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

RUNNING TITLE: Social context and immigrant viability

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ABSTRACT

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, which vary in individual personality as well as the group personality compositions across sites, to test if the strength of selection against immigrants (i.e., mortality rates) differs depending on whether spiders are transplanted i) as individuals and remain alone, ii) join pre-existing colonies at their new non-native environment, or iii) 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 suffer higher mortality rates compared to individuals transplanted as singletons, regardless of whether or not they are 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 colonies' 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) favored 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.

KEYWORDS: Immigrant inviability; personality; natural selection, group composition;
reproductive isolation; local adaptation

INTRODUCTION

Ecology has often considered individual variation in animal behavior 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 inter-individual variation in behavior represents an ecologically and evolutionarily significant behavioral phenomenon, often dubbed ‘animal personality’ (Gosling, 2001; Ingley & Johnson, 2014; Reale, Dingemanse, Kazem, & Wright, 2010; Sih, Bell, & Johnson, 2004; Wolf & Weissing, 2012). The field of animal personality describes inter-individual behavioral tendencies that are consistent through time (either short or long term) and across various ecological contexts (e.g., mating, feeding, or inter-specific interactions), which has been a pattern of interest to psychologists for decades (Gosling, 2001; Reale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih et al., 2004). Animal personalities, like their human analogues, are often heritable (Reale 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’; a.k.a. ‘behavioral types’) often co-vary 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 (Reale et al., 2007; Sih et al., 2004; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2012).

Because animal personality variation is often linked with individual fitness in a site-specific manner (Dall, Houston, & McNamara, 2004; Dingemanse & Reale, 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 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 who move 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 vs. 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 favor an increasingly aggressive colony composition as they increase in size, while the opposite is favored 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 i) 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 ii) 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 behavior [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.

MATERIALS AND METHODS

Reciprocal Transplant Experiment

Colony Collection and Lab Maintenance

A. 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 egg cases (Watts, Ross, & Jones, 2015); using only recently matured females allowed us to avoid potentially confounding effects of age and reproductive state on behavioral measures. We determined age by carefully monitoring populations' phenology to ensure we conducted behavioral assays at the moment 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 inter-individual 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 lab for no longer than 48-72 hours prior to being deployed into the field.

Inter-individual Distance Test

In order 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 24h 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 inter-individual distance measure $<7\text{cm}$. Females that exhibited an inter-individual distance $>7\text{cm}$ were scored preliminarily as aggressive. However, each female that tested as aggressive in this first trial was retested with a known docile female. This is because one of the

two spiders that tested as aggressive in the first test might actually be docile, but was prevented from aggregating because of the aggressiveness of the other spider. A distance of 7cm corresponds with a natural break/lull in the distribution of inter-individual distance measures in this species and most social *Anelosimus* (Pruitt & Goodnight, 2014; J. N. Pruitt, S. E. Riechert, & T. C. Jones, 2008). These inter-individual distance measures are highly repeatable and heritable in *A. studiosus* (Pruitt & Goodnight, 2014). We refrain from referring to these phenotypes as “aggregative” vs. “solitary” here and elsewhere because both phenotypes can be found in isolation and within multi-female colonies. Moreover, multi-female colonies have higher success when both phenotypes are present (Pruitt & Riechert, 2011a) potentially because of division of labor (Wright, Holbrook, & Pruitt, 2014).

We used a subset of individuals from each site to confirm that the docile/aggressive distinction is repeatable in these populations of *A. studiosus* (Melton Hill N = 20, IC King N = 14, Chilhowee N = 18, Cheoah N = 15). Individuals were assayed once every three days for 12 days (totaling 4 observations per individual). As seen in previous studies, we detected very high intraclass correlation coefficients (ICC) for each population using the ICC Package in R (Melton Hill ICC = 0.58 [0.37, 0.79], IC King ICC = 0.35 [0.05, 0.65], Chilhowee ICC = 0.51 [0.27, 0.75], Cheoah ICC = 0.75 [0.58, 0.92]). This finding reiterates a high degree of temporal consistency in these traits (Pruitt & Goodnight, 2014; Pruitt & Riechert, 2009, 2011b; Jonathan N. Pruitt, Susan E. Riechert, & Thomas C. Jones, 2008).

