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Social environment determines the effect of boldness and activity on survival

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Abstract

Populations of animals are composed of individuals that differ in ecologically relevant behaviors. Building evidence also suggests that individuals occupy different social niches. Here, in a mark–recapture experiment, we show evidence of an interacting effect of behavior and social niche on survival in the wild: Bold individuals had higher survival if they were initially captured in groups, while shy, inactive individuals had higher survival if they were initially captured when alone. These findings provide support for the hypothesis that behavioral type–environment correlations can be favored by natural selection.

KEYWORDS

boldness, exploratory behavior, *Gasterosteus aculeatus*, maintenance of variation, three-spined stickleback

1 | INTRODUCTION

A large body of evidence has shown that individuals of the same species can differ consistently in behavior across time or context, a phenomenon known as animal personality (Dall, Houston, & McNamara, 2004; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). These consistent differences in behavior can have important implications for the ecology of individuals, populations, and communities (Bolnick et al., 2011; Mittelbach & Ballew, 2014; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2012). While several mechanisms have been proposed to explain the existence of consistent individual differences in behavior (Dingemanse & Wolf, 2010; Luttbeg & Sih, 2010; Sih et al., 2015; Wolf & Weissing, 2010), we are far from a consensus about the causes and consequences of animal personality.

The connection between animal personality traits and fitness is well documented (Smith & Blumstein, 2008). Several animal personality traits have the potential to affect survival by determining how vulnerable an individual will be to predation. For example, relatively high boldness (willingness to take risks) has been shown to affect the risk of predation (McGhee, Pintor, & Bell, 2013; Réale & Festa-Bianchet, 2003; Smith & Blumstein, 2010). Personality traits might also influence survival by determining an individual's ability to acquire resources (Brodin & Johansson, 2004; Dingemanse, Both, Drent, & Tinbergen, 2004; Le Galliard, Paquet, Cisel, & Montes-Poloni, 2012; Webster, Ward, & Hart, 2009). Indeed, Ward et al. (Ward, Thomas, Hart, & Krause, 2004) showed that bolder three-spined stickleback consumed more food items in scramble competition and had faster growth rates than relatively shy stickleback. It is likely that the fitness consequences of personality traits are determined by how they affect the trade-off between growth and mortality (Stamps, 2007). For example, animals that engage in more exploratory behavior might gain a greater knowledge about the availability of resources, but they are also likely to have a relatively high predator encounter rate.

Group living is a feature of an individual's ecology that can strongly influence survival (Krause & Ruxton, 2002). Group living might reduce mortality through enhanced predator detection (Lima & Dill, 1990; Pulliam, 1973) or evasion (Foster & Treherne, 1981; Turner & Pitcher, 1986). Group living might also influence survival by affecting the rate or efficiency of foraging if, for example, group members share in the task of searching for food (Day, MacDonald, Brown, Laland, & Reader, 2001; Zahavi & Ward, 1973) or being vigilant for predators (Pulliam, 1973).

The extent to which group living affects survival might be personality-dependent. For example, the antipredator benefits of social living might be especially important for individuals that have a propensity to be less cautious. Living in close proximity to conspecifics might increase competition for food (Beecham & Farnsworth, 1999; Ekman, 1979; Janson & Goldsmith, 1995), and the impact of competition might disproportionately impact shy individuals that are poor competitors (Ward et al., 2004; Webster, Ward, & Hart, 2007).

In this study, we used mark–recapture to estimate the relationship between survival and two behavioral traits that are commonly studied in the context of animal personality: boldness and level of activity in a novel environment. It should be noted that we chose to increase our sample size at the cost of omitting repeated measures of behavior in this study. We therefore apply the "individual gambit" and must use caution when interpreting our results (see Niemelä & Dingemanse, 2018, for further discussion). We also recorded each individual's social environment (solitary or in a group) when they were initially captured, which allowed us to assess whether the social environment influenced the relationship between behavior and survival.

