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Personality trait differences between mainland and island populations in the common frog (*Rana temporaria*)

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Abstract Understanding and predicting species range expansions is an important challenge in modern ecology because of rapidly changing environments. Recent studies have revealed that consistent within-species variation in behavior (i.e., animal personality) can be imperative for dispersal success, a key process in range expansion. Here we investigate how habitat isolation can mediate differentiation of personality traits between recently founded island populations and the main population. We performed laboratory studies of boldness and exploration across life stages (tadpoles and froglets) using four isolated island populations and four mainland populations of the common frog (*Rana temporaria*). Both tadpoles and froglets from isolated populations were bolder and more exploratory than conspecifics from the mainland. Although the pattern can be influenced by possible differences in predation pressure, we suggest that this behavioral differentiation might be the result of a disperser-dependent founder effect brought on by an isolation-driven environmental filtering of animal personalities. These findings can have important implications for both species persistence in the face of climate change (i.e., range expansions) and ecological invasions as well as for explaining rapid speciation in isolated patches.

Introduction

In many species, individuals exhibit relatively stable, consistent differences in behavior across multiple contexts (e.g., in how they feed, cope with predators, interact with conspecifics, mate, or disperse) (Sih et al. 2004a, b). These consistent individual differences in behavior are referred to as animal personality traits. Animal personality is a recent and very exciting conceptual development in the study of animal behavior (aka temperament, behavioral type, and behavioral syndrome; Dall et al. 2004; Sih et al. 2004a, b; Bell 2006; Reale et al. 2007; Sih and Bell 2008). Both empirical and theoretical studies suggest that individual personality can have important ecological and evolutionary implications (Dingemanse and Wolf 2010; Luttbeg and Sih 2010; Stamps and Groothuis 2010; Sih et al. 2012 and refs therein). For example, it has been shown that bold and asocial individuals of the invasive mosquitofish (*Gambusia affinis*) are more prone to disperse and, through that, potentially lead the invasion of new areas (Cote et al. 2010a). In recent years, it has also become evident that individual personality often is a crucial determinant for important fitness correlates, such as growth, reproduction, and survival (Smith and Blumstein 2008). While studies on individual variation are becoming common, studies of personality trait differences on population level, and what might generate such differences, are still few (however, see Bell 2005; Dingemanse et al. 2007). Personality differentiation between populations can arise as a result of stochastic evolutionary processes (e.g., drift or founder effect) or as a result of natural selection favoring optimal trait combinations (Dingemanse et

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al. 2007). For example, Bell (2005) suggested that predators might shape personality in sticklebacks, generating population differences depending on level of predator pressure. This was later confirmed both experimentally (Bell and Sih 2007) and statistically in a field study by Dingemanse et al. (2007) where they showed that personality of 12 populations of sticklebacks differed predictably depending on predator presence.

Another plausible reason for creating personality differences between populations, at least in earlier parts of the population history, is personality-dependent dispersal. Recent studies in different systems showed that individuals exhibit personality-dependent dispersal, e.g., where boldness, sociability, or aggressiveness is associated with dispersal tendency (Fraser et al. 2001; Dingemanse et al. 2003; Cote and Clobert 2007; Duckworth and Badyaev 2007; Cote et al. 2010a, 2011). While personality-dependent dispersal has been demonstrated in only a few species, it has been suggested as a widespread phenomenon with important ecological consequences (McCauley et al. 2010; Cote et al. 2010b).

One determining factor for colonization of habitats is patch isolation. Isolation can be an important selective agent, and both the distance between patches and the type of matrix isolating a habitat island are important, as illustrated by studies that have shown matrix-dependent colonization success (Ricketts 2001). This suggests that colonization of isolated habitats might be possible exclusively for individuals with a very specific phenotype. If this is the case, one could see what, if any, environmental filtering of phenotypes preceded colonization by comparing phenotypes of newly colonized populations with phenotypes of the main population. In other words, what phenotypic characteristics were needed to reach and colonize the isolated area, and how the magnitude of these traits change with distance traveled could be evaluated. Such behavioral differences between individuals that have recently colonized habitats differing in their level of spatial isolation would indicate that the impact of immigrants (i.e., as predators and/or competitors) on a patch varies across space and cannot be estimated solely on the basis of the average behavior of colonists across all distances from source populations (McCauley et al. 2010).

