Variable individual consistency in timing and destination of winter migrating fish

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Migration is an important event in the life history of many animals, but there is considerable variation within populations in the timing and final destination. Such differential migration at the population level can be strongly determined by individuals showing different consistencies in migratory traits. By tagging individual cyprinid fish with uniquely coded electronic tags, and recording their winter migrations from lakes to streams for 6 consecutive years, we obtained highly detailed long-term information on the differential migration patterns of individuals. We found that individual migrants showed consistent site fidelities for over-wintering streams over multiple migratory seasons and that they were also consistent in their seasonal timing of migration. Our data also suggest that consistency itself can be considered as an individual trait, with migrants that exhibit consistent site fidelity also showing consistency in migratory timing. The finding of a mixture of both consistent and inconsistent individuals within a population further our understanding of intrapopulation variability in migration strategies, and we hypothesize that environmental variation can maintain such different strategies.

Keywords: differential migration; individual consistency; roach; Rutilus rutilus

1. INTRODUCTION

During the course of a year, most habitats vary in their profitability regarding both potential growth rates and mortality risks [1,2]. Migrating animals exploit this variation by moving according to temporal changes in the profitability of different habitats [2,3]. Central questions in animal migration studies arise from the widespread observation that there is significant variation in migratory behavioural traits within populations, e.g. in the time of migration or in the final destination—a phenomenon known as ‘differential migration’ [4,5]. Several studies have focused on how conditional traits can explain differential migration, whereas less attention has been paid to individual consistencies in differential migratory traits, i.e. how fixed the migratory traits are within individuals [6,7]. Here, we assess individual consistency in migratory traits in a common cyprinid fish, the roach Rutilus rutilus, and ask whether this consistency is a general trait or found only in some individuals within a migratory population.

Behavioural consistency is usually inferred from statistical correlations over time at the population level. However, population-level analyses can mask the fact that not all individuals behave consistently within a population, even if a significant correlation is found. The degree to which individuals are consistent may vary, yet few studies have considered consistency in behaviour as a trait in itself. Here, we present a study investigating population-level consistency in two key migratory traits: the timing and destination of migration. We also show that, in our study species, the roach, consistency itself can be considered a trait that exhibits considerable variation among migratory individuals.

2. MATERIAL AND METHODS

(a) Study system

The study was conducted in the 3.4 km², shallow, macrophyte-rich Lake Krankesjön in southern Sweden (for lake description, see [8,9]). Parts of the roach population in the Lake Krankesjön are known to overwinter in either of the three connected streams: Silväkrabäcken, Lånsmansbäcken or Alabäcken [10].

(b) Fish migration

Between 2003 and 2007, we captured, measured, tagged with passive integrated transponders (PIT-tags) and released 2908 roach in the Lake Krankesjön during autumn (see electronic supplementary material). Directional migration of fish between the lake and the streams was monitored by using a modified PIT-tag antenna system consisting of two antennas and a recording station in each stream (for details see [9]). Migration was monitored from October 2003 to June 2009, i.e. for six consecutive migration periods. The occurrence of site fidelity and the extent of consistency in timing of migration were analysed at the individual level. For data treatment, see the electronic supplementary material.

3. RESULTS

(a) Site fidelity

Of the 2909 fish tagged between 2003 and 2007, 424 individuals (15%) migrated both during the first and the second winter after tagging, which enables analyses of individual consistency in differential migration. Of these 424 fish, 239 individuals (56%) migrated into only one of the three streams in both years, whereas the rest migrated into multiple streams during at least one of the two winters. We found that individual fish that migrated into multiple streams during the first winter were also more likely to migrate into multiple streams during the second winter as compared with fish that migrated into only one stream during the first winter ($X^2 = 4.46; n = 432; p = 0.035$).

Of the 239 fish that migrated into only one of the streams during the first two winters after tagging, 151 individuals (63%) chose the same stream in both years, which was significantly more than if fish chose streams randomly ($X^2 = 60; n = 239; p < 0.001$; figure 1). The same pattern was found when comparing individual over-wintering sites in both the first and the third winter after tagging ($X^2 = 26.6; n = 58$;
the population level (linear mixed model; between-year variation in the date of outmigration at significant effect of the random factor ‘year’ indicates occurred around mid-October (data not shown). The and spring, but the highest peak in outmigration (

Individual fish left the lake throughout autumn, winter (

In this study, we have had a unique opportunity to track the migration behaviour of a large number of individually tagged fish for a number of years, and thereby we were able to describe consistency in differential migration at both the population and the individual levels. Studies on intrapopulation differentiation into consistent and inconsistent individuals focus most often on differences in foraging behaviour and foraging-based traits, where individuals are classified as either generalists or specialists [11]. However, intrapopulation differentiation may also occur in behavioural consistency, which, as we show here, extends into migration-related traits. This further illustrates that an underlying intrapopulation mixture of consistent and inconsistent individuals can shape population-level differential migration.