The subjects of our study were three-spined sticklebacks (*Gasterosteus aculeatus*). Sticklebacks are ideal for this work, as numerous studies have documented consistent individual differences in behavior in this species (Bell, 2005; Bensky, Paitz, Pereira, & Bell, 2017; Dingemanse et al., 2007; Laskowski & Bell, 2014; Ward et al., 2004; Webster et al., 2009). In a previous study (Pearish, Hostert, & Bell, 2013), we found repeatable differences in boldness and exploratory behavior in the freshwater population of three-spined stickleback that are the focus of this study. Laboratory experiments with three-spined sticklebacks have demonstrated a link between personality traits and important determinants of survival, such as vulnerability to predation (McGhee, Pintor, Suhr, & Bell, 2012) and ability to compete for food (Ward et al., 2004; Webster et al., 2009). Here, we build upon our understanding of how these behavioral traits affect survival in the field and extend it by considering the impact of social context.

2 | METHODS

Juvenile three-spined sticklebacks (25.1 mm ± 0.2 SE) were collected from a 240-m stretch of the Navarro River, CA (39°03'N, 123°27'W), between July 20 and August 7, 2013. The Navarro River experiences natural annual cycles of high flow (winter and spring) and low flow (summer and fall). However at the time of our study, the water had dropped to unusually low levels due to drought. Large sections of the Navarro River, including the sections immediately upstream and downstream of our research site, were dried up. This drying had the effect of concentrating aquatic species that had previously benefited from much greater access to habitat and much lower competition into the limited habitat that was available. Although we do not have predation pressure data to provide a comparison, it appeared

that piscivorous predators were also concentrated at our research site. We frequently observed a group of common mergansers (*Mergus merganser*) engaged in behavior that appeared to be pursuit of fish prey (Video S1), and mergansers are known to prey on juvenile three-spined sticklebacks (Reimchen, 1994). In addition to mergansers, other avian predators (*Ardea alba, A. herodias, Phalacrocorax auritus*), predatory fish (*Cottus* species), and aquatic invertebrates (*Odonata* species) that are known to prey on sticklebacks were also abundant at the site. Therefore, we expect that mortality, and the potential for phenotypic selection, was especially high at the time of our study.

Sticklebacks were collected using a trout landing net lined with a 2-mm-mesh, nylon net. Before approaching, we observed the focal fish from a distance ≥ 2 m for 30 s and then recorded whether it was solitary (*n* = 145) or in a shoal (<4 body lengths from another fish; Pitcher, 1993) (*n* = 286). Previous studies have shown that individual differences in social environment use are consistent over time in three-spined sticklebacks (Greenwood et al., 2015; Jolles et al., 2015; Laskowski & Bell, 2014; Pearish, Hostert, & Bell, 2017; Ward et al., 2004); therefore, we assumed that an individual's social environment at the time of initial capture was a reliable predictor of the social environment that individual was most likely to occupy for the remainder of the study.

We used procedures similar to those used in other studies to quantify activity in a novel environment (open field test; Verbeek, Drent, & Wiepkema, 1994; Walsh & Cummins, 1976) and boldness (simulated predator strike; Bensky et al., 2017; Krause & Godin, 1996; Stein & Bell, 2014).

During a behavioral observation, an individual was allowed to acclimate in an opaque refuge (10 cm diameter, 10 cm height) in the center of a circular plastic pool (150 cm diameter) for 3 minutes. Lines on the bottom divided the pool into nine equally sized sections: eight perimeter sections surrounding one central section that contained the refuge (Figure 1). Each perimeter section contained a rock. A researcher behind a blind pulled a string to remove a rubber

FIGURE 1 Experimental arena showing the acclimation chamber (center) and model sculpin (foreground)

stopper from a 5-cm hole in the side of the refuge, allowing the fish to emerge. Following emergence, we recorded the number of times the individual moved into a different section of the pool (transitions), which we interpret as activity in a novel environment. Previous studies have found this behavior to be repeatable in this population (Laskowski & Bell, 2014; Laskowski, Pearish, Bensky, & Bell, 2015; Pearish et al., 2013). After 3 minutes, we simulated a predator attack by moving a clay sculpin model (20 cm length; Figure 1) toward the focal fish. Sculpins (genus: *Cottus*) are a natural predator to freshwater populations of sticklebacks (Pressley, 1981) and were observed consuming stickleback during the course of this study. We recorded the time the focal fish remained frozen after the simulated attack (time frozen). Remaining motionless is an effective predator defense for stickleback (McGhee et al., 2012), and individuals exhibit consistent individual differences in this behavior (Bensky et al., 2017; McGhee et al., 2013). Therefore, we interpret shorter freeze times as relatively "bolder" behavior (Réale et al., 2007).