In this study, we explore a set of personality traits (consistent behavioral characteristics) of recently established populations of the common frog (*Rana temporaria*). We choose to study two traits, boldness and exploratory behavior. Boldness is a personality trait that has been associated with both predation risk and dispersal propensity (Dugatkin 1992; Fraser et al. 2001) and can be broadly defined as a willingness to accept a higher degree of risk in return for potentially greater returns while foraging or mating (Ward et al. 2004). Bold individuals are characterized by more risk-prone behaviors such as being quicker to emerge from shelter in a novel environment (Cote et al. 2010a). Exploration can be defined as an individual's

response to a novelty and is often assayed as exploration of a novel environment (Verbeek et al. 1994; Cote et al. 2010a).

We explored boldness and exploratory behavior of frogs on isolated coastal land-rise islands, and compare them with source populations from the mainland. This system is ideal for studying mechanisms underlying behavioral changes during range expansion since we have replicates of recently colonized isolated islands (Lind et al. 2011). Also, here, we aim to discuss whether the most parsimonious reason for these changes are behavioral flexibility, differential selection pressures across populations or the result of a founder effect in contrast to other studies of adaptive behavioral differences during range expansions (Suarez et al. 1999; Bearhop et al. 2005).

Methods

Study area/organism

All experiments were conducted in an aquatic laboratory facility at Umeå University, Sweden. The common frog (*R. temporaria*) breeds in temporary and permanent waters across Sweden (Gasc et al. 1997). Recent studies on islands in the archipelago within the Gulf of Bothnia, outside Umeå, northern Sweden, found local adaptation in development time and size at metamorphosis (Johansson et al. 2005; Lind and Johansson 2007) caused by divergent natural selection (Lind et al. 2011). Populations from pools that dried out faster had smaller sizes at metamorphosis and shorter development times than those from more permanent pools. To control for potential behavioral effects caused by this pattern, we chose island populations from the entire range of the drying regime.

Eggs were collected from four mainland populations and from four islands in the archipelago. All these populations are situated within a radius of 20 km from the center of Umeå city. One island has only permanent pool present (Storhaddingen), one has temporary pools (Sävar-Tärnögern), and two have pools that are intermediate in their drying (Svart Lass and Petlandsskär). The islands are all comparatively young, spanning a range of 350–800 years (Johansson et al. 2005), and have risen above the sea level as a consequence of ongoing postglacial land rise in the area (~8 mm/year). The mainland populations were from three permanent (Mariehem, Djäkneböle, and Grössjön) pools and one temporary (Tvärån) pool. Between May 9 and 13, 2009, 40–50 eggs were sampled from 10 different egg clutches from each population. The samples were transported to the laboratory where they were kept at 4 °C until all eggs were collected. At this temperature, no egg development occurs. Each egg clutch corresponds to the yearly offspring of one female because the females of *R.*

temporaria in this region breed only once a year and produce only one egg clutch (Elmberg 1991). When all of the eggs were collected, the temperature in the climatic controlled room was raised to 22 °C with a light/dark cycle of 18:6, corresponding to the natural light/dark cycle in the area. Experiments were started when tadpoles entered Gosner stage 23 (active swimming) (Gosner 1960). Ten tadpoles from each female were randomly chosen and placed individually into plastic containers (9.5×9.5 cm, height 10 cm) filled with 750 ml of tap water previously aged and aerated in a tank together with dried deciduous leaves. The leaves were removed when the water was transferred to the experimental containers. The plastic containers were distributed in a predetermined random pattern in the climatically controlled room. The tadpoles were fed, and the water was replaced every fourth day. The tadpoles were given 26 mg of food for the first 8 days. During the following 8 days, the food levels were increased to 51 mg, and from day 16 until the tadpoles had reached Gosner stage 42, the tadpoles were given 103 mg/day. This represents an ad libitum situation for the tadpoles. The food given to the tadpoles was a mixture of finely ground commercial fish flakes and rabbit food in a weight ratio of 1:1. At Gosner stage 42 (the forelimbs are visible), feeding was terminated and the water was drained and replaced with moist moss that covered the bottom of the containers where the tadpoles were kept until metamorphosis was completed (Gosner stage 46).