Social treatments

A subset of assayed females were deployed at foreign sites that exhibited the opposite resource levels of the individuals' site of origin in one of three social settings. All members of a colony

were passed through the personality assays, following which each female was assigned a number, and a focal female selected using a random number generator. Focal females were all individually marked using non-toxic colored paint pens. A unique sequence of colored dots was painted atop their cephalothorax prior to being deployed to the field, allowing us to track the mortality of individual females and estimate the proportion of individual mortality events attributable to colony extinctions. A subset of females was marked and released as singleton individuals outside of any colony (Chilhowee→Cheoah, N = 29; Cheoah→Chilhowee, N = 29; Melton Hill → IC King, N = 29; IC King→Melton Hill, N = 28). This treatment mimicked individual dispersal events and allowed us to test viability of individual immigrants in their non-native resource environment. These individuals are potentially important in this context because pre-mated females have the ability to establish a colony on their own. A second subset of females was marked and released with all original colony members placed as a group at a foreign site with a mismatched resource environment (Chilhowee→Cheoah, N = 16; Cheoah→Chilhowee, N = 15; Melton Hill → IC King, N = 17; IC King→Melton Hill, N = 18). This treatment allowed us to mimic colony dispersal events, and test viability of immigrants when dispersing with their native colonies to foreign environments with contrasting resource levels. A third subset of females was marked and introduced individually into a pre-existing colony at a new site (Chilhowee→Cheoah, N = 15; Cheoah→Chilhowee, N = 13; Melton Hill → IC King, N = 16; IC King→Melton Hill, N = 17). This treatment allowed us to mimic a situation where immigrants join existing colonies to form a chimeric colony. Spiders were released in May 2015. Although likely somewhat rare, dispersal events of the magnitude and social contexts simulated here have been documented in nature and are thus ecologically relevant (Jones & Parker, 2002; Riechert & Jones, 2008).

Following release, we monitored the survival of marked focal females (one per colony) twice weekly for the next three months and recorded whether each female survived long enough to produce an egg case and for that egg case to hatch. *A. studiosus* has obligate parental care, thus the viability of egg cases is contingent on their mother's survival (Jones, Riechert, Dalrymple, & Parker, 2007), so all females that die prior to the hatching of their egg cases have a fecundity of 0. We therefore only modeled survival as a binary response (yes or no), rather than looking at the time of death. We also monitored colony survival and recorded whether individual mortality events were linked with colony extinction events. A range of 30-90% of *A. studiosus* colonies go extinct each year, and colony extinction events are thought to be the major driver of individual mortality in this species (Pruitt, 2012, 2013; Pruitt & Goodnight, 2014). We define a colony extinction event as a case where we observe no surviving colony members, mass mortality (spider carcasses), and no new colonies appearing in a 3-meter vicinity. Approximately 95-99% of individuals disperse within 2 meters of their parental colony when they disperse (unpublished data), thus, if we observe no new colonies in the immediate vicinity, then we can conclude with high levels of certainty that the colony has gone extinct.

Control treatments

To assess the degree to which manipulating and transplanting colonies impacts their viability, we compared the extinction rates of three different classes of colonies: i) colonies that were disassembled, reassembled and deployed at a foreign site with a resource level that mismatched the source levels of individuals' home sites (see above for sample sizes); ii) colonies that were disassembled, reassembled and deployed at a foreign site that matched the resource levels of individuals' home sites (Chilhowee → Melton Hill, N = 13; Melton Hill → Chilhowee, N = 13;

Cheoah → IC King, N = 11; IC King → Cheoah, N = 14); and iii) control colonies that remained completely unaltered and remained at their original home site (Chilhowee, N = 13; Melton Hill, N = 10; Cheoah, N = 11; IC King, N = 17). A prior study showed that survival rates of experimental colonies that are disassembled, reassembled and redeployed at their native site are statistically indistinguishable from unaltered control colonies (Pruitt & Goodnight, 2014), even with very large sample sizes (318 colonies deployed across 6 sites). Thus, if there is any effect of our manipulations on colony survival rates, it must be very small indeed. A graphical description of the transplant experiments and controls is found in Fig. 1.