Timing of migration is crucial for over-wintering success, and the optimal time of migration is dependent on environmental variation, such as temperature or food availability [2,9]. However, besides external control, the individual timing of migration may also be dependent on individual migration history or be under genetic control as seen in both birds [12] and fish [13]. Accordingly, we found that individual timing of migration in fish was related to the individual time of migration in the preceding year. There may be a number of mechanisms maintaining the variation in endogenous control of migration in a population. Other studies have shown that the primary aim of winter migration in cyprinids is to avoid predation over winter [2,14]. Surviving migrants should therefore be considered as having successful migration strategies, and individuals should thus retain migratory behaviours between years. Alternatively, consistency in individual variation in timing may also be maintained through density-dependent selection on a threshold in the circannual rhythm [15], where individuals staying in the lake longer before migrating out would benefit from decreased competition from individuals leaving earlier.

Migratory direction has been shown to be under genetic control in birds migrating long distances to their winter quarters [16,17]. Here, individual phenotypes may end-up migrating to unfavourable sites and thus be selected against [18]. However, for short-distance migrants, e.g. fish in lakes, migrating in a fixed compass direction would provide little accuracy in reaching preferred wintering sites, as outmigration from the lake has to go through the mouth of the

(b) Timing of migration

Individual fish left the lake throughout autumn, winter and spring, but the highest peak in outmigration occurred around mid-October (data not shown). The significant effect of the random factor ‘year’ indicates between-year variation in the date of outmigration at the population level (linear mixed model; \( F_{1,348} = 22.2; p < 0.001 \)), but the timing of outmigration from the lake to the streams for individual fish in the second winter after tagging was significantly related to the timing of outmigration during the first year of migration (linear mixed model: \( F_{1,348} = 3.98; p = 0.047 \)). Size (total length) of the migrating individual had no significant effect on timing (linear mixed model: \( F_{1,348} = 1.94; p = 0.164 \)).

(c) Migratory consistency as a trait

As described above, individual consistency was found within the population in both the timing of migration and in the over-wintering site. However, consistency varied between individuals and individuals consistent in one trait were generally also consistent in the other. More specifically, we found that the probability of site fidelity increased with smaller between-year difference in the timing of outmigration from the lake (logistic regression: Wald\(_{237} = 19.7; p < 0.001\); figure 2).

4. DISCUSSION

In this study, we have had a unique opportunity to track the migration behaviour of a large number of individually tagged fish for a number of years, and thereby we were able to describe consistency in differential migration at both the population and the individual levels. Studies on intrapopulation differentiation into consistent and inconsistent individuals focus most often on differences in foraging behaviour and foraging-based traits, where individuals are classified as either generalists or specialists [11]. However, intrapopulation differentiation may also occur in behavioural consistency, which, as we show here, extends into migration-related traits. This further illustrates that an underlying intrapopulation mixture of consistent and inconsistent individuals can shape population-level differential migration.

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Figure 1. Site fidelity between years 1 and 2 of migration in roach overwintering in three different streams: Silvåkra-bäcken (black bar), Lånsmansbäcken (white bar) or Alåbäcken (grey bar). The y-axis shows the number of individuals in each stream during the second year. Arrows indicate site fidelity. Fish generally choose to migrate to the same stream as they did in a preceding winter, for the three potential over-wintering streams.

\[ p < 0.001; \] electronic supplementary material, figure S1a), and in the second and the third winter after tagging \( (\chi^2 = 34; n = 74; p < 0.001) \); electronic supplementary material, figure S1b).

Figure 2. The relationship between the individual degree of consistency in the timing and individual site fidelity (solid line) from a logistic regression for winter-migrating roach in the Lake Krankesjön. Bars show the frequency distribution in deviation in the timing of fish that either showed site fidelity (upper bars) or not (lower bars).
streams, which are usually narrow. It therefore seems more likely that the site fidelity in the winter-migrating roach is caused by experience from successful migrations in previous years, so that learning potentially maintains consistency in this trait. Individual variation in site fidelity could be a result of differences in the degree to which individuals store or use information gathered from previous experiences of migration.

In summary, we found a general individual consistency in both the timing of migration and in the over-wintering site for migratory roach. However, for both traits, the degree of consistency varied in the population, i.e. there is a mixture of both consistent and inconsistent individuals within the population. In accordance with the result that individuals with more consistent timing of migration also showed a higher likelihood of site fidelity, we conclude that some individuals are simply more consistent than others in multiple traits, which suggest that behavioural consistency can be regarded as a trait in itself. The differences in individual consistency in migratory behaviour could reflect underlying variation in animal personality [19], which has recently been shown to play a role in migratory behaviour in this species [20]. The responsiveness axis of animal personality has been reported in a number of species, and referred to how animals respond to environmental stimuli [21]. ‘Responsive’ individuals are sensitive to stimuli, whereas ‘unresponsive’ individuals form routines and are consistent and less flexible in their behaviour. In migratory roach, consistent migrants can be viewed as unresponsive individuals, which should be selected for when the correlation between proximate cues and optimal time of migration is low, i.e. when present environmental conditions in one habitat offer little possibility to predict differences in profitability of alternative habitats, and at a low degree of spatial and temporal environmental stochasticity. Previous studies have shown that migratory consistency differs between populations, but we show here that migratory consistency also varies within populations.

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