Measuring boldness and exploration in a novel environment

Boldness and exploration levels were assessed by recording these behaviors in a novel environment (Yoshida et al. 2005; Brown et al. 2007): a well lit, opaque, round plastic tank (diameter=120 cm, height=90 cm) filled with 10 cm of well water for tadpoles, while for froglets, the bottom was only slightly moist. Design of behavioral assays of tadpoles and froglets were almost identical, and hence we present the full design for tadpoles and only the adjustments of the design for the froglets. Tadpole behavior was estimated at Gosner stage 37 (when the toes of the hind limb are separated) and froglet behavior at Gosner stage 46 (when the tail is resorbed and metamorphosis is completed).

To estimate boldness and exploration in tadpoles, a tadpole was added gently to an upright, cylindrical (9 cm diameter, height 90 cm), gray, opaque, covered refuge chamber placed 4 cm from the wall of the tank. The cylinder had a circular opening (diameter=3 cm), covered by a lid, facing towards the center of the tank. After 10 min, we remotely opened the lid of the refuge chamber, allowing tadpole access to the experimental arena while digital cameras recorded behavior. Trials ended either 5 min after tadpoles left the refuge, or was terminated after 20 min (1,200 s). For froglets, the behavior trial was allowed to

go on for 10 min longer before terminated (1,800 s) since test trials had shown a much longer latency to leave refuge in that life stage.

Boldness was estimated as the maximum time allowed for tadpoles to exit the refuge (1,200 s; 1,800 s for froglets) minus the actual latency to exit from refuge; shorter latency to exit indicates higher boldness. Exploratory tendency was estimated as the area covered (see below) during the 5-min assay after the individual had left the refuge. While some have suggested that latency to emerge in a novel environment should be termed exploratory behavior and not boldness (Reale et al. 2007), we follow several earlier papers (Yoshida et al. 2005; Brown et al. 2007; Cote et al. 2010a) in our assessment that a short latency to emerge alone from a dark refuge into an open, novel environment represents risk taking (i.e., boldness), while exploratory tendency is measured as space use after emergence from refuge.

Video files were exported as image stacks (1 frame per second) using FFmpeg (http://www.ffmeg.org/). These image stacks were imported into ImageJ (http://rsbweb.nih.gov/ij/) where the tadpole's position was tracked over the 5-minute assay. Area explored incorporates both the distance an individual moved and the spatial pattern of those movements. Given x-y coordinates from each frame, we tracked each individual's continuous path (assuming that movements between frames were straight). As the water level in the tank was low (10 cm or no water), we only track movement in 2D. Explored area was calculated (in Matlab R2007) as the percentage of the arena that fell within 4 cm (approx. two body lengths) of the tadpole's path.

Weight

After the experiments were finished, froglet weight (Gosner stage 46) was estimated on a balance. We did not estimate weight of tadpoles, but weight is correlated across metamorphosis in these populations (Johansson et al. 2010), and we therefore used weight at metamorphose in our tadpole analyses as well. We also measure size as body length, head width, femur length, tibia length, and foot length, but due to an unfortunate mistake, the measurements from one population were lost. We therefore only use weight as our size estimate. However, repeating the analysis with size (excluding the missing population) gave qualitative the same results.