Following behavioral observation, the fish was weighed, measured for standard length (tip of nose to base of caudal fin), uniquely marked with fluorescent implants (Visible Implant Elastomer Tags; Northwest Marine Technology, Inc.), and released in the location from which it was collected. A control group was collected, weighed, measured, marked, and released without undergoing behavioral observation, allowing us to confirm that behavioral observations did not affect the probability of recapture (recapture of observed [n = 310] vs. control [n = 121], χ^2 = .75, df = 1, p = .39).

The fish were recaptured approximately 2 weeks (16.6 d ± 0.5 SE) after initial capture to estimate the effect of behavioral traits on survival. To improve the likelihood of recapturing all individuals, we started at the downstream end of the study site and moved methodically up the river using block nets to isolate fifteen-meter sections (Figure 2). Two block nets were constructed with a 1.6-mm-mesh, polyester netting (Delta Knotless Netting, Stock # 1000–8; Memphis Net and Twine Co., Inc.). Ten-centi meter-diameter, cylindrical, polyethylene foam floats were used to raise the entire top

edge of the block nets above the surface of the river and 8-mm chain was embedded in the bottom edge of the block nets to anchor them to the riverbed. The bottom edge was manually buried in gravel after the nets were secured in position upstream and downstream of a fifteen-meter section.

We used two methods for recapture (seining, snorkeling) in an effort to avoid biasing capture toward particular behavioral types (Biro & Dingemanse, 2009; Wilson, Coleman, Clark, & Biederman, 1993). Recapture methods precluded us from being able to reassess social environment at the time of recapture. Recapture efforts continued in each section until two consecutive seine net sweeps yielded less than 3% of the initial yield. For example, a typical first seine sweep in a section would yield approximately 300 sticklebacks. In this section, we would continue alternating between recapture methods until two consecutive seine net sweeps yielded nine or fewer sticklebacks. After a section was exhausted, we moved fish to a darkened tent and used violet light (VI Light; Northwest Marine Technology, Inc.) to identify fish that were marked with fluorescent implants.

We used logistic regressions to test for the main and interacting effects of social environment and behavior on recapture. Behavior variables were $\log_{10}(x + 1)$-transformed to improve normality. Behavioral traits were not tightly correlated (R^2 = 0.15), and therefore, we treated them as independent and analyzed them separately. To aid in interpretation of significant interactions, we calculated Cohen's d, a metric of effect size. Cohen's d values less <.2, <.5, or <.8 are considered to be small, medium, or large effects, respectively (Cohen, 1988). Finally, in cases where we detected effects of behavior on survival, we calculated one-way ANOVAs to examine the estimated distribution of behavior across social environments in the initial sample of fish and then separately with only the fish that had been recaptured. We used R 3.0.2 (R Core Team, 2013) for all analyses.

2.1 | Ethical Note

The protocol for this study was reviewed and approved by the IACUC of the University of Illinois Urbana-Champaign (protocol #09204). This work was permitted by the California Department of Fish and Wildlife (scientific collecting permit #SC-11126).

3 | RESULTS

We recaptured 118 of the 431 marked individuals (27%). Recapture rate did not differ between social environments (solitary = 30%, in shoal = 26%, χ^2 = .57, df = 1, p = .45). We did not detect an effect of body size on the probability of recapture (recaptured 25.1 ± 0.3 SE mm, not recaptured 25.1 ± 0.2 SE mm).

