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The Ecological Importance of Extrinsic and Intrinsic Drivers of Animal Movement

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The Ecological Importance of Extrinsic and Intrinsic Drivers of Animal Movement

Josh E. Rasmussen

A dissertation submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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ABSTRACT

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Doctor of Philosophy

The movement of individuals is foundational to many ecological processes. For example, the movement of an organism from one place to another alters population density at both sites and has potential for affecting the genetic dynamics within the new population. Individual movement events may be in synchrony with overall trends in populations, e.g. spawning migrations, or may be atypical (asynchronous). This latter movement type can affect population and metapopulation dynamics, depending on its prevalence within a population. Nevertheless, given the complexity of interactions, the causative factors of movement are understood vaguely, much less for aquatic organisms. Drivers of movement are extrinsic (e.g. habitat quality, predation or habitat heterogeneity) and intrinsic (e.g. sex, size, or behavioral tendencies). Interactions among these drivers provide crucial insight into the patterns of movement observed within populations. Habitat is here shown to affect observed movement patterns of populations of southern leatherside chub (*Lepidomeda aliciae*). Streams with higher-quality habitat were inhabited by populations exhibiting lower overall movement compared to lower-quality streams. However, observations of individual long distance movement relative to the norm within the population suggest that movement may also be behaviorally based. In further tests, it is shown that, indeed, behavioral tendencies of individuals can be measured and are predictive of annual movement by individuals. Other drivers, habitat availability and quality, were also found to influence movement on a yearly basis. Movement patterns are also affected by the presence or absence of predators. A tropical livebearer (*Brachyrhaphis rhabdophora*) has a higher percentage of individuals classified as generally moving when predators are absent from the environment compared to predator sites. Predation environment also significantly affects individual body shape with predator sites possessing caudal peduncles with greater surface area, an adaptation likely promoting burst speed for greater escape abilities. Classification of individuals as generally moving or generally not moving was also significantly related to variation of body shape of these fish. However, biological significance is ambiguous given the absence of obvious morphology trends explained by this factor. It is critical to understand these drivers to better understand the dynamic interface between ecology and evolution.

Keywords: dispersal, restricted movement paradigm, *Lepidomeda*, *Brachyrhaphis*, morphometrics, habitat quality, behavioral syndromes

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Chapter 1: Movement of Freshwater Stream Fishes: Linking Ecological Processes with Evolutionary Patterns

Abstract

Movement of organisms is an important activity that has ecological and evolutionary implications, including individual reproductive success and survival, population growth and persistence, local adaptation and gene flow. Expression of movement behavior has traditionally been termed dispersal and measured relative to home ranges; however, this simplistic approach belies the complexity of the movement process and consequences. Movement of freshwater fish has long been viewed as predominantly restricted in nature, but recent research challenges this paradigm. Some level of movement invariably exists in every population. A better research emphasis is to understand conditions which may promote or limit movement. Thus, a review and discussion of movement and related factors is warranted. Movement behavior by individuals is often synchronized with the majority of the population, but asynchronous movement may also occur. Drivers of movement can be categorized as extrinsic environmental factors, e.g. habitat quality, habitat variability, and the presence of predators, and intrinsic conditions of the fish, e.g. sex, body size and condition, and ontogenetic stage. One intrinsic trait that has received relatively little attention is the inherent behavioral tendency of an individual to be sedentary or mobile. Clarification of movement patterns and consequences will only occur when ecological and evolutionary forces are considered jointly. Future research of movement behavior should focus on the interaction of extrinsic and intrinsic drivers to better understand the evolutionary and ecological implications of movement.

Keywords: restricted movement paradigm, synchronous movement, movement drivers

Introduction

Movement of individuals is an important ecological process that occurs at the individual level, but has ramifications across many levels of ecological organization with potentially far-reaching evolutionary effects (Dodson 1997). Individuals within populations often display little movement over long periods punctuated by relatively brief, but important, periods of movement (Schlosser 1995; Vokoun and Rabeni 2005) such as coordinated migrations or individual dispersal events. Understanding animal movement depends on our ability to understand the ecological causes and the evolutionary outcomes of such events. Over-simplification of the inherent patterns in populations must be avoided by viewing such patterns as variable phenotypic expressions, and instead treat such patterns as a continuous variable.

Recent reviews have covered movement behavior generally (Bowler and Benton 2005; Bullock et al. 2002; Clobert et al. 2001; Ronce 2007), in relation to metapopulation dynamics (Clobert et al. 2004), gene flow (Bohonak 1999), plants and seed dispersal (Cousens et al. 2008; Levin et al. 2003), mammals (Chepko-Sade and Halpin 1987; Matthysen 2005; Stenseth and Lidicker 1992), birds (Clarke et al. 1997; Matthysen 2005; Nichols and Kaiser 1999), and insects (Cook and Holt 2006; Hopper 1999; Ockinger and Smith 2008; Service 1997; Woiod et al. 2001). Surprisingly, references to freshwater fish as examples are limited in general reviews of dispersal. Few reviews have been conducted on the movement behavior of fish; exceptions include marine fish movement (McCormick et al. 1998; Woodson and McManus 2007) and freshwater fish, primarily focused on salmonids (Banks 1969; Gowan et al. 1994; Leggett 1977; Lucas and Baras 2001; Northcote 1992; Rodriguez 2002). Data concerning larval movements or movements within lacustrine environments is germane, but to focus and simplify the scope of

this review is limited to include movement behavior of adult and juvenile freshwater stream fish, including information from other systems or ontogenetic stages where pertinent.

The limited inclusion of fish movement research in freshwater streams is surprising, given that these are excellent systems to better understand this process. The linearity of freshwater streams can greatly reduce the complexity of models of movement compared to terrestrial, lacustrine, or marine models; although the dendritic nature of stream systems does add elements of complexity. Additionally, recent advances in capture and tagging techniques permit utilization of fish with minimal invasiveness to individuals, which often occur in relatively high densities (Gowan et al. 1994; Juanes et al. 2000; Northcote and Lobon-Cervia 2008). Lastly, the inherent diversity and plasticity of freshwater stream fish (e.g. life-span, life history traits, and reproductive systems) presents a myriad of opportunities to explore the numerous correlations of movement patterns with other important ecological and evolutionary processes (Lucas and Baras 2001).