Colony Creation and Establishment

Prior to being deployed at their release site, females were placed individually or in groups in 59ml or 590ml clear plastic containers, respectively. Containers each housed a tangled ball of poultry wiring to facilitate web construction. Spiders were provided three days to construct a web. On the fourth day spiders were provided an *ad libitum* meal of termite workers. The following day spiders were deployed at their various field sites. Release localities were identified using a natural pre-existing web of comparable size as an indicator of site quality. The resident colony was removed and the experimental colony was placed in the same locality by adhering the poultry wiring to foliage using topiary guide wires.

Statistics

To compare survival rate of marked individuals released in different social contexts, and to determine if individual personality traits affected survival of marked individuals, we conducted logistic regression with survival as the response variable, release site as a random effect, and

social context (i.e., singleton, foreign colony, or chimeric colony) and individual personality of marked individuals (i.e., aggressive, docile) as fixed effects. We also included an interaction term between social context and the personality of marked individuals to determine if the effect of individual personality on survival varied with social context. To determine if colony extinction events are a primary driver of mortality of individuals within groups, we conducted a generalized linear mixed model (GLMM). For this model we used individual survival as a response variable, site pair as a random effect, and colony extinction (extinct or not extinct) as a fixed effect. We ran an independent GLMM for each of the two colony social settings (i.e., chimeric colony and foreign colony). To determine if transplanting colonies had an effect on colony survival, we conducted a logistic regression model with colony extinction as the binary response variable, transplant condition (i.e., control, matched resource site, and mismatched resource site) as a fixed effect, and release site as a random effect. To test for differences in proportion of survivors within sites but among social contexts, we conducted a pairwise Fisher's exact test with a Bonferroni correction for multiple comparisons. Model assumptions were met for all analyses described above.

Genetic Structure of Natural Populations

In 2014, *A. studiosus* individuals (N = 213, 46-59 per population) were collected from single female nests and multi-female colonies in four populations (Chilhowee Dam, Melton Hill, Melton Lake, and Boone Lake, all in Tennessee) that ranged from 5 to 200 km apart. The former two sites are high resource and the latter two are low resource environments. Of these, two localities were adjacent to, but not overlapping with, populations that were subsequently used in experimental manipulations. *A. studiosus* have a patchy distribution; thus, sampling within each

site was performed opportunistically by canoeing down the edge of the lake/river and spotting patches of *A. studiosus*. We collected 2-3 individuals from distinct colonies in each patch, recorded their locality using a portable GPS unit, and canoed on to the next patch. We were prevented from using the identical set of populations for both components of our study for two reasons: i) Boone Lake and Melton Lake suffered large population die-offs prior to the start of our transplant experiments, and ii) special care was taken not to deplete the Boone Lake because this population is a shared resource with collaborators from East Tennessee State University (TJ Jones) and the University of Tennessee- Knoxville (SE Riechert). Nevertheless, the geographic scope of the sampling and the experiment were similar.

Individuals were preserved in 95% ethanol. We extracted DNA using DNeasy Blood and Tissue protocols for insects. We sequenced short reads across a subset of the genome using a low-density ddRAD approach (Brelsford, Dufresnes, & Perrin, 2016; Parchman et al., 2012) on an Illumina HiSeq 2500. Briefly, these reads were demultiplexed with the `process_radtags` command in Stacks (Catchen, Amores, Hohenlohe, Cresko, & Postlethwait, 2011) and mapped to a rough draft *A. studiosus* genome with Bowtie (Langmead & Salzberg, 2012). Markers were sorted and aligned with SAMtools (Li et al., 2009), and filters were applied in VCFtools (Danecek et al., 2011) to remove low quality sequences ($\text{minGQ} = 20$), to remove markers with too much missing data ($\text{max-missing} = 0.8$), and to remove markers below a minimum allele frequency threshold ($\text{maf} = 0.05$). The remaining high quality markers were retained for further population genetic analyses.