The mark–recapture data suggest that the social environment in which the fish was initially captured and the way the fish behaved during observations had interacting effects on the probability of survival (Table 1). Among solitary fish, less active individuals (fewer transitions) were more likely to be recaptured (behavior

FIGURE 2 Block nets used to isolate sections of the river during recapture

TABLE 1 Logistic regressions testing for social context-dependent survival of different behaviors. a) Model testing for the effect of social environment, transitions, and their interaction on the probability of recapture. b) Model testing for the effect of social environment, time frozen, and their interaction on the probability of recapture. Positive estimates of the effect of social environment indicate that the probability of survival is higher for solitary fish. $N = 310$

Factor	Estimate	Estimate SE	p value
a)			
Social environment (solitary vs. in shoal)	2.3	1.1	.04*
Transitions	1.8	0.8	.03*
Social environment*transitions	1.9	1.0	.06
b)			
Social environment (solitary vs. in shoal)	1.4	0.8	.10
Time frozen	0.6	0.4	.16
Social environment*time frozen	−1.1	0.6	.04*

*Factors that are signficant with a *p*-value < 0.05.

of recaptured vs. not recaptured, Cohen's d = .43). In contrast, the probability of recapture was not related to activity in a novel environment among the fish initially captured in shoals (Cohen's d = .04). Similarly, the probability of recapture depended on an individual's boldness (time frozen) and social environment, with a significant interaction between the two (Table 1b). Among solitary fish, relatively shy individuals with long freeze times were more likely to survive to the time of recapture (Cohen's d = 0.29). In contrast, bold individuals with short freeze times were more likely to survive among the fish initially captured in shoals (Cohen's d = .22).

These patterns are consistent with the hypothesis that social environment mediates the effect of behavioral traits on survival; shy fish suffered higher mortality than bolder fish in shoals, but shy, inactive fish actually had relatively low mortality outside of shoals.

Another way to examine the effect of behavior and social environment on the probability of recapture is to visualize the distribution of behavior across social environments before versus after recapture. Examination of all fish sampled during the initial capture shows that the number of transitions and time frozen were equally distributed across the two social environments (Table 2, Initial

sample): active individuals were equally common in shoals and by themselves (Figure 3a,c). Similarly, bold individuals occurred in both social environments at comparable frequencies (Figure 3e,g). However, a comparison of fish that were found in the recapture sample shows a non-random distribution of number of transitions and time frozen across the two social environments (Table 2, Recaptured sample). In the subset of fish that were recaptured, shoalers were more active (Figure 3b vs. 3d) and stayed frozen for a shorter duration (Figure 3f vs. 3h) compared to solitary fish.

4 | DISCUSSION

The results of this study provide evidence that the social environment can mediate the influence that behavioral traits have on survival. Bold individuals had higher survival if they were initially captured in groups, while shy, inactive individuals had higher survival if they were alone at initial capture. These findings could have important implications for understanding the role of natural selection in maintaining variation in animal personality traits.

Regular observations of avian and aquatic predators actively consuming stickleback at the field site lead us to speculate that high mortality due to predation may have been the cause of the patterns we observed. We hypothesize that timid behavior was favored among solitary fish because reduced activity and increased freezing behavior can be effective antipredator strategies when sticklebacks are by themselves (McGhee et al., 2012). On the other hand, individuals that reduce activity when threatened might have suffered higher mortality in a group setting, because here the best antipredator strategies, such as dilution (Foster & Treherne, 1981) or predator confusion (Milinski & Heller, 1978; Neill & Cullen, 1974), depend on coordinated movements. Indeed, our data suggest that a tendency to freeze is disadvantageous for individuals that occur in groups.

An alternative mechanism that might cause boldness to be favored in the highly social context of a fish shoal is competition for food. Bold stickleback outcompete shy stickleback in direct competition for food items (Ward et al., 2004); thus, shy individuals that occur in shoals might be more likely to die of starvation or other causes of death that are indirectly related to poor body condition (predation: Booth & Beretta, 2004; disease: Alcorn, Pascho, Murray, & Shearer, 2003).