This review 1) presents a brief sketch of the general topic of dispersal research and terminology, 2) discusses long-standing and recent paradigms specific to freshwater fish movement, 3) reviews evidence for extrinsic and intrinsic drivers of movement, and 4) discusses the linkage of ecological patterns and evolutionary outcomes.

General Dispersal Research

Customarily, individual movement in excess of daily movement behavior has been termed “dispersal.” Spatial and temporal scales vary with the organism of interest and must be considered to assess individual movement properly (Albanese et al. 2003; Armstrong et al. 1998; Cooper et al. 1998; Labbe and Fausch 2000; Nathan 2005; Petty et al. 2005; Turchin 1998).

Nevertheless, dispersal is typically defined as travel by an individual farther than the average home range size (Stenseth and Lidicker 1992). A single dispersal event is often partitioned into three stages: 1) emigration, 2) transit, and 3) immigration. Emigration is the act of abandoning the current area occupied by the individual, and eventually transitions into the transit stage which is the actual travel by the individual. This second stage is often characterized by exploratory behavior and evaluation of patches, and includes important variables such as travel distance and direction (Bowler and Benton 2005; Doerr and Doerr 2005). Finally, the individual becomes established in a new patch (i.e. immigration) (Bowler and Benton 2005).

Migrations are special instances of dispersal in which organisms return to the original area from which they emigrated (Cooke et al. 2008; Dingle 1996; Dodson 1997). A common migration of many freshwater fishes occurs annually during spawning and post-spawning movements; often coinciding with spring and fall seasonal changes (Godinho et al. 2007; Grant and Maslin 1999; Gresswell and Hendricks 2007; Hilderbrand and Kershner 2000; Kuhn et al. 2008; Schrank and Rahel 2004). In addition to habitat quality, spawning migrations often correlate with other potential drivers, such as lack of breeding or social resources, predation risk, and genotypic variation (Jennings et al. 1996; Lucas and Baras 2001; Naslund 1993; Ovidio et al. 1998). Return movements of individuals often span a broad range of distances (Kuhn et al. 2008; Ovidio 1999; Schrank and Rahel 2004). Important migrations also occur due to significant ontogenetic differences within species for feeding or refuge resources (Northcote 1978, 1984).

As described above, scale is integral in describing movement patterns (Crook 2004; Koster and Crook 2008; Labbe and Fausch 2000). Movements typical of acquiring essential resources for daily survival or exploratory excursions, while important, are typically smaller in

scale than what is classically considered a dispersal event or are circular, i.e. movements center on a hub possibly with brief periods of absence (Mikheev 2005; Smithson and Johnston 1999; Van Dyck and Baguette 2005). Even so, when viewed across many time increments these minor movements may combine to produce a movement signature of a longer distance type that potentially has weighty evolutionary implications. Long distance movements may also occur over much shorter periods of time (Lucas and Baras 2001).

Usage of the term “dispersal” can be vague (e.g. poorly defining specific movement parameters) or incomplete (e.g. narrowly focusing on one stage). The same term is applied to natal movement from birth sites, spawning movements of adults, and individual movements related to these other two. This is in part due to the complexity of these processes, but also exposes an attempt to simplify a highly variable process primarily in a phenomenological context with discrete outcomes, e.g. did or did not disperse. For many taxa, this discrete approach and term (i.e. dispersal) accurately reflect population dynamics, particularly applying to natal movement events, e.g. plant seed dispersal and density-dependent insect dispersal (Cousens et al. 2008; Stenseth and Lidicker 1992; Woiod et al. 2001). However, in many instances the more general term “movement,” more accurately reflects the true continuous, plastic nature of this behavior and allows for greater flexibility in addressing and conceptualizing broad patterns and linking these to other important processes, such as evolutionary processes, without necessarily requiring such patterns to be categorized into discrete groupings (Neville et al. 2006).

The study of movement behavior is complicated by the inherent intricacies and interactions within and among individuals, populations, communities, and a multitude of abiotic factors (Drakou et al. 2009; Ewers and Didham 2006). Movement by an individual may increase

or decrease survival probability, body condition, fitness, or any number of parameters (Clobert et al. 2004; Fraser et al. 2001; Hilderbrand and Kershner 2004; 2007; Schradin and Lamprecht 2002). The same movement event may also significantly affect population (Bohonak 1999) or metapopulation dynamics (Daniels et al. 2008; Hanski and Gaggiotti 2004), as well as inter-specific interactions (Bowler and Benton 2005; Drakou et al. 2009; Hitt and Angermeier 2008; Peterson and Fausch 2003). One noteworthy potential outcome of individual movement is the flow of genes, with all its attendant issues, such as out-breeding depression or genetic rescue (Carlsson et al. 1999; Tallmon et al. 2004). Barriers, habitat fragmentation and disturbance also significantly influence movement patterns within and among populations; such factors may affect broad-scale population resiliency or species-level extinction risk (Ewers and Didham 2006; Meffe 1990; Neely and George 2006; Pluym et al. 2008; Rahel et al. 1996; Roghair 2005; Sheldon and Meffe 1995; Van Dyck and Baguette 2005). It is difficult to think of any other ecological process that has more universal implications throughout the domain of ecological study.

History of the Study of Freshwater Fish Movement

The fact that some individuals within a population are mobile while others largely sedentary is widely recognized; however the prevalence of movement within populations is a subject of much recent debate (Gerking 1959; Gowan et al. 1994; Jackson 1980; Rodriguez 2002). The principal paradigm in fish dispersal, presented in a review by Gerking (1959), held that salmonids are predominantly sedentary and that mobile individuals, “strays” in his terminology, are uncommon and therefore abnormal (Kahler et al. 2001). For example, Knouft and Spotila (2002) determined that nearly 96% of all recaptures of resident brown trout (*Salmo*

trutta) remained within 800 m after 6 months. This restricted movement paradigm (RMP; Gowan et al. 1994) has also been widely adopted for other freshwater species and systems ([Table 1](#)). However, the RMP was challenged as data, particularly turnover rates, from salmonid and other freshwater taxa indicated that movement was potentially much more common than previously believed ([Table 1](#)). For example, Riley and Fausch (1995) proposed that immigration of unmarked stream-dwelling brook trout (*Salvelinus fontinalis*), brown trout, and rainbow trout (*Oncorhynchus mykiss*) into improved habitat areas accounted for the increase of densities in these areas given low recapture rates of marked fish and relatively high proportions of unmarked individuals. Similarly, Young (1994) reported that 65% of marked brown trout within two Wyoming streams had estimated home ranges of greater than 50 m. These and other data lead authors to conclude that perhaps the RMP was incorrect, possibly due to flawed methods of data collection which tended to overemphasize non-moving recaptured individuals while ignoring unmarked individuals or not accounting for long-distance movers (Albanese et al. 2003; Fausch et al. 1995; Gowan and Fausch 1996b; Gowan et al. 1994).