Statistical analysis

The personality variables, boldness for tadpoles and exploration for tadpoles and froglets, were log transformed before analyses to meet the assumption of normality. Boldness of froglets showed a truncated distribution and was therefore analyzed with a Kaplan–Meier survival analysis. To compare behavior between mainland and island populations, we

ran mixed-model ANCOVAs with environment (mainland and island) as fixed factor, population as random factor (nested in environment), and weight as covariate.

To explore if drying rate of pools affected behavior, we compared both exploration and boldness between the different drying regimes using two-way ANOVA with drying regime and environment (and the interaction) as factors.

Repeatability is defined as the proportion of phenotypic variation explained by differences between individuals (Lessells and Boag 1987), which can be caused by a variety of factors: genetic, developmental, and environmental (Reale et al. 2007; Bell et al. 2009).

Repeatability was estimated as suggested by Lessells and Boag (1987) using boldness and exploration in tadpoles and froglets. Behavioral correlation between boldness and exploration was analyzed separately for tadpoles and froglets. In addition, we estimated behavioral repeatability in the tadpole stage over 12 days. We were not able to test for repeatability in the froglet stage since they had to be released directly back into the wild for animal care reasons after the estimates of behaviors and size. Spearman rank correlation was used to estimate behavioral correlations because some of our variables did not meet the assumptions of normality.

Results

Boldness

Boldness in tadpoles differed significantly between mainland and island populations ($F_{1,54}=6.94$, $p=0.03$, with tadpoles from islands being more bold; Fig. 1). Weight did not affect boldness of tadpoles ($p=0.83$).

Boldness in froglets showed the same pattern as for tadpoles. Froglets from island were bolder compared to

Fig. 1 Mean boldness and exploration in tadpoles and froglets and weight (g) in froglets from island and mainland population. *Error bars* denote SE. Note that boldness is shown as the maximum time allowed for froglets or tadpoles to exit the refuge minus latency (s) to exit from refuge; shorter latency to exit indicates higher boldness
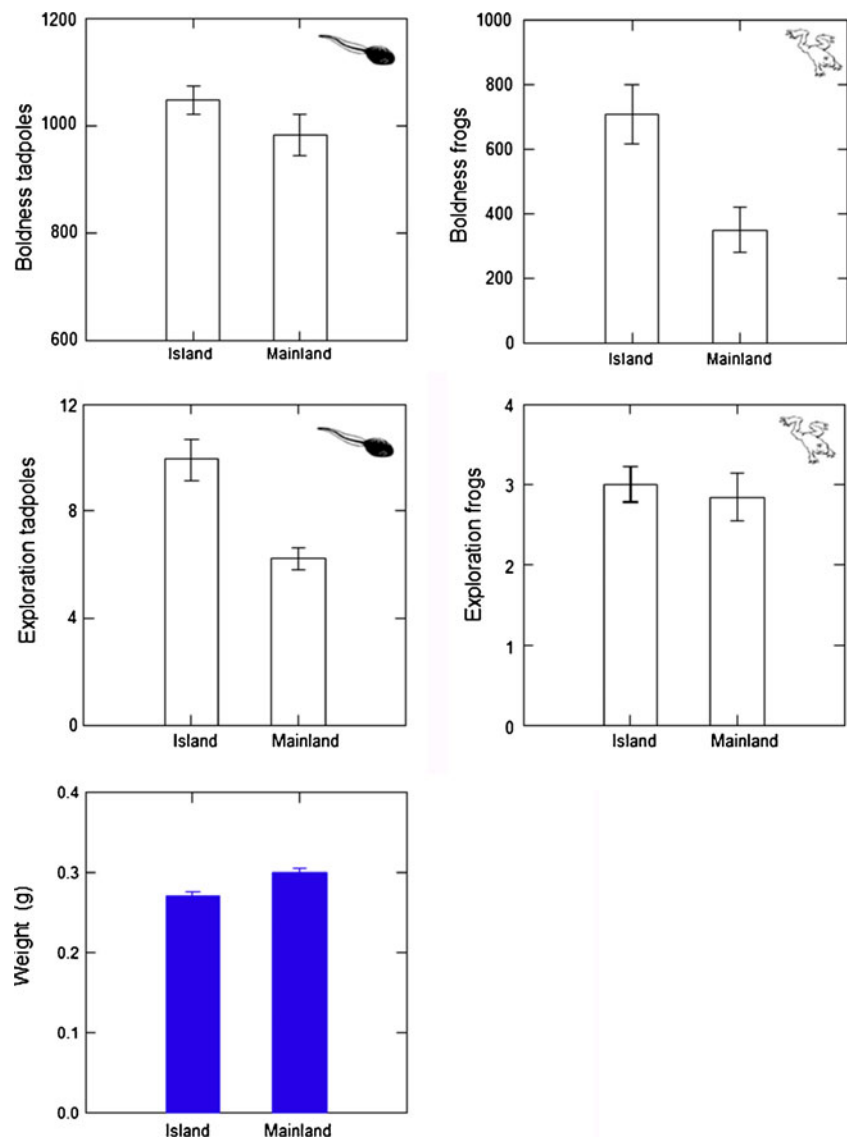
mainland populations (Fig. 1). This difference was supported by the Kaplan–Meier analysis (χ^2=5.09, p=0.02). Froglet weight affected boldness significantly in that heavier froglets (those on mainland) were less bold (χ^2=6.94, p=0.008).

