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International Society for Behavioral Ecology

Ecology

Behavioral Ecology (2016), 27(6), 1635-1641. doi:10.1093/beheco/arw084

Original Article Thermal effects on survival and reproductive performance vary according to personality type

Celine T. Goulet,^{a,*} Spencer J. Ingley,^{b,*} Inon Scharf,^c and Jonathan N. Pruitt^d

^aSchool of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia, ^bDepartment of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599, USA, ^cDepartment of Zoology, Tel Aviv University, Tel Aviv 6997801, Israel, and ^dDepartment of Ecology, Evolution and Marine Biology, University of California–Santa Barbara, Santa Barbara, CA 93106, USA

*These authors have contributed equally to the study, and names have been listed alphabetically.

Received 19 February 2016; revised 28 April 2016; accepted 8 May 2016; Advance Access publication 21 June 2016.

Understanding the ecological and evolutionary consequences of individual behavioral variation has become a major focus in behavioral ecology, yet we still know remarkably little about how abiotic and biotic factors influence personality-dependent fitness trade-offs in naturally occurring systems. In particular, fitness trade-offs associated with abiotic factors remain underrepresented in the animal personality literature. Here, we examine the interacting effects of personality and temperature on survival and reproduction—both at the individual and colony level—using the socially polymorphic spider *Anelosimus studiosus* as a model system. Overall, temperature had a profound effect on survival and reproduction, but the effect differed according to both individual personality and the personality composition of colonies. Temperature was positively correlated with mortality rates but negatively correlated with reproductive rates in aggressive individuals, whereas the opposite was true in docile individuals. Colonies composed of either all aggressive or all docile individuals suffered reduced reproductive rates in high and low temperatures, respectively. In contrast, colonies composed of a mixture of aggressive and docile individuals performed equally well at both high and low temperatures, suggesting that some aspect of colony living helps buffer individuals with ill-suited personalities from environmental conditions that would otherwise lead to their demise. Our study demonstrates the need to consider both abiotic and biotic (i.e., social) context when assessing the impact of personality on fitness.

Key words: Araneae, behavioral syndrome, metabolism, pace-of-life, personality, thermal gradient.

INTRODUCTION

Behavioral ecology has traditionally considered individual variation in animal behavior within populations to be mere noise around an adaptive mean or to be due to human sampling or observational error (Wilson 1998; McCarthy 2000; Stamps 2007; Biro and Stamps 2008; Careau et al. 2008; Smith and Blumstein 2008; Réale et al. 2010). However, accumulating evidence from a range of animal taxa has demonstrated that among individual variation in behavior represents an ecologically and evolutionarily significant phenomenon, namely, "animal personality" (a.k.a. "behavioral syndromes" or "temperament"; Sih et al. 2004a, 2004b; Biro and Stamps 2008; Bell et al. 2009; Stamps and Groothuis 2010; Ingley and Johnson 2014). Animal "personality" refers to interindividual

Address correspondence to C.T. Goulet. E-mail: celine.goulet@monash.edu.

behavioral differences that are consistent-both over time and across contexts-such that, for example, an individual acting more aggressively in one context (e.g., towards prey) is likely to act more aggressively in other contexts (e.g., toward mates; Sih et al. 2004a; Bell 2007). Among the range of personality types frequently considered, an individual's level of aggression has become of particular interest due to its frequent association with fitness (Sih et al. 2004b; Wray et al. 2011; Wolf et al. 2013). Differential expression of aggression among individuals often results in fitness tradeoffs (for review, see Stamps 2007; Biro and Stamps 2008; Smith and Blumstein 2008; and references within). For instance, more aggressive individuals might benefit from increased growth rates and fecundity due to increased foraging efficiency (Boon et al. 2007; Stamps 2007; Biro and Stamps 2008), but may also run the risk of encountering more predators or engaging in maladaptive reproductive behavior (e.g., excessive precopulatory cannibalism;

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Johnson and Sih 2005; Pruitt and Riechert 2012). Because the nature of fitness trade-offs with respect to personality type are likely context dependent (Coleman and Wilson 1998), we argue that it is crucial to identify both abiotic and biotic drivers of trade-offs in naturally occurring systems. Fitness trade-offs associated with the former (i.e., abiotic factors) are currently underrepresented in the animal personality literature.