However, this assertion that high turnover rates were necessarily indicative of high movement rates was also challenged. Rodriguez (2002), using data from 28 salmonid populations, compared pooled distributions (i.e. up- and downstream movers were combined) of recaptured individuals to a negative logistic distribution using non-linear regression methods, from which he estimated median distances moved and turnover rates. This analysis purported to show that high turnover rates can also be associated with low median distances moved.

In summary, the RMP has been mainly tested in salmonid systems with mixed results. The problem with the RMP (aside from the lack of support across diverse taxa) is that it is

intended to describe movement patterns, but has no theoretical basis. In other words, proponents of either side of the debate ask readers to subscribe to their perspective with no underlying mechanism to provide support for their argument. It is important, therefore, to refocus the debate towards a better understanding of actual patterns of fish movement within and among populations (Lucas and Baras 2001).

The first step to comprehension of movement patterns and their evolutionary importance is to understand the impetus for movement. In general, a distinction can be made among the drivers of movement behavior as those extrinsic and those intrinsic to an individual. However, interactions between these drivers certainly occur and are an important element affecting the eventual movement phenotype displayed (McMahon and Matter 2006).

Drivers of Movement

There are important distinctions between the types of movement an individual may perform throughout its life. Many movement events are carried out in synchrony with all or most other individuals in the population (population-level movement). These events include spawning and post-spawning migrations and movements avoiding substandard habitat conditions, i.e. anchor ice or hypoxia. The events are seemingly better described by the term dispersal. Population-level movements are often ecologically based, responding to specific ecological forces such as temperature cues, lack of resources, or predation risk. The vast majority of individuals in a population will respond to these situations or conditions in much the same way. In contrast to population-level movement events, individuals may move independent of the normal or average behavior of the rest of the population, asynchronous movement. These individual-level movement events are much more difficult to understand or attribute to a single

causative factor, but may include many intrinsic as well as extrinsic factors (Lucas and Baras 2001; McMahon and Matter 2006).

Extrinsic Factors

Habitat Quality

Habitat quality includes available resources, abiotic environmental conditions and predator environment and is closely tied to population movement patterns in many instances ([Figure 1](#); Lucas and Baras 2001). Higher quality habitats typically produce less mobile individuals than poorer quality habitats (Aparicio and De Sostoa 1999; Kahler et al. 2001). For example, habitat structure deemed desirable for trout, e.g. large woody debris, was determined by several researchers to provide settlement areas for otherwise “transient” individuals (Fausch et al. 1995; Gowan and Fausch 1996a), but Harvey (1998) observed that large woody debris did not increase immigration of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) into manipulated areas. Food, or the lack thereof, was not an important factor in causing emigration movements of juvenile Coho salmon (*Oncorhynchus kisutch*) during simulated winter conditions in artificial channels (Giannico and Healey 1998); however, Mikheev (2005) noted that fish inhabiting uniform habitat tend to use a variety of foraging behavior to improve food searching techniques, including increased mobility. The opposite is true when resources are adequate (Mikheev 2005). Indirect measures of habitat quality (i.e. population densities) often do not correlate with movement patterns (Heggenes 1988; Natsumeda 2003) of adults, but may reflect movement patterns of juveniles (Petty and Grossman 2004).

Abiotic conditions, e.g. water temperature and water current or flows, often correlate with seasonal movements or spawning migrations, even of land-locked populations (i.e.

potamodromy) (Curry et al. 2002; Lucas and Baras 2001). Frequent examples involve upstream movements as temperatures increase (Albanese et al. 2004; Grabowski and Isely 2006; Sakaris et al. 2005) and downstream movements as temperatures decrease (Homel and Budy 2008; Jakober et al. 1998), but in some instances changes in temperature were determined to not correlate with movement patterns or in some instances to reduce movement (Giannico and Healey 1998; Mellina et al. 2005; Monnot et al. 2008; Natsumeda 2003, 2007). Rates of flow also significantly affect the movement patterns of many freshwater fish species with both positive and negative relationships, i.e. both higher and lower rates of movements have been associated with increased flows (Giannico and Healey 1998; Koster and Crook 2008; Mellina et al. 2005; Natsumeda 2003, 2007; Schaefer 2001; Simpson and Mapleston 2002; Steingrimsson and Grant 2003). Schlosser (1995) found that downstream movement from a beaver pond primarily occurred during high flow events, but upstream movements occurred across a broad range of flows.

Abiotic environmental factors also consist of physicochemical characteristics of the water body (e.g. temperature and dissolved oxygen). For instance, six species of fish emigrated from a desiccating wetland complex in patterns closely tied to water quality and physiological tolerances of each species (Cucherousset et al. 2007). Several centrarchid species have been observed to emigrate from backwater areas when hypoxic conditions increase (Gent et al 1995; Knights et al. 1995). Likewise, experimental manipulation of Atlantic salmon (*Salmo salar*) parr exposure to two estrogenic compounds (estradiol-17 and tert-octylophenol) reduced migratory behavior relative to control individuals (Bangsgaard et al. 2006). Given the transitory nature of

abiotic conditions, movement in response to these conditions is also typically temporary (Lucas and Baras 2001).