We investigated the genetic structure of the four populations using a Bayesian clustering approach implemented in STRUCTURE 2.3.4 (Pritchard, Stephens, & Donnelly, 2000; Pritchard, Wen, & Falush, 2010). We retained 1075 markers with a single nucleotide

polymorphism, each of which aligned to a unique genomic scaffold, for this analysis. We replicated simulations 10 times for each K-value (1-6) using the Admixture Model, and we repeated the analyses with 10 replicates for each K-value (1-6) using the LOCPRIOR model, which uses sampling locality as a prior in the model (Hubisz, Falush, Stephens, & Pritchard, 2009). For all analyses, models were run with a burn-in period of 20,000 followed by 100,000 Markov Chain Monte Carlo iterations. For each model, we used the method proposed by Evanno, Regnaut, and Goudet (2005) to infer the number of genetic clusters. Figures were generated in STRUCTURE PLOT (Ramasamy, Ramasamy, Bindroo, & Naik, 2014). In complement, we performed hierarchical *F*-analyses of variance to investigate differentiation among spiders based on colony of origin and population of origin, implemented in HIERFSTAT (Goudet, 2005).

RESULTS

Social context was a strong predictor of survival rates of marked individuals (social context: L-R $\chi^2_2 = 43.101$, $P < 0.001$). Individual personality did not predict survival rate of marked individuals (personality: L-R $\chi^2_1 = 0.013$, $P = 0.919$), and this result did not vary among social contexts (social context x personality: L-R $\chi^2_2 = 0.318$, $P = 0.853$). Overall, marked individuals deployed into non-native resource environments along with their native colony members suffered significantly lower survival than did individuals deployed as singletons or individuals deployed into a local colony (chimeric colonies; Fig. 2). Notably, colony extinctions explained the majority (74% in Chilhowee; 60% in Cheoah; 89% in Melton Hill; 68% in IC King) of mortality events of marked individuals at all sites (colony extinction, foreign colonies: L-R $\chi^2_1 = 48.494$, $P < 0.001$; colony extinction, chimeric colonies: L-R $\chi^2_1 = 44.575$, $P < 0.001$). Finally,

control colonies transplanted into sites with similar resource environments to those of their site of origin (matched colonies) exhibited similar extinction rates to colonies that were entirely unmanipulated, and both kinds of colonies exhibited higher survival rates than colonies transplanted into sites with non-native resource levels (transplant condition: L-R $\chi^2_2 = 34.993$, $P < 0.001$; Fig. 3). This finding shows that differences in colony extinction rates among transplant conditions were not an artifact of the transplant process.

Analyses of genetic variation reveal that population structure was stronger among nests than among localities based on 1075 polymorphic markers distributed throughout the genome. The hierarchical F_{ST} analyses revealed that the F_{ST} between localities within the total population was 0.0059 (95% confidence intervals: 0.0051-0.0067), while the F_{ST} between nests within the total population was 0.0729 (0.0712-0.0766) and between nests within locality was 0.0684 (0.0658-0.0711). In the STRUCTURE analysis that included collection locality as a prior, the optimal cluster number was two ($K = 2$). The models that did not include locality as a prior had an optimal cluster number of four ($K = 4$; Evanno et al. 2005). Patterns of differentiation between individuals reveal a pattern of colony structure and proliferation that likely dates back several generations, since three or more contemporary colonies share the same underlying genetic structure (Online Appendix A). Several demographic scenarios would be consistent with the low level of differentiation among localities. For instance, there may be enough gene flow across populations to prevent substantial isolation by distance. Alternatively, the *A. studiosus* populations sampled for this study may have recently expanded into the current range in Tennessee, not yet accumulating differential mutations across distant localities. Either way, these results suggest that occasional migrants successfully colonize or disperse into distant habitats in different drainages (and different resource environments), but the majority of

dispersal events would be localized around successful colonies. This is consistent with previous empirical observations of dispersal (Jones & Parker, 2002; Riechert & Jones, 2008), and coupled with our current findings suggest that individuals that immigrate as singletons may provide a conduit for gene flow among populations from divergent resource environments.