Further analyses showed that both tadpole and froglet boldness differed between environments ($F_{4, 72}$=4.00, p=0.049 and $F_{4, 62}$=8.13, p=0.006 resp.) but was unaffected by drying regime ($F_{4, 72}$=0.09, p=0.91 and $F_{4, 62}$=2.38, p=0.10 resp.) and the interaction ($F_{4, 72}$=0.001, P=0.972 and $F_{4, 62}$=3.37, p=0.072 resp.). To explore if the extreme drying rate of pools (high–low) might affect boldness in our system, we compared the two island populations that differed most in pool drying: Storhaddingen (permanent) and Sävar-Tärnögern (temporary) using one-way ANOVAs. Tadpoles and froglets from the permanent and the temporary pool populations did not differ in boldness: $F_{1,18}$=0.005, p=0.94 and $F_{1,16}$=2.86, p=0.11, respectively.

Exploration

Tadpoles from islands had a higher exploration index than tadpoles from mainland populations (Fig. 1; $F_{1,54}$=27.01, p=0.001). Weight affected exploration significantly in that heavier tadpoles had a higher exploration index ($F_{1,54}$=6.50, p=0.013).

Froglets did not differ significantly in exploration between island and mainland populations (Fig. 1; $F_{1,54}$=3.78, p=0.09). Heavier froglets had a higher exploration index ($F_{1,54}$=7.18, p=0.013). One mainland population (Grössjön) had an extremely high exploration index which was on average 52 % higher than the second highest among the mainland populations. When we excluded this outlier population from the analysis of exploration, island populations had significant higher exploration values ($F_{1,45}$=25.14, p<0.003) .When this population was excluded from the analysis, weight still had a significant effect on froglet exploration ($F_{1,45}$=4.58, p=0.04). In addition, a subsequent analysis showed that both tadpole and froglet exploration was significantly affected by environment, island and mainland, ($F_{4, 62}$=14.81, p=0.0005 and $F_{4, 52}$=5.08, p=0.029 resp.) but not by drying regime ($F_{4, 62}$=2.74, p=0.073 and $F_{4, 52}$=0.46, p=0.631 resp.) or the interaction ($F_{4, 62}$=0.52, p=0.48 and $F_{4, 52}$=2.48, p=0.122 resp.).

For exploration we again compared the temporary pool population (Sävar-Tärnögern) with the permanent pool population (Storhaddingen) using one-way ANOVAs. Tadpoles and froglets from the permanent and the temporary island populations did not differ in exploration: $F_{1,18}$=1.92, p=0.18 and $F_{1,16}$=1.81, p=0.19, respectively.