Habitat Heterogeneity

Spatial and temporal heterogeneity are significant drivers of movement behavior (McPeck and Holt 1992). Habitats with greater inherent complexity have higher probabilities of supplying an individual's requirements, and therefore often elicit reduced movement behavior (Albanese et al. 2004; Baras 1992), but not always. Roni and Quinn (2001) observed higher proportions of individuals moving in an artificial system with complex habitat relative to the simple habitat. Macro-habitat variation, e.g. relationship of pools, runs, and riffles, is frequently correlated with movement patterns. Isolation of pools by riffles constrained movements of fantail (*Etheostoma flabellare*), riverweed (*E. podostemone*), and Roanoke darter (*Percina roanoka*) in addition to effects from micro- and mesohabitat (Roberts and Angermeier 2007). Likewise, individuals from two Arkansas stream assemblages emigrated from pools bounded by "short" riffles at rates three times higher than individuals in pools bounded by "long" riffles, and movement from "long-riffle" pools were directed downstream in a higher proportion than from "short-riffle" pools (Lonzarich et al. 2000). In contrast, riffle and glide habitats were not barriers to blue shiner (*Cyprinella caerulea*) movement (Johnston 2000).

In freshwater streams, heterogeneity often results from temporally recurring events, e.g. flooding or other forms of disturbance. Disturbance can result in involuntary movement (e.g. flushing) or avoidance movements (Albanese et al. 2004; Allibone et al. 2003; Chapman and Kramer 1991), but such movements are typically short-term or temporary (Fischer and Kummer 2000). However, responses to disturbance events may vary; individuals have been documented

to move upstream during flood events (Albanese et al. 2004). Gowan and Fausch (2002) proposed that temporal variation in optimal feeding site distribution for brook trout required that dominant individuals move to maintain possession of optimal foraging sites producing a cascade of displacement and movement by lower-ranking individuals throughout the local area. In contrast, seasonal heterogeneity did not appear to correlate with *Cottus gobio* movement patterns (Knaepkens et al. 2005).

Predators

Relatively little research has been conducted on broad movement patterns of freshwater fish as attributable to co-occurring predators. Killifish, *Rivulus hartii*, exhibited higher rates of movement through areas inhabited by predators (Gilliam and Fraser 2001). Individual size and water levels interacted with predation threat (Gilliam and Fraser 2001). Similarly, movement of three cyprinid species was apparently stimulated by predation threat in an artificial system (Schaefer 2001). In contrast, Roberts and Angemeier (2007) observed constrained movement patterns by fantail, riverweed, and Roanoke darter, accounted for, in part, by predator density. Brassy minnows (*Hybognathus hankinsoni*) and hornyhead chubs (*Nocomis biguttatus*) were found to move from preferred habitats into shallow raceway and riffle refugia in the presence of smallmouth bass (*Micropterus dolomieu*) predators (Schlosser 1988a, b)

Intrinsic Factors

Body Size and Condition

Comparisons of body size between putative mobile and sedentary individuals within populations reveal that mobile individuals are often larger (Croft et al. 2003; Natsumeda 2007; Sakata et al. 2005; Young 1994) and grow faster (Kahler et al. 2001; Roni and Quinn 2001;

Steingrímsson and Grant 2003). This is contrary to assumptions that competitively inferior individuals that have been displaced comprise mobile portions of populations (Gerking 1959). However, instances of no difference or higher rates of mobility at smaller body sizes and poorer growth of movers have also been documented (Nakamura et al. 2002; Natsumeda 2007; Schrank and Rahel 2006). Hughes and Reynolds (1994) and Hughes (1999) proposed that a “larger-older-fish-upstream distribution pattern” of Arctic grayling (*Thymallus arcticus*) is maintained by progressive upstream movement such that older fish recruit into higher reaches as they age. Likewise, some patterns of interactions between movement and body size indicate that rapid yearly growth may promote upstream movement where poor growth produces the opposite pattern (Hughes 1999). Similar patterns of larger fish upstream were documented in fish inhabiting lowland rivers in England (Linfield 1985). Body size is frequently strongly correlated with distance traveled by mobile individuals. Larger individuals regularly move greater distances including female guppies (*Poecilia reticulata*; Croft et al. 2003), post-spawn bull trout (*Salvelinus confluentus*; Monnot et al. 2008), sub-adult and adult Colorado Pikeminnow (*Ptychocheilus lucius*; Osmundson et al. 1998), cutthroat trout (Schrank and Rahel 2004), and flathead catfish (*Pylodictus olivaris*; Travnichek 2004). Mobile individuals may exhibit poorer body condition than predominantly sedentary individuals (Gowan and Fausch 1996b; Hilderbrand and Kershner 2004), but these differences may only be temporary (Hilderbrand and Kershner 2004). Exceptions to this have been observed in populations of brook trout (no difference) and Bonneville cutthroat trout (negative relationship) (Peterson and Fausch 2003; Schrank and Rahel 2006).

Sex

Differences of movement outside of spawning migration between the sexes have received relatively little attention, in part due to the emphasis of spawning migration research and the perceived similarities of the sexes outside of spawning season. However, broad-scale movement of galjoen (*Dichistius capensis*) in southern Africa was unrelated to sex and age (Attwood and Cowley 2005). In contrast, male guppies were documented to have much higher movement rates than females, similar to other internal reproducers (e.g. mammals) (Croft et al. 2003).

Behavioral Phenotype

Putative “mobile” and “sedentary” individuals within populations have been documented for many freshwater species ([Table 2](#)). Asynchronous movement among individuals is best understood as a behavioral phenotype reflecting expression of divergent life history strategies (Cucherousset et al. 2005; Lucas and Baras 2001). For example, broad ranges (e.g. 1 km to greater than 30 km) of movement by individuals within the same population have been documented for several species (Baras 1992; Lucas and Batley 1996; Lucas et al. 1998); however, the causes of the differences are little understood. Differences in the upstream, range-expansion movement of brook trout was observed such that many fish moved along the “front of invasion” while others exhibited long-distance or jump invasion moving very far distances (Peterson and Fausch 2003). Movement behavior of individuals may be relatively constant through life or may alternate between mobile and sedentary (Knaepkens et al. 2005; Knaepkens et al. 2004; Mellina et al. 2005; Nakamura et al. 2002).