Recent work suggests that ambient temperature could be a particularly strong abiotic factor in determining individual differences in aggression due to the close link between temperature and metabolic rate, and in turn between metabolic rate and personality (Biro et al. 2010; Biro and Stamps 2010; Kralj-Fiser and Schuett 2014). Furthermore, metabolic rates might be a key mechanism underlying links between personality and life-history strategies (Biro and Stamps 2010; Réale et al. 2010), which play a direct role in fitness among individuals with different personality types (Biro et al. 2013). Regarding aggression specifically, high temperatures have been shown to cause an increase in aggressive behavior in arthropods (Baird and May 2003; Pruitt, Demes, et al. 2011), fish (Biro et al. 2010), lizards (Flores et al. 1994; Stapley 2006), and snakes (Brodie and Russell 1999), and even modest shifts in the thermal environment can elicit dramatic behavioral responses (Biro et al. 2010). Despite mounting empirical evidence that thermal environment can influence the expression of personality traits (e.g., aggression) and that different personality traits enjoy different fitness benefits, little is known about the interaction between personality types and thermal environment with respect to fitness. Given the variation in fecundity, growth, and survival among docile versus aggressive types (Biro and Stamps 2010; Réale et al. 2010; Le Galliard et al. 2013), it is likely that variation in temperature itself could produce opposing fitness outcomes as a function of one's personality type. Among aggressive individuals, for example, the level of aggressive behavior may surpass a given threshold in response to increased temperature, resulting in a reduction in reproductive success through unrestrained aggression toward mates and/or a higher avoidance by potential suitors (Pruitt and Riechert 2012). This can be particularly important in ectotherms, where metabolic rate increases exponentially with a rise in temperature (Clarke and Johnston 1999). Survivorship could also decline if these personality types become more vulnerable to predation or if increased aggression raises an already high metabolic rate and causes greater levels of oxidative stress, and therefore low immune function (Arnold et al. 2015). Conversely, docile individuals may attain a fitness advantage from elevated temperatures in that encounter rates with mates and food resources could increase, promoting higher reproductive output while still maintaining metabolic rates and predator interactions within an optimal range. Given the increasing frequency with which organisms are facing extreme and even unseasonal changes in ambient temperature (e.g., via global climate change; Welbergen et al. 2008) and the preponderance of urban heat islands (Foley et al. 2005), it is surprising that more studies have not evaluated the interacting effect of temperature and personality on fitness.

Here, we examine the interaction between temperature, personality, and fitness using the socially polymorphic spider *Anelosimus studiosus* (Araneae, Theridiidae) as a model system. Specifically, we test how altered temperature regimes affect survival and reproductive success (i.e., egg case production) among different personality types at both the individual and the colony level. At the individual level, we test for a temperature effect on survival and egg case production. At the colony level, we test for temperature and colony personality composition effects on colony egg production. *Anelosimus studiosus* is an ideal system for such an investigation as females of this species exhibit a marked personality polymorphism, and colony performance depends largely on the mixture of personality types found within a colony (Pruitt and Goodnight 2014). Individuals can readily be categorized as either a docile or aggressive phenotype (Pruitt et al. 2008), which has been shown to be both highly repeatable and heritable (Pruitt and Goodnight 2014). Throughout its distribution, which ranges across the Americas, both personality types occur in varying proportions within colonies and as singleton individuals (Pruitt et al. 2008). The frequency of aggressive individuals and colonies has been shown to decrease with latitude, possibly in response to climatic conditions (Jones et al. 2007). Furthermore, previous studies (Pruitt, Demes, et al. 2011; Pruitt and Ferrari 2011) have not only demonstrated that the behavior of this species imposes fitness consequences, but that it readily responds to temperature as well, suggesting that temperature may, in turn, have an interactive effect on survival and reproduction as a function of personality, both at the individual and colony level. We predict that, at the individual level, survival and egg case production in aggressive individuals will decrease as temperature increases, but will show the opposite pattern in docile individuals. We predict a similar pattern at the colony level, with increased egg case production by colonies composed of aggressive individuals at low temperatures, and the opposite pattern occurring in colonies composed of docile individuals.