DISCUSSION

The amount of gene flow that occurs among populations plays an important role in mediating a range of possible outcomes, from the emergence of genetic divergence if gene flow is low, to the erosion of local adaption if gene flow is high. Where trade-offs associated with local adaptation are strong, maladapted immigrants can suffer decreased survival, thus reducing mating opportunities among individuals from different populations and limiting genetic homogenization among diverging populations. Despite the apparent ubiquitous nature of this source of reproductive isolation (Nosil, 2012), we still know little about how divergent selective regimes act on specific traits to contribute to patterns of gene flow. Social organisms provide us with an interesting study for the topic because trait-environment mismatches can occur at one or both of two levels—individual traits and collective traits (Gardner, 2015)—each of which may be required to drive the cessation of gene flow. Our results here demonstrate that, despite strong ecological selection against immigrant groups, gene flow between populations in contrasting environments can be maintained in the absence of strong selection on individual level traits. This inference is reinforced by the finding that control colonies that were transplanted into foreign sites with similar resource levels to their site of origin had success rates similar to those of unaltered control colonies (Fig. 3). Thus, the mismatching of resource levels, native vs. foreign, appears to be the driver of selection against immigrant colonies.

Social Context, not Individual Personalities, Drives Selection against Immigrants

In *A. studiosus*, individual survival rate varied significantly based on the social context in which an individual immigrates (Fig. 2). Individuals that were transplanted into a new resource environment with their native group suffered high levels of mortality that, by and large, resulted from increased colony extinction rates. Data from numerous studies have shown that a major determinant of group extinction events in *A. studiosus* is groups' personality compositions and the relationship between this composition and success depends on a site's resource levels—the personality compositions that beget success at some sites doom colonies elsewhere (Pruitt, 2012, 2013; Pruitt & Goodnight, 2014; Pruitt & Modlmeier, 2015). In contrast, individuals that immigrated as singletons outside of a colony, and individuals that immigrated as singletons that were assimilated into a locally adapted colony, suffered much lower mortality rates. Overall, our study confirms that groups of foreign individuals do poorly in foreign environments, potentially because their collective traits mismatch those favored in their new environment.

Importantly, we found that individual personality (i.e., docile or aggressive) did not influence survival and therefore immigrant inviability. A growing body of work has demonstrated that individual personality has a strong link to fitness in a variety of taxa (Smith & Blumstein, 2008), yet our results deviate from this trend. Rather, individual survival in *A. studiosus* depended largely on colony survival, and colonies transplanted from different resource environments suffered increased extinction rates relative to those that were moved to matched resource environments. Although the extinction rates of the foreign colonies that we measured were too high to link colony composition to viability of immigrant colonies, previous studies in this system have shown that colony survival is linked to the colony's mixture of docile versus

aggressive phenotypes (Pruitt & Goodnight, 2014). Our study highlights the need to consider social context and collective attributes of the group, particularly in social animals, in determining the viability of immigrant individuals, rather than focusing solely on individual traits. *A. studiosus* provides us with a particularly illuminating reminder because the power of selection on group attributes in this system may supersede the viability associated with individual level traits, since much of the mortality in this system is driven by colony-level extinction events.

Immigration as Individuals: Avenues for Gene Flow?

Individuals that immigrated into divergent resource environments as singletons had increased survival rates relative to those who immigrated with their native group (Fig. 2). However, this pattern could paint a misleading picture regarding the long-term viability of these immigrants and the colonies that they could spawn. Previous work has shown that the personality type of founding individuals of *A. studiosus* can influence the life histories of their colonies and their long-term viability (Pruitt, 2012, 2013). If pre-mated females were to disperse from one resource environment to another, these founding females could potentially prime their newfound colony for extinction by creating a descendant colony that hones its personality composition to match that selected for by their native environment (Pruitt & Goodnight, 2014). In other words, lineages that proceed from immigrant females could be doomed from their conception. New data suggest that this is likely (Pruitt, Goodnight & Riechert *in revision*). Thus, although individual immigrants appear to have high fitness (i.e., survival through reproduction) in opposing resource environments when they ‘go it alone,’ selection on the groups that emerge from these individuals could potentially eliminate immigrant lineages in the long term. That is, unless these colonies are rescued by gene flow from locally adapted residents.