Variation in movement behavior has been correlated with other behavioral traits suggesting that behavioral syndromes may provide important insight into movement patterns

(Dingle 2001; Sih et al. 2004a; Sih et al. 2004b). Laboratory assessments of boldness of *Rivulus hartii* predicted distance moved after release into natural environments even after the effects of size and sex were accounted for (Fraser et al. 2001). Similarly, observations of foraging behavior in a natural environment were correlated with movement behavior in a novel setting (i.e. aquaria; Wilson and McLaughlin 2007). Yet, dominance in trout does not appear to significantly relate to short-term movement behavior (Hojesjo et al. 2002; Nakano 1995).

Genetically based variation in movement behavior is supported by evidence with walleye (*Sander vitreus*; Jennings et al. 1996), salmonids (Lucas and Baras 2001), and threespined stickleback (*Gasterosteus aculeatus*; Snyder and Dingle 1989; Snyder 1991). It remains to be determined how genotype and environment interact to produce the expression of a given movement phenotype, and how much of the behavior is due to plasticity in the response of the individual to extrinsic drivers.

Linking Ecology and Evolution

Movement may be categorized as either consistent with prevailing population trends, i.e. the majority of individuals are moving in synchrony with each other (dispersal), or movement during a period when the majority of individuals are predominantly sedentary (asynchronous movement). These types of movement are not necessarily mutually exclusive, but each will create unique evolutionary forces within populations. Both dispersal and asynchronous movement are life-history strategies with alternative phenotypes; however, they are not two alternatives of the same behavior. Dispersal more accurately reflects either-or-type movement events, while asynchronous movement is expressed variably along a continuum by individuals ([Figure 2](#); Southwood 1988). Frequency dependent dynamics may act on the population or

metapopulation such that neither phenotype goes to fixation in a population; however, such dynamics are likely to occur across an evolutionary time frame rather than an ecological time frame. Both behaviors involve movement from one location to another, but seem to be driven by very different ultimate factors.

Individuals jointly participating in synchronous movements will typically belong to the same population. Synchronous movement tends to homogenize and synchronize populations genetically, behaviorally, and phenotypically given that these types of movements often result in congregated gatherings for reproduction promoting genetic admixture. Likewise, seasonal movements driven by abiotic conditions frequently produce restricted distributions, assuring similar selective pressures. Such occurrences tend to produce greater opportunity for local adaptation.

Asynchronous movement events can affect evolutionary dynamics of both populations and metapopulations, even if such events are rare. Such movements are influential at an ecological level if the distance traveled is within the confines of the population and if differences in important parameters, such as survival, growth, or fitness, between mobile and sedentary individuals occurs. However, extreme expressions of an asynchronous movement phenotype will result in individuals, and thus genes, crossing population boundaries (Stiver et al. 2007; Wilson et al. 2004). High rates of asynchronous movement will reduce genetic isolation and local adaptation ([Figure 3](#)) and may contribute to synchrony between populations. For example, component populations pertaining to a metapopulation may have synchronous spawning runs; however, this synchrony may be a result of habitat requirement restrictions or relatively high rates gene flow due to individual-level asynchronous movements (Stenseth and Lidicker 1992).

Therefore, understanding probabilities of rates and distances of asynchronous movement is essential to link these two fields.

Connecting drivers, extrinsic and intrinsic, with probabilities of rates and magnitude of movement within and among populations should be approached through a synthesis of mathematical, empirical, and experimental means to generate and test predictions (Johnson and Gaines 1990; Wilson et al. 2004). Emphasis in research should be directed towards heuristic detection of empirically generated patterns that appear consistently across taxa and environments, and in so doing a clearer picture of the strength and directional of certain drivers on movement behavior will emerge. Based on this model of population- and individual-level movement differences, predictions can be made with associated tests of movement in relation to other factors. High levels of habitat heterogeneity should favor sedentary individuals under the assumption that the probability that realized benefits will exceed realized costs is low (Adams et al. 2004; Albanese et al. 2004; Hamilton and May 1977), but dispersal rates should be unaffected by this factor. However, temporal and spatial variability may work counter to each other (Dieckmann et al. 1999; Johnson and Gaines 1990).

Within other vertebrates, inbreeding avoidance has received much attention as a likely evolutionary driver of movement patterns. Freshwater fish present a multitude of reproductive strategies that may allow testing of this hypothesis. A prediction may be that species utilizing paired spawning may exhibit some form of sex-biased dispersal patterns at some stage throughout development. In contrast, group spawning species may lack this pattern given that the probability of spawning with a close relative may be relatively low. Asynchronous movement rates would likely be unaffected by these differences in reproductive systems. The

study of correlation between reproductive strategies and movement patterns should yield fertile ground for linking ecology with evolution.

In the end it is likely that the intersection of extrinsic factors and intrinsic traits can be implicated in nearly every movement event (McMahon and Matter 2006). Extrinsic factors certainly can affect a multitude of intrinsic factors which may further interact with each other potentially altering movement behavior (Ovidio et al. 1998). Likewise, the inclusion of movement behavior, especially asynchronous movements, in consideration with behavioral syndromes will be especially useful in elucidating the evolutionary implications of movement and how they correlate with individual behavior in other situations (Sih et al. 2004a; Sih et al. 2004b). It is at these junctures (i.e. interactions) where the majority of significant information will be found concerning the drivers of fish movement.

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Tables

Table 1 Recently published reports of movement patterns of freshwater fish species in relation to the prevailing restricted movement paradigm and conclusions drawn by the researchers (e.g. generally restricted or prevalent). Prevalent refers to movement in relative terms and may not imply that mobile components of the population were the majority of individuals