Altogether our results are consistent with the hypothesis that selection in the form of social environment-dependent mortality might

TABLE 2 Comparisons of the behavior (mean ± SE) of solitary fish versus fish that were in shoals at the time of capture. The "initial sample" includes data from all fish that were captured (left), and the "recaptured sample" uses only the data of fish that were recaptured (right). Means and standard errors are back-transformed from $\log_{10}(x + 1)$-transformed data. The average behavior of fish that were solitary versus in a shoal did not differ in the initial sample. However, in the subset of fish that were recaptured, shoalers were more active (more transitions) and bolder (stayed frozen for a shorter duration) compared to solitary fish

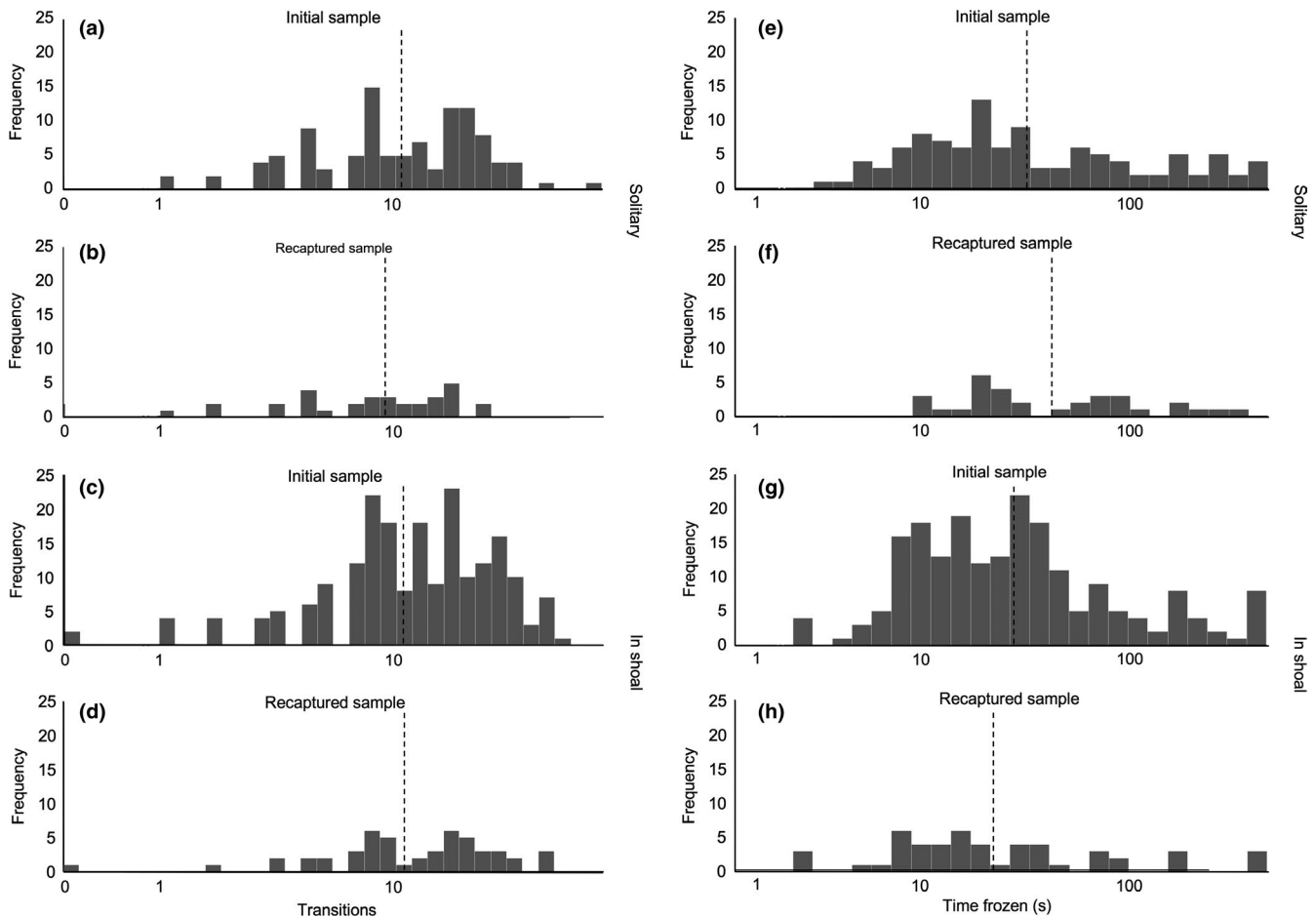|	Initial sample				Recaptured sample			
	Solitary	In shoal	$F_{1,309}$	p value	Solitary	In shoal	$F_{1,80}$	p value
Transitions	10.5 [9.8–11.2]	11.3 [10.8–11.9]	0.89	.35	8.4 [7.4–9.4]	11.5 [10.4–12.7]	4.08	.047
Time frozen	34.1 [30.3–38.4]	29.4 [27.2–31.7]	1.19	.28	44.0 [36.9–52.4]	23.9 [20.1–28.5]	4.93	.021