Immigration as a singleton and assimilation into a locally adapted colony may be the most viable route for gene flow among diverging populations of *A. studiosus*, and could explain strong evidence of occasional gene flow among geographically distant populations (Fig. 4). We reason that immigrant singletons in chimeric colonies may benefit from the collectively adapted traits of the colonies into which they immigrate. In a sense, these individuals could use their new social context to dampen the effects of an alien selective regime. However, it is intriguing to note the possibility that increased levels of immigration could ultimately adulterate a native colony's traits (e.g., composition) enough to contribute to its demise. In other words, reproducing immigrant females could potentially alter the composition of their newly adopted colony across generations, potentially sending these colonies down a path to extinction. It is unknown if or how frequently this might occur in nature, and if colonies have the ability to regulate overall colony trait mixtures to combat the potentially deleterious effects of immigration. However, given strong evidence for gene flow among these populations, it appears plausible that immigrant individuals could assimilate into native colonies at rates high enough to alter overall colony composition. Finally, we note that it is possible that natural dispersers could be a non-random sample of their given source population with regards to individual personality traits. In some animals, personality is a strong predictor of dispersal tendencies, and an individual's personality could even affect the likelihood of successful colonization in a new habitat (Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Fogarty, Cote, & Sih, 2011; Nilsson, Bronmark, Hansson, & Chapman, 2014). Although we did not test this in our current study, future studies in this system could attempt to identify non-random dispersal patterns and the potential consequences for viability of immigrants.

Concluding Remarks

We have demonstrated that survival of immigrants in their non-native environments is highly dependent on the social context in which they occur. Immigrating with one's native colony into a site of dissimilar resource levels appears to result in almost certain extinction, while immigrating into a local colony appears to shield immigrants from selective forces that could otherwise cause their demise. Furthermore, we have shown that individual personality does not drive immigrant inviability in *A. studiosus*. This points to the need to evaluate collective traits of a group (e.g., personality composition) in addition to individual traits (e.g., personality) when evaluating the success of immigrants in their non-native environments. Success of immigrants that join native colonies appears to indicate a promising avenue of gene flow explaining the lack of genetic isolation among populations from divergent resource environments. These results are important because they provide a first look into the simultaneous roles of social context, individual traits, and collective traits in driving patterns of gene flow among populations from divergent selective regimes.

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Figure Captions:

Fig. 1: Schematic representation of the reciprocal transplant experimental design. Solid arrows represent transplants from one resource environment to another, with the direction of the arrow indicating the direction of the transplant. Sample sizes for social treatments indicate either the number of individuals (for ‘Singletons’) or colonies (for ‘Foreign Colonies’ and ‘Singleton Colonies’) deployed and tracked through the end of the reproductive period. Dashed arrows represent matched colony controls (i.e., colonies that were disassembled, reassembled, and deployed at a site that matched their native site ecology).

Fig. 2: Survival rates for each of three social treatments used in this study: singleton individuals deployed to foreign resource environments (‘F Single’); singleton individuals deployed with their native colony to a foreign resource environment (‘F Group’); and singleton individuals deployed into a foreign resource environment with a native colony (‘Chimeric’). Individuals from four sites were evaluated: a) Chilhowee (high-resource); b) Cheoah (low-resource); c) Melton Hill (high-resource); and d) IC King (low-resource). Transplant details can be found in the text and Fig. 1. Significance to a level of 0.05 is denoted in each panel.

Fig. 3: Colony survival rates for each of three colony transplant conditions: colonies deployed to sites with matched resource environments (‘Matched’), mismatched resource environments (‘Mismatched’), and colonies left untouched in their native resource environments (‘Control’). Colonies from four sites were evaluated: a) Chilhowee (low-resource); b) Cheoah (high-resource); c) Melton Hill (low-resource); and d) IC King (high-resource). Transplant details can be found in the text and Fig. 1. Significance to a level of 0.05 is denoted in each panel.

656

657 **Fig. 4:** Population genetic analyses reveal little genetic structure between geographically distant
658 populations. The STRUCTURE plot is based on a model wherein locality is included as a prior
659 and $K = 2$. Columns represent each individual in the analysis ($N = 213$), and they are arranged
660 according to their population of origin (BL = Boone Lake, CH = Chilhowee Dam, MH = Melton
661 Hill, ML = Melton Lake). The colors represent inferred populations, and the proportion of each
662 color in a given column represents the proportion of the genome of an individual that originated
663 from each inferred population. The major population structure that emerges in this model is
664 centered upon individuals from three different colonies in Melton Lake; these colonies were
665 presumably propagules from the same colony one or more generations in the past.

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Figure 1

Figure 2

Figure 3

Figure 4