METHODS AND MATERIALS

Collection and maintenance

Colonies of late instar A. studiosus were collected at IC King Park in Knoxville, TN, in April 2008. Colonies were collected by placing the colony in a plastic garbage bag and then trimming off the supporting foliage using pruning snips. Colonies were then transported back to the laboratory at the University of Tennessee, Knoxville. The number of spiders within each colony was counted, and each spider was isolated in a 59-mL deli cup containing a small ball of poultry netting to facilitate web construction. Spiders were fed an ad libitum diet of termite workers twice weekly (Tuesdays and Thursdays) until they matured. Water was provided once a week (Wednesday) by misting each spider's web with water using a plastic spray bottle. On reaching maturity, each virgin female was mated with a haphazardly selected male that came from a colony >5 m away from the female's source colony. All matings were conducted at the same temperature (21-23 °C), although the second yolking phase (which follows shortly after mating) occurred in the various temperature treatments described below. Although receptivity of females could vary by temperature, our study used only virgin females, which exhibit very high levels of receptivity (Pruitt and Riechert 2009), and only rarely did we intervene in trials to prevent females from killing males. Furthermore, we took care to feed females prior to mating them. Thus, although it is possible that altering temperature at the mating phase could have influenced the relationship between temperature and reproductive success in the experimental phase, we deem this alternative explanation unlikely due to the high levels of receptivity observed in our test animals. Prior to administering our temperature treatments, we determined each female's personality type (docile or aggressive) using an interindividual distance test (see below) and then assigned them to one of 2 social settings: solitary (1 singleton female per web) or multifemale colony (6 females per web). When constructing multifemale colonies, care was taken not to mix individuals from multiple source colonies, as to preserve natural levels of within-colony relatedness (Duncan et al. 2010).

Interindividual distance test

To determine each female's personality type, 2 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 interindividual distance measure <7 cm. Females that exhibited an interindividual distance >7 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 2 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. Seven centimeters corresponds with a natural break/lull in the distribution of interindividual distance measures in this species and most social Anelosimus (Pruitt et al. 2008; Pruitt, Iturralde, et al. 2011). These interindividual distance measures are highly repeatable and heritable in A. studiosus (Pruitt and Goodnight 2014).

Colony establishment

Females were assigned to one of 2 social settings prior to being subjected to a temperature treatment. Two days after a routine feeding event, singleton females were placed individually in a 200-mL pill vial containing a tangled ball of poultry wiring to facilitate web construction. Multifemale colonies were likewise established 2 days after a routine feeding event. Multifemale colonies were established by placing individual spiders into a 200-mL pill vial one at a time, with 10-min intervening periods in order to provide each spider time to settle within the vial. Singleton females were either docile or aggressive, whereas multifemale colonies were constructed with one of 3 personality compositions: 6 aggressive, 3 aggressive and 3 docile, or 6 docile spiders. Spiders were given 3 days to construct webs in their new containers before being subjected to one of the various temperature treatments.

Temperature treatments

Singleton female spiders were subjected to one of 6 temperature treatments: 24 °C (aggressive: n = 12; docile: n = 9), 26 °C (aggressive: n = 12; docile: n = 12; sive: n = 16; docile: n = 19), 28 °C (aggressive: n = 14; docile: n = 19), 30 °C (aggressive: n = 22; docile: n = 22), 32 °C (aggressive: n = 22), 32 °C sive: n = 16; docile: n = 21), or 34 °C (aggressive: n = 20; docile: n = 9). These temperature treatments were selected to resemble and exceed the high summer temperatures endured by A. studiosus throughout the Tennessee summer which range from 29.3 to 31.2 °C during June through September. In contrast, multifemale colonies of various personality composition were subjected to one of only 2 temperature settings: 24 °C (all aggressive: n = 12; all docile: n = 9; 50% aggressive 50% docile: n = 18) or 32 °C (all aggressive: n = 6; all docile: n = 11; 50% aggressive 50% docile: n = 22). Temperature treatments were administered by housing colonies in 6 Percival I22-LV HID Growth Chambers. Each chamber can produce 2 independent temperature and humidity settings. Thus, each temperature treatment was replicated in at least 2 chambers. Humidity was maintained at 65% in all chambers. Spiders were maintained at these temperatures using our standard feeding and watering regime until they either perished or until they produced an egg case. Chambers were checked daily for mortality events and for the production of egg cases. Singleton females were removed from the chamber when or if they produced an egg case. Females in multifemale colonies remained in the chamber until all individuals perished or had produced an egg case. Survival, whether or not singleton females produced an egg case, and the total number of egg cases produced by an entire colony were recorded over a period of 40 days and used for our analyses.