In summary, tadpoles and froglets from island population were bolder and more exploratory. However, since these effects sometimes covaried with weight, we performed correlations between the weight estimates and personality indices for each population separately. In total, this includes 32 correlations (eight populations×weight×four personalities). Of these 32 correlations, five showed a positive and three a negative significant relationship. Hence, there was no clear trend with regard to the relationship between behavior and weight, suggesting that weight does not affect personalities at the population level. Since population where used twice in these test, we also corrected for multiple test with Bonferroni corrections; after which, none of the correlations were significant.

Repeatability

In parallel with the main study, boldness trials of 60 tadpoles showed that boldness was repeatable over a time period of 12 days (p=0.012, r=0.34). In contrast, repeatability across life stages for both boldness and exploration was nonsignificant and lower (r=0.25 and r=0.25, respectively). In addition, if we pooled all four mainland populations or all four island populations, repeatability in boldness between the life stages was still nonsignificant and fairly low for both the mainland (r=0.29) as well as for the island individuals (r=0.23). Similarly, there was nonsignificant repeatability in exploration (correlation between exploration in tadpoles and froglets) for both the mainland (r=0.23) and the island individuals (r=0.30).

Behavioral correlations

Cross trait correlations between boldness and exploration were negative, but not significant, in both tadpoles (r_s=−0.208, n=63, p=0.08) and froglets (r_s=−0.167, n=63, p=0.19). When analyzing correlation between boldness and exploration of mainland and island populations separately, we still found no significant correlations (mainland tadpoles, r_s=−0.29, n=37, p=0.08; island tadpoles, r_s=−0.06, n=35, p=0.72; mainland froglets, r_s=−0.04, n=34, p=0.83; island froglets, r_s=−0.24, n=29, p=0.20).

Discussion

Our study is a multi-life-stage study that illustrates population differentiation in personality traits between isolated populations and source populations. In this island system with isolated populations that are connected with mainland populations through migration (Lind et al. 2011), the current study clearly shows that newly established populations of *R. temporaria* on isolated islands (Johansson et al. 2005) differ from the ancestral mainland populations in several personality traits. It should be noted that the froglets and juvenile frogs are dispersal stages in *R. temporaria* since the tadpole

larvae is completely aquatic and that the low salinity in the sea allows dispersal.

We show that both tadpoles and froglets from isolated populations are bolder and more exploratory when compared to less isolated mainland populations. Our results are in line with what could be expected if colonizers of isolated islands are not a random draw of the founder population but instead, the small subset of the founder population that is bolder and more exploratory than the average random frog. This combination of trait expressions is the behavioral type that could be expected to successfully disperse to isolated islands. Earlier studies of personality-dependent dispersal have shown that dispersers often express a different behavioral type than residents; they can be bolder (Fraser et al. 2001; Chapman et al. 2011), more exploratory (Dingemanse et al. 2003), or less sociable (Cote et al. 2010a). Hence, our findings are in accordance with previous studies of personality-dependent dispersal (Fraser et al. 2001; Dingemanse et al. 2003; Cote and Clobert 2007; Cote et al. 2010a; Cote et al. 2011). However, to our knowledge, this is the first study to indicate a connection between environmental filtering (via isolation) of animal personalities through personality-dependent dispersal and population differentiations in the wild. The temporal persistence of these effects is still unknown. Trade-offs between traits correlated with dispersal and other traits determining fitness may lead to a shift in the population over time towards a phenotypic composition more similar to highly connected habitats (Hill and Caswell 1999; Duckworth and Badyaev 2007) or populations may diverge even more. However, the populations are young, 23–267 generations (Johansson et al. 2005), and connected to the mainland by continuous gene flow (Lind et al. 2011), which suggests that they are continuously receiving an inflow of bold dispersers.

However, since we did not collect the dispersing individuals on their way to the islands but instead, the offspring of individuals that had successfully dispersed and also established themselves in the local breeding population, there are possible alternative explanations for the personality differences found between island and mainland populations.