| Species | Conclusions | Reference |
|---|-------------|--------------------------------|
| Barbo de cola roja – <i>Barbus haasi</i> | Restricted | Aparicio and De Sostoa (1999) |
| Blackbanded darter - <i>Percina nigrofasciata</i> | Restricted | Freeman (1995) |
| Blue shiner - <i>Cyprinella caerulea</i> | Restricted | Johnston (2000) |
| Brown trout - <i>Salmo trutta</i> | Prevalent | Milner et al. (1979) |
| Brown trout - <i>Salmo trutta</i> | Prevalent | Carlsson et al. (2004) |
| Bullhead - <i>Cottus gobio</i> | Restricted | Fischer and Kummer (2000) |
| Bullhead - <i>Cottus gobio</i> | Prevalent | Knaepkens et al. (2004) |
| Common carp - <i>Cyprinus carpio</i> | Restricted | Crook (2004) |
| Cutthroat trout- <i>Oncorhynchus clarkii</i> | Prevalent | Schmetterling and Adams (2004) |
| Cutthroat trout- <i>Oncorhynchus clarkii</i> | Prevalent | Gresswell and Hendricks (2007) |
| Galjoen - <i>Dichistius capensis</i> | Restricted | Attwod and Cowley (2005) |
| Giebel - <i>Carassius auratus</i> | Restricted | Penczak (2006) |
| Golden perch - <i>Macquaria ambigua</i> | Restricted | Crook (2004) |
| Green sunfish - <i>Lepomis cyanellus</i> | Restricted | Gatz (2007) |
| Gudgeon - <i>Gobio gobio</i> | Restricted | Penczak (2006) |
| Loach - <i>Barbulata barbulata</i> | Restricted | Penczak (2006) |

Continued on next page

| Species | Conclusions | Reference |
|---|-------------|--------------------------------|
| Mottled sculpin - <i>Cottus bairdii</i> | Restricted | Brown and Downhower (1982) |
| Mottled sculpin - <i>Cottus bairdii</i> | Restricted | Petty and Grossman (2004) |
| Perch - <i>Perca fluviatilis</i> | Restricted | Penczak (2006) |
| Redbreast sunfish - <i>Lepomis auritus</i> | Restricted | Freeman (1995) |
| Rhone streber - <i>Zingel asper</i> | Prevalent | Labonne and Gaudin (2005) |
| Roach - <i>Rutilus rutilus</i> | Restricted | Penczak (2006) |
| Roanoke darter - <i>Percina roanoka</i> | Prevalent | Roberts et al. (2008) |
| Slimy sculpin - <i>Cottus cognatus</i> | Prevalent | Schmetterling and Adams (2004) |
| Tench - <i>Tinca tinca</i> | Restricted | Penczak (2006) |
| Yellowfin shiner - <i>Notropis lutipinnis</i> | Restricted | Goforth and Foltz (1998) |

Table 2 Recent studies in which evidence for at least two distinct behavioral phenotypes (i.e. mobile and sedentary) was reported for freshwater fish species.

| Species | Reference |
|---|--------------------------------|
| Barbell - <i>Barbus barbus</i> | Hunt and Jones (1974) |
| Bullhead - <i>Cottus gobio</i> | Knaepkens et al. (2004) |
| Bullhead - <i>Cottus gobio</i> | Knaepkens et al. (2005) |
| Cutthroat trout - <i>Oncorhynchus clarkii</i> | Gresswell and Hendricks (2007) |
| Cutthroat trout - <i>Oncorhynchus clarkii</i> | Hildebrand and Kershner (2000) |
| Cutthroat trout - <i>Oncorhynchus clarkii</i> | Schmetterling and Adams (2004) |
| Eurasian minnow - <i>Phoxiunus phoxinus</i> | Kennedy and Pitcher (1975) |
| European chub - <i>Leiciscus cephalus</i> | Nicolas et al. (1994) |
| Gudgeon - <i>Gobio gobio</i> | Stott (1967) |
| Hardhead - <i>Mylopharodon conocephalus</i> | Grant and Maslin (1999) |
| Largemouth bass - <i>Micropterus salmoides</i> | Paller et al. (2005) |
| Masu salmon - <i>Oncorhynchus masou</i> | Sakata et al. (2005) |
| Pikeperch - <i>Sander lucioperca</i> | Fickling and Lee (1985) |
| Rainbow trout - <i>Oncorhynchus mykiss</i> | Meka et al. (2003) |
| Sacramento pikeminnow - <i>Ptychoheilus grandis</i> | Grant and Maslin (1999) |
| slimy sculpin - <i>Cottus cognatus</i> | Schmetterling and Adams (2004) |
| Surubum - <i>Psuedoplatystoma corruscans</i> | Godinho et al. (2007) |

Figures

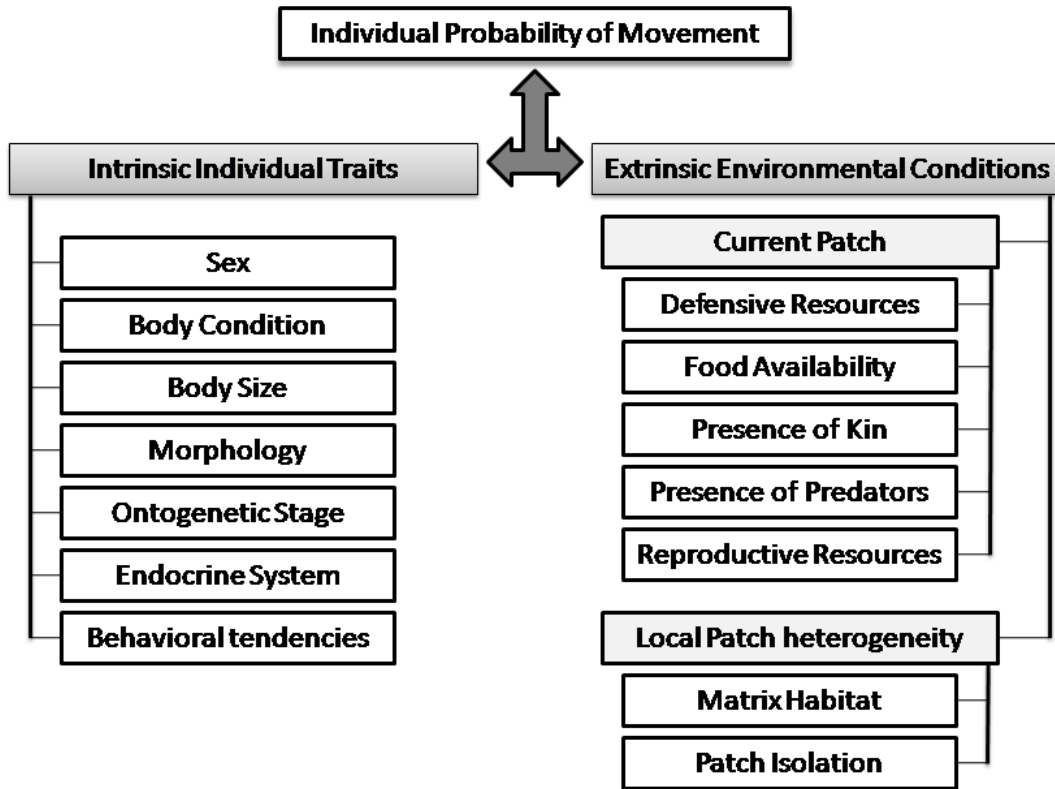


Figure 1 Schematic of selected intrinsic and extrinsic factors that potentially affect the probability of an organism to emigrate from its current patch. Lines connecting white boxes indicate potential interactions among those factors and highlight the inherent complexity of this ecological process.