Statistics

To assess whether temperature or personality influenced survival or reproductive performance, we used generalized linear models (GLM) using SPSS v. 20.0. Three separate models were generated, two at the individual level and one at the colony level. Temperature and personality type (individual or colony composition) as well as their interaction were included as fixed effects and individual egg production (binary: "egg case produced" or "no egg case"), individual survival (binary: "yes" or "no"), and colony egg production (count) were included as response variables. Models predicting individual egg production and survival used the binary response "negative binary logistic" that assumes a binomial distribution while that predicting colony egg production used a Poisson distribution and "log" link function. Pearson chi square was used as the scaling parameter in order to adjust for overdispersion. Significance was determined by the Wald χ^2 -statistic.

RESULTS

Individual survival and reproductive rates

A total of 112 solitary females (56%) survived to 40 days, and of those 65 (58% of survivors; 33% of individuals overall) produced egg cases. The day of death for nonsurvivors ranged from 2 to 38 (mean = 20.06 ± 9.61). Based on the GLMs, individual survival was influenced by temperature ($\chi^2 = 1.874$, degrees of freedom [df] = 1, P < 0.001) as well as its interaction with personality ($\chi^2 = 8.678$, df = 3, P = 0.003; Table 1). Overall survival was highest at 28 °C and lowest at 34 °C, with docile personality types surviving more than aggressive types (Table 2). When considering the interactive effect of temperature and personality, docile individuals

Table 1

Results of the generalized linear model used to evaluate the effects of temperature, personality type, and their interaction on individual survival, individual performance, and colony performance in *Anelosimus studiosus*

Parameter	Estimate (\pm SE)	df	χ^2	Р
Individual survival				
Temperature	$0.031 (\pm 0.023)$	1	1.874	< 0.001
Personality type	5.043 (±1.278)	1	1.700	0.171
Temperature \times	$-0.198(\pm 0.046)$	1	8.678	0.003
personality				
Overall model		3	48.816	0.001
Individual egg produ	ction			
Temperature	$-0.119(\pm 0.042)$	1	8.054	0.005
Personality type	$12.065 (\pm 1.738)$	1	48.191	< 0.001
Temperature ×	$-0.442 (\pm 0.061)$	1	51.848	< 0.001
personality				
Överall model		3	52.599	< 0.001
Colony egg production	on			
Temperature	0.077 (±0.019)	1	16.962	< 0.001
Personality type	$2.43 (\pm 0.449)$	1	30.369	< 0.001
Temperature ×	$-0.089(\pm 0.017)$	1	28.363	< 0.001
personality				
Overall model		3	36.484	< 0.001

SE, standard error.

Temperature	\mathcal{N}		Number of individuals surviving (>40 days)			Number of reproductive individuals			
	Docile	Aggressive	Docile	Aggressive	Total	Docile	Aggressive	Total	
24	9	12	3 (33%)	6 (50%)	9 (43%)	0	6 (50%)	6 (29%	
26	19	16	15 (79%)	11 (69%)	26 (74%)	7 (37%)	9 (56%)	16 (17%	
28	19	14	15 (79%)	11 (79%)	26 (79%)	5 (26%)	7 (50%)	12 (36%	
30	22	22	16 (73%)	6 (27%)	22 (50%)	11 (50%)	3 (14%)	14 (2%)	
32	21	16	18 (86%)	2 (13%)	20 (54%)	15 (71%)	0	15 (41%	
34	9	20	6 (67%)	3 (15%)	9 (31%)	2 (22%)	0	2 (7%)	
Overall	99	100	73 (74%)	39 (39%)	112 (56%)	40 (40%)	25 (25%)	65 (33%	