First, one might argue that the island populations live in a more unstable environment, for instance, with a higher risk of pond drying, forcing island tadpoles to be more bold and exploratory to be able to grow and develop rapidly to escape pond drying thru metamorphosis (Johansson et al. 2005; Lind et al. 2011). This explanation seems unlikely for several reasons. Ponds used in the study represent the entire gradient of drying regimes, from temporary rock-pools to permanent waters bodies. The ponds were chosen to avoid systematic errors that pond-drying regime might invoke. In addition, our results are independent of the drying regime and hence support our conclusion that personality differentiation might be the result of personality-dependent filtering thru isolation.

Second, the behavioral differentiation could be an effect of different predator environments. Earlier studies have shown that predation can be a major force in differentiating personality traits between populations (Bell 2005; Dingemanse et al. 2007). In our case, if the island populations experience less predation pressure than the mainland populations, it could explain those populations being bolder and more exploratory. Examples of more risk-prone individuals in environments with low predation pressure are numerous (Lima and Dill 1990; Anholt and Werner 1998; Brodin and Johansson 2004) and bolder individuals have been shown to have a higher probability of mortality by predation (Dugatkin 1992; Ward et al. 2004; Bell and Sih 2007). However, there are also studies showing selection for bolder individuals in high predation environments (Brown et al. 2005). In an earlier study, Scherlund (2003) showed that the mainland and island frog populations have similar behavioral responses when facing a caged predator. Four antipredator behaviors were measured (swimming activity, feeding activity, spatial avoidance, and escape distance), and mainland and island populations showed similar responses in all measured traits. Thus, frogs from mainland and island populations respond similarly to predators. Although the results of Scherlunds (2003) do not exclude the possibility of differentiated predation pressure between islands and mainland, they do not support it either. Hence, we cannot discard the possibility that predation pressure might, at least partly, be a factor in differentiating island and mainland frog populations studied here.

Third, behavioral differentiation between island and mainland could be condition dependent, since individual condition has been shown to potentially affect animal behavior (McNamara and Houston 1994; Mikolajewski et al. 2004). We found significantly heavier froglets from mainland populations when compared to island populations. However, although mainland (heavier) tadpoles/froglets are less bold and exploratory than island (lighter) tadpoles/froglets, there is no correlation between weight and tadpole boldness. In addition, when we analyzed the effects of weight on personality traits for each population separately, there were no significant relationships found for any life stage. This strongly suggests that individual weight and personality trait expression is independent in this study. Thus, we can conclude that two plausible explanations for this population differentiation in personality traits remain. It could either be the result of founder effects caused by personality-dependent environmental filtering of dispersing frogs or the result of differing predation pressure or maybe even a combination of both. Since the sea is a very hostile and risky matrix to disperse thru (individuals will either make it to the island or die trying), we expect the selection to be strong and only a very narrow "phenotypic window" will be open for successful dispersers.

Therefore, although we cannot out rule the possibility that the differences in personality traits between mainland and island populations are influenced by other factors than dispersal since differences in predation pressure can result in similar patterns, the known history of the populations as recently colonized islands with substantial gene flow from the mainland (Lind et al. 2011) and the close match to predictions (Fraser et al. 2001; Chapman et al. 2011) makes personality-dependent dispersal a strong candidate for the present result.

An interesting behavioral outlier among the mainland populations is Grössjön. For being a mainland population, it is quite isolated from other ponds or lakes and has no inlet or outlet (as opposed to the other mainland populations). One could say that Grössjön could be regarded as an island on land. The matrix surrounding Grössjön is land, with vegetation and plenty of cover, and hence not as hostile and exposed as the sea matrix surrounding the island populations. This could explain why the Grössjön populations only have high exploration and not high boldness. Exploration is needed to travel long distances independent of matrix but high boldness should not be as important if there is plenty of cover and refuges present in the isolating matrix (as is on land).

