24 h to settle and construct webbing. Docile females tend to aggregate with conspecifics, whereas aggressive females demand space from conspecifics. Females were deemed docile if they exhibited an interindividual distance of <7 cm. Females that exhibited an