Table 2	
Summary of survivorship and reproductive success at the individual level	

The number of individuals and their proportion (in parentheses) surviving past 40 days and producing egg cases are presented by personality type and temperature treatment.

exhibited the highest level of survival at 32 °C (Figure 1). The production of egg cases among solitary females, on the other hand, was influenced by temperature and personality as well as their combined effect ($\chi^2 = 8.054$, df = 1, P = 0.005; $\chi^2 = 48.191$, P < 0.001; and $\chi^2 = 51.848$, P < 0.001, respectively). The overall number of reproductive individuals was highest at 32 °C and lowest at 30 °C. When considering the interactive effect of temperature and personality type on reproductive output, aggressive individuals generally decreased the number of egg cases produced as temperature increased, whereas docile individuals exhibited an opposite pattern from 24 °C to 32 °C after which there was a steep decline (Figure 2). The greatest level of variation between personality types occurred at the extreme temperatures; no egg cases were produced by docile individuals at 24 °C and none were produced at 32 °C or 34 °C for aggressive individuals.

Colony-level reproductive rates

A total of 75 colonies (96%) successfully reproduced resulting in a total of 114 egg cases (Table 3). Overall, all colonies (n = 40) composed of mixed personality types produced eggs, whereas 95% of docile (n = 20) and 89% of aggressive (n = 18) colonies were successful at producing eggs. Mixed colonies exhibited the highest level of productivity (49% colony members being reproductive) followed by aggressive colonies (44% colony members) and docile colonies being the least productive (41% colony members). The GLM revealed that temperature ($\chi^2 = 16.962$, df = 1, P < 0.001; Table 1), personality type ($\chi^2 = 30.369$, df = 1, P < 0.001), and its interaction with temperature ($\chi^2 = 28.363$, df = 1, P < 0.001) had a significant effect on egg production at the colony level. Reproductive output was lowest among aggressive colonies at high temperatures, and lowest among members of docile colonies at low temperatures (Figure 3). The proportion of reproductive colony members followed a similar pattern. Docile colonies had the lowest proportion of reproductive colony members at low temperatures, whereas aggressive colonies had the lowest proportion of colony members at high temperatures (Figure 4).

DISCUSSION

Our study provides insight into the personality-dependent effects of abiotic factors (i.e., temperature) on both individual- and colonylevel performance. At the individual level, we found that the interaction between personality type and temperature had a significant effect on both survival and reproduction. At the colony level, we detected similar effects: colony-level performance at different temperatures depended greatly on the personality composition of the colony. Importantly, we also detected evidence for some mediating

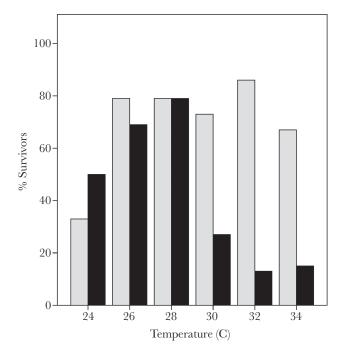


Figure 1

Proportion of docile (gray) and aggressive (black) individuals that survived to 40 days at 6 different temperature treatments.

effects of social context: Personality types that were unable to survive and reproduce at particular temperatures as singleton individuals were able to persist and reproduce at these temperatures when they occupied colonies of mixed personality types.