FIGURE 3 Distributions of number of transitions (left panels) and time frozen (right panels). The top four panels represent solitary fish, while the bottom four panels show fish that occurred in shoals. Histograms show all fish if marked "Initial sample" (*N* = 310) or only those fish that were recaptured if marked "Recaptured sample" (*N* = 81). Mean transitions did not differ between shoalers and solitary fish in the initial sample (a vs. c). However, a difference in mean activity is seen when the histograms include only individuals from the recaptured sample (b vs. d). The difference in mean time frozen after a simulated predator attack seen in the initial sample (e vs. g) is much larger in the histogram that includes only the recaptured sample (f vs. h). $Log_{10}(x + 1)$ transformations were used in analyses, so data are plotted on a log scale. Dashed lines represent means that are back-transformed from $log_{10}(x + 1)$-transformed data

cause non-random associations between behavioral types and the social environment. However, this inference makes three important assumptions.

First, it assumes that an individual's behavior as assessed at the time of capture reflects long-lasting individual differences in behavior. Previous studies offer support for this assumption because they have shown that time freezing and activity are repeatable in this system (Bensky et al., 2017; Laskowski & Bell, 2014; Laskowski et al., 2015; McGhee et al., 2013; Pearish et al., 2013), and sticklebacks from the Navarro River showed greater behavioral consistency when compared to another Californian population (Bell, 2005). However, it should be noted that studies that rely on a single observation to quantify individual differences in behavior have applied the "individual gambit" and conclusions reached from these data should be taken with caution. Repeatability tells us the portion of the variation in behavior that occurs among individuals (generally approximately 40%; Bell, Hankison, & Laskowski, 2009). The roughly 60% of behavioral variation occurring at

the within-individual level cannot be captured with a single measurement.

Our second assumption is that individuals that were initially captured in shoals were likely to continue to shoal over time (although not necessarily with the same shoal) and that solitary fish were likely to continue to occur alone. This assumption is well supported by the literature showing that variation in shoaling behavior in sticklebacks has a genetic basis (Greenwood et al., 2015; Greenwood, Wark, Yoshida, & Peichel, 2013) and is repeatable (Jolles et al., 2015; Laskowski & Bell, 2014; Pearish et al., 2017; Ward et al., 2004). However, as with boldness and activity, multiple measures of social environment would have provided greater confidence that the true patterns were captured by this study.

Finally, it assumes that recapture is a good proxy for survival. This assumption is likely to be true because dispersal outside of the study area was prevented by dried-up sections of river upstream and downstream of the study site. Also, our study coincided with a period in which mortality was especially high due to unfavorable

environmental conditions (i.e., low water levels due to drought). This might explain our recapture rate (27%) and why behavioral traits were not non-randomly distributed across social environments at the outset of our study. The drought might have caused a bottleneck that accelerated phenotypic selection.

A major question in the study of animal personality has to do with the processes that can maintain individual variation within populations (Dingemanse & Wolf, 2010). Our results provide support for the hypothesis that heterogeneity in the social environment can maintain variation. It is interesting to consider that selection might favor mechanisms that make adaptive behavioral type–environment correlations more likely, for example, a genetic correlation between social environment preference and boldness (Ravigné, Dieckmann, & Olivieri, 2009; Saltz & Nuzhdin, 2014). Such a genetic correlation could further amplify variation if, for example, bold behavior is favored to overcome the challenge of competition within shoals; shoals composed of bolder-than-average individuals could increase the strength of selection and potentially accelerate the emergence of bold behavior even further (indirect genetic effect; Moore, Brodie, & Wolf, 1997). Further appreciation of the mechanisms and consequences of behavioral type–environment correlations could provide considerable insight into the causes of consistent individual differences in behavior.

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CONFLICT OF INTEREST

None.

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SUPPORTING INFORMATION

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