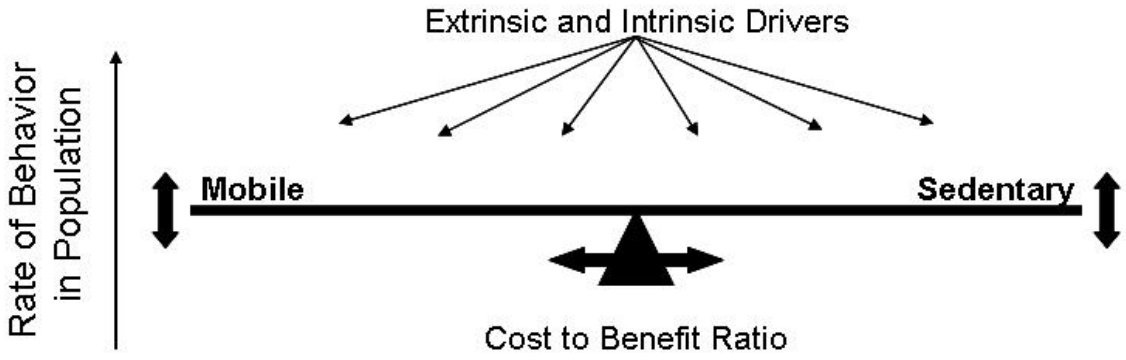


Figure 2 Rates of individual-level movement behavior within a population may be viewed as a sea saw ranging between 0 and 1, and always summing to 1. Drivers variably affect the probability of asynchronous movement, though the interaction and relative strengths of such effects are often unknown. The fulcrum on which the figure rests may also shift laterally dependent on the cost to benefit ratio of the movement behaviors such that when costs outweigh benefits the fulcrum will shift away from that behavior, increasing the prominence of the other within the population.

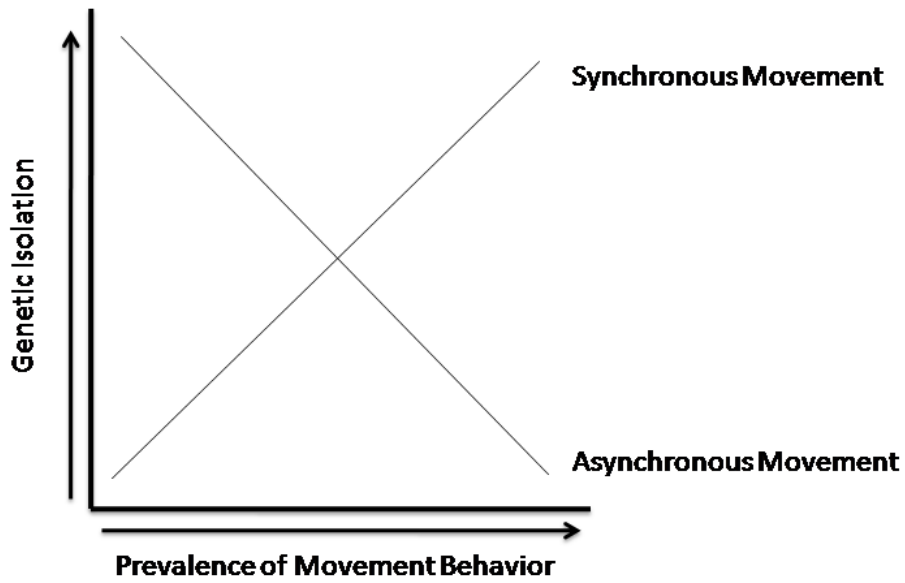


Figure 3 Relationship of population genetic isolation to the prevalence of synchronous (i.e. population-level) dispersal and asynchronous (i.e. individual-level) movement behavior.

Chapter 2: Variation in Movement Behavior Among and Within Populations of Southern Leatherside Chub (*Lepidomeda aliciae*)

Abstract

Movement of freshwater fishes has long been considered to be generally restricted both in scope and prevalence in populations, and as such a relatively homogeneous trait. However, recent research has both supported and contradicted this paradigm of restricted movement. In addition to providing a test of the prevalence of movement in freshwater fish populations, we clarify the contribution of some drivers of movement to apparent movement patterns by assessing the variation of behavior among five populations of southern leatherside chub using mark-recapture techniques over four years. Broad habitat characteristics, such as abundant instream structure and deep pools, appear to affect movement of individuals, as the streams classified as poor quality habitat exhibited much higher movement and turnover rates than populations in good habitat. Furthermore, the occurrence of a small group ($n = 26$) of long-distance movers (0.5 – 2 km) in Salina Creek provides evidence for variation in movement behavior within populations. This data reveals the importance of adaptive management techniques, e.g. sampling methods should be tailored to specific stream types dependent on habitat characteristics. Likewise, movement behavior is a polymorphic trait and thus it is invalid to characterize such patterns with means only; analysis of means and variances and tests for bimodality may be required.

Keywords: *Lepidomeda*, habitat quality, long-distance movement

Introduction

Variation in phenotypic expression can be an important determinant of evolutionary stability and adaptability of populations. However, the resolution at which observations are conducted may affect the apparent patterns of variation (Adams et al. 2004). Movement of organisms is central to the temporal and spatial dynamics of populations and metapopulations. Effects of movement occur at diverse resolutions such as ecological, e.g. population growth and density, source-sink dynamics (Dieckmann et al. 1999; Hovestadt and Poethke 2006; Labonne and Gaudin 2006; Larson et al. 2002) and colonization or range expansion (Lonzarich et al. 1998; Taylor 1997), and an evolutionary level, i.e. gene flow (Bohonak 1999). Attempts to simplify or classify observed patterns of dispersal into discrete categories may lead to disregard of the importance of variation in dispersal behavior among and within populations.