Individual-level differences in survival and reproduction

We found a consistent interacting relationship between temperature and survival among individuals with different personalities, although overall survivorship did not differ among personality types. Survivorship decreased with increasing temperature among aggressive individuals, but generally increased with increasing temperatures among docile individuals (Figure 1). This leads us to ask: Why is there this interaction between temperature and personality with respect to survival? One possible explanation could stem from differences in baseline metabolic rate among docile and aggressive individuals, given that metabolic rate frequently increases as temperature increases (Clarke and Fraser 2004). Although explicit measurements of metabolic rate have not been performed for this species, recent evidence suggests that docile individuals are more resistant to starvation than aggressive individuals (Lichtenstein and Pruitt 2015). These differences in starvation resistance could possibly be indicative of differences in underlying metabolic rate (i.e., higher metabolic rate in aggressive individuals causes increased susceptibility to starvation). Consistent with this line of reasoning: Laboratory studies on other species of web-building spiders have shown a positive association between boldness/aggressiveness and heart rate (Shearer and Pruitt 2014). Aggressive A. studiosus are also more active than docile individuals (Pruitt et al. 2008; Pruitt, Demes, et al. 2011). If more active and aggressive individuals do in fact have a higher baseline metabolic rate, it is possible that they are brought to a critical thermal "tipping point" more quickly than docile individuals when encountering high temperatures. The increased production of reactive oxygen species (ROS) could be a possible underlying mechanism leading to increased mortality rates of aggressive individuals in high-temperature treatments. High metabolic rates promote the production of ROS which, in turn, results in higher levels of oxidative stress (Arnold et al. 2015). Thus, if aggressive individuals have a higher baseline metabolic rate,

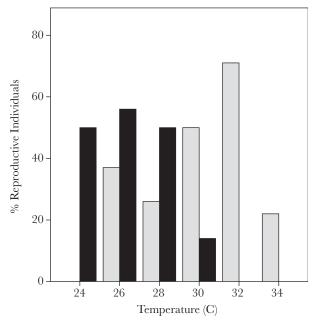


Figure 2

Proportion of docile (gray) and aggressive (black) survivors that reproduced (i.e., produced egg cases) at 6 different temperature treatments.

Table 3

Summary of reproductive output at the colony level

increased temperatures could increase metabolic rate and therefore the production of ROS to lethal levels.

We found that both temperature and personality type affected reproductive success of individuals, but that the nature of this relationship in a given temperature changed as a function of personality type. Overall, docile individuals reproduced more frequently than aggressive individuals (Table 2). Generally, the number of aggressive individuals that produced egg cases decreases as temperature increased, whereas the number of docile individuals that produced egg cases exhibited the opposite pattern, with the exception of individuals at the highest temperature treatment (where egg production declined sharply). Extreme temperatures appeared to have a strong effect on reproduction. No docile individuals reproduced in the lowest temperature treatment, and no aggressive individuals reproduced at the highest temperature treatment (Figure 2). These results suggest that, beyond survival, temperature has a strong effect on individual fitness, as does an individual's personality, but that the nature of this effect is dependent on an individual's personality.

Temperature and personality-dependent differences in reproductive output at the colony level

We detected a clear relationship between temperature and colonylevel egg case production. Temperature had a significant effect on performance for colonies composed of either all docile individuals or all aggressive individuals, but did not affect performance of mixed colonies (Figure 3; Table 3). In docile colonies, egg case production increased with temperature. This was likely due to a positive relationship between temperature and the proportion of reproductive individuals within the colony (Figure 4). We saw the opposite pattern in aggressive colonies: Egg case production decreased with increases in temperature. Likewise, this was probably driven by a negative relationship between the number of reproductive individuals and temperature. These patterns resemble those detected for singleton individuals with different personalities and suggest that the effects of temperature on individual survival and reproduction scale up to the colony level when colonies are composed of only one personality type (all aggressive or all docile). In contrast, colonies composed of a mixture of aggressive and docile individuals appear to be robust to temperature differences, performing equally well at both high and low temperatures. This suggests that some aspect of colony living helps shield individuals with illsuited personalities (e.g., aggressive individuals in high temperatures) from environmental conditions that would otherwise lead to their demise. Our finding that the proportion of reproductive individuals did not differ between mixed colonies and the performance

	N		Number of reproductive colonies		Number of egg cases produced		% Reproductive colonies		% Reproductive colony members	
Colony personality	24 °C	32 °C	24 °C	32 °C	24 °C	32 °C	24 °C	32 °C	24 °C	32 °C
Docile	9	11	8	11	$14(1.56 \pm 0.29)$	35 (3.18±0.35)	89	100	26	53
Mixed	18	22	18	22	$55(3.06 \pm 0.17)$	$62(2.82\pm0.17)$	100	100	51	47
Aggressive	12	6	12	4	$42(3.5\pm0.26)$	$6(1.00\pm0.37)$	100	67	58	17
Overall	39	39	38	37	$111(2.84 \pm 0.174)$	$103(2.64 \pm 0.185)$	97	95	47	44

The number and proportions of colonies producing egg cases and the number of egg cases produced are presented by personality type and temperature treatment. Averages and standard errors are given in parentheses.