In a recent study of the island system, Johansson et al. (2012) found that the genetic variance and covariance matrix of life-history traits (including weight) in tadpoles from the island system is significantly different than the matrix derived from tadpoles on the mainland. One possible explanation for this pattern is that the frogs that have colonized the island system are a nonrandom subset of the frogs present on the mainland. Although our study provides no direct evidence supporting this explanation, it does show that bold froglets, decedents from frogs colonizing the islands, weigh less than the shy and large mainland froglets. Hence, a subset of frogs not only in terms of life history but also in terms of behavior might have colonized the islands. Such a pattern would be in accordance with a recent paper by Biro and Stamps (2008) in which they suggest that life history and personality could be tightly linked.

Behavioral correlations may differ in stability depending on what mechanism underlies the correlation. Individual differences in single traits of animal personalities (e.g., boldness) are usually moderately heritable and relatively stable over an individual's life (Koolhaas et al. 1999; van Oers et al. 2005). Most stable over time (many generations) are phenotypic correlations caused by strong genetic correlations (van Oers et al. 2005; Bell 2005) such as pleiotropy, where the correlated behaviors (e.g., boldness and exploration) are governed by a shared genetic mechanism. Evidence for strong genetic correlation between behavioral traits suggests that behavioral traits are correlated because they are controlled by the same hormones (Koolhaas et al. 1999;

Ketterson and Nolan 1999) or genes (van Oers and Mueller 2010). Components of personality may therefore be difficult to decouple (Ketterson and Nolan 1999). Another mechanism generating behavioral correlations is linkage disequilibrium caused by correlational selection. Correlational selection is selection for optimal trait combinations (Barton and Turelli 1991), and theory predicts that correlational selection will eventually produce an adaptive genetic correlation between traits because alleles influencing one trait will be co-inherited together with alleles influencing the other trait (Jones et al. 2003). In this study, we found no correlation between individual tadpole and froglet personality-trait expressions. This finding was slightly unexpected since an earlier study of "carry-over effects" between distinctly different life stages showed that personality traits can, indeed, be carried over from larvae in one environment to adult in a completely different environment (Brodin 2009). That study on damselflies showed that active and bold larvae gave rise to active and bold adults, illustrating a behavioral syndrome from an aquatic life stage to a terrestrial life stage. Here, however, we present contrasting results with no correlation between the two life stages despite a very similar scenario where aquatic larvae metamorphose and move into a terrestrial habitat. The mismatch of the results from these studies is very intriguing and adds new information about the stability and generality of carry-over effects. Actually, our results fit well with earlier theories that have suggested that selection should uncouple a behavioral syndrome through ontogeny when environmental conditions experienced by juveniles differ substantially from those experienced by adults (Sih et al. 2004a, b). Indeed, it is very likely that the selection pressures experienced by *R. temporaria* below and above the water surface differ. For example, a highly exploratory larva may be favored in a low predation site but a highly exploratory adult might be more easily spotted by a predatory bird or could have a higher probability of ending up in unfavorable (as well as favored) patches. Previous studies have also found decoupling of locomotion performance in amphibians between the tadpole and froglet stage when controlling for body size (Watkins 2001; Johansson et al. 2010).

This study adds a valuable piece of information on how colonization of isolated habitats may lead to behavioral differentiation between new populations and the founder population. How this behavioral difference in turn affects ecosystem effects of colonizers and population viability remains to be explored. Trade-offs between traits correlated with dispersal and other traits determining fitness may lead to a shift in the population over time towards a phenotypic composition more similar to highly connected habitats (Hill and Caswell 1999; Duckworth and Badyaev 2007) or populations may diverge even more. An interesting continuation of this study would be to evaluate the temporal persistence

of this behavioral differentiation. Finally, since amphibians are one of the most threatened vertebrate group, with over 30 % threatened with extinction (Stuart et al. 2008), studies like ours that provide new understanding about amphibian dispersal and colonization are crucial for helping us understand how to increase the chance of persistence for species in jeopardy.

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