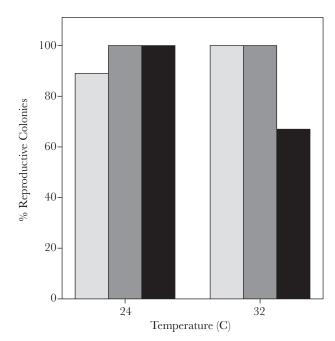


Figure 3

Proportion of colonies that reproduced at low (24°) and high (32°) temperature treatments. Docile (light gray) and aggressive (black) colonies were composed of either all docile or all aggressive individuals. Mixed colonies (dark gray) contained equal numbers of individuals with each personality type.

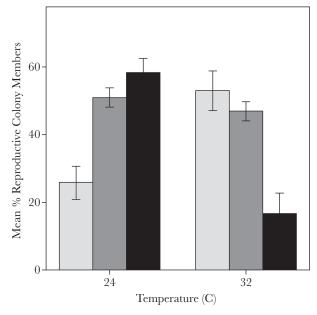


Figure 4

Means and standard errors of the proportion of reproductive colony members (i.e., individuals that produced egg cases) from docile (light gray), mixed (dark gray), and aggressive (black) colonies at low (24°) and high (32°) temperature treatments.

of monotypic colonies under their ideal conditions further suggests that mixed personality colonies somehow buffer individuals from costly personality-temperature mismatches. Likewise, mixed colonies produced the highest number of egg cases at both high and low temperatures. Positive effects of within-group behavioral variation have been observed in a number of other taxa (Michelena et al. 2010; Pruitt and Riechert 2011; Wray et al. 2011; Kralj-Fiser and Schneider 2012; Modlmeier et al. 2012; Holbrook et al. 2014), yet the underlying mechanisms by which heterogeneous groups realize higher levels of productivity remains unresolved. One theory put forth proposes that intracolony variation allows trade-offs associated with particular personality types to be circumvented, or at least moderated (Modlmeier et al. 2012). Although monotypic colonies express only an all-or-nothing response, mixed colonies are more effective at meeting colony needs because members with different personalities are more specialized in performing different roles or tasks (Modlmeier et al. 2012; Holbrook et al. 2014).

CONCLUSIONS

How personality drives fitness trade-offs under different abiotic conditions remains largely unexplored. Our study provides valuable insight into this question by demonstrating that personality and abiotic factors (i.e., temperature) have an interacting effect on individual fitness and colony-level success. Temperature had a profound effect on survival and reproduction, yet the effect differed according to both individual personality and the personality composition of colonies. Furthermore, we showed that colonies composed of either all aggressive or all docile individuals suffered reduced reproductive rates in high and low temperatures, respectively, but that colonies composed of a mixture of aggressive and docile individuals performed equally well across a wide range of temperatures. Thus, some aspect of colony living apparently helps buffer individuals with ill-suited personalities from environmental conditions that would otherwise lead to their demise. But, this effect is only apparent within behaviorally diverse societies. Our results stress the need to consider both abiotic and biotic (i.e., social) context when assessing the impact of personality on fitness, especially in the face of global change that broadly affects temperature regimes of both human altered (e.g., urban "heat islands") and natural environments.

FUNDING

S.J.I. was supported by a NSF Postdoctoral Research Fellowship (#1523621). J.N.P. was supported by NSF IOS grants #1352705 and #1455895. J.N.P. and I.S. were supported by BSF grant #2013086.

We thank Dr S. Nakagawa and 2 anonymous reviewers for insightful comments that helped improve the manuscript.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Ingley et al. (2016).

Handling editor: Shinichi Nakagawa

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