To date, much of the research on freshwater fish has been to quantify patterns, with limited effort to clarify the underlying biological and ecological processes that produce such variation (Albanese et al. 2004; Heggenes 1988; Penczak 2006). In his review of fish movement patterns, Gerking (1959) maintained that freshwater fish movement within streams is restricted in terms of both distance and prevalence among individuals of a population. However, Gowan et al. (1994) challenged this paradigm (termed by them as the restricted movement paradigm; RMP) using movement data of brook trout (*Salvelinus fontinalis*) in several Rocky Mountain streams. Gowan et al. (1994) argued that movement was much more variable within populations than previously proposed given high turnover rates in distinct sections of rivers. The perspective that high rates of movement are common is contradicted (Aparicio and De Sostoa 1999; Freeman 1995; Johnston 2000; Penczak 2006) and supported (Adams et al. 2004; Kahler et al. 2001;

Labonne and Gaudin 2005; Smithson and Johnston 1999) by research within freshwater fish populations. Furthermore, Rodriguez (2002) challenged the paradigm of higher rates of movement reviewing recapture distributions of 28 salmonid populations and concluding that high turnover rates are not necessarily indicative of high levels of movement. However, even individuals who support a restricted movement paradigm, including Gerking (1959) and Rodriguez (2002), acknowledge that variation of movement behavior may exist among and within populations (Allibone et al. 2003).

Freshwater fish are an excellent model for dispersal research due to the predominantly linear or longitudinal structure of stream systems (which can reduce the complexity of models) and the relative ease with which large numbers of individuals can be sampled. Similarly, advances in mark-recapture techniques permit non-destructive marking of large groups of individuals, which are then available for recapture over multiple events, often years, with relatively high efficiency (Gowan and Fausch 1996; Gowan et al. 1994; Rodriguez 2002). Our purposes are twofold: 1) evaluate movement in a series of systems that differ in their habitat quality in a way that allows for a comparison of movement across a variety of habitats and detection of long-distance movers, and 2) seek further clarification of the RMP by incorporating analysis of the role habitat variation and behavioral dimorphism play in movement patterns. To accomplish this we compare movement patterns among and within populations of a small western North American cyprinid *Lepidomeda aliciae*, southern leatherside chub.

Southern leatherside chub is a rare desert fish occurring in streams or small rivers in the Utah Lake and Sevier River drainages of the Bonneville Basin in Utah (Johnson et al. 2004; Wilson and Belk 2001). This species provides a good system with which to achieve these

objectives due to the variation in habitat quality among several populations. Likewise, the several populations chosen provide sufficient numbers of individuals necessary to successfully undertake a mark-recapture study, a circumstance relatively rare given the decline of population numbers.

Methods

In August 2003, we initiated a multi-year mark-recapture study at two locations: Salina Creek and Lost Creek ([Figure 4](#)). Three additional study sites were added in 2004 - Mammoth Creek, San Pitch River, and Soldier Creek. Salina Creek was resampled each year until 2006; and Lost Creek was resampled in 2004 and 2005 ([Table 3](#)). All three sites initiated in 2004 were resampled in 2005. Southern leatherside chub co-exists with brown trout in three of these streams, Mammoth, Lost, and Soldier creeks. However, in Salina Creek and San Pitch River larger predatory fish are absent.

Qualitative differences in apparent habitat quality among the streams exist. Salina and Lost Creeks present relatively good habitat for southern leatherside chub (Walser et al. 1999; Wilson and Belk 2001). Habitats in these streams consist of heterogeneous instream structure, such as deep pools (> 1 m), riffles, cover from riparian vegetation (longbar willow [*Salix exigua*], yellow willow [*Salix lutea*], and Russian olive [*Eleagnus angustifolia*] being the most prominent), and undercut banks. In contrast, San Pitch River and Soldier Creek provide few, if any, of these beneficial habitat characteristics. These streams are relatively shallow (typically 0.2 – 1 m) with few deep pools and relatively devoid of instream or riparian structure to provide cover or refuge (Walser et al. 1999; Wilson and Belk 2001). Available habitat within Mammoth Creek is composed of some deep pools, cut banks, and backwater areas; however, similar to San

Pitch River and Soldier Creek, this stream possesses negligible riparian vegetation, which translates into a volatile channel and unstable banks. In contrast, vegetation in the channel was very common at Mammoth Creek in 2004. However, Mammoth Creek experienced extremely high flows (>100 year return period) in the summer of 2005 with flows (239.9 m³/s) an order of magnitude higher than the previous year (48.6 m³/s). This event significantly altered instream habitat structure by scouring all in-stream vegetation from the channel.

At all of the sites selected southern leatherside chub co-exist with several native species, speckled dace (*Rhinichthys osculus*), mountain sucker (*Catostomus platyrhynchus*), and mottled sculpin (*Cottus bairdii*). Each of these species presents another potential habitat effect, that of competition. However, competition is probably an insignificant factor affecting leatherside chub movement behavior, given that the chub typically feed in the drift and the others are primarily demersal or benthic feeders.

First year sampling of each site consisted of capturing, tagging, and releasing southern leatherside chub. In each stream, four contiguous 50-m segments were blocked downstream with a net (mesh size approximately 1 cm) while fish were removed during three successive passes with a backpack electroshocker. We estimated the number of southern leatherside chub per 50 m of each stream based on our three-pass removal sampling. We used a closed capture model (Pollock and Otto 1983) within Program CAPTURE to calculate the density estimates. Estimates were produced for each of the four original 50-m segments, averaged for each year where data existed, and standardized to densities per 100 m. Following each pass with the electroshocker, individuals were sorted into aerated holding tanks according to species. Species other than southern leatherside chub were counted and released after sampling was completed.

Southern leatherside chub were measured (standard length; SL) and marked using Visual Implant Elastomer (VIE; Northwest Marine Technology, Inc., Shaw Island, Washington, USA). Mark location reflected size class of the individual at the time of marking (40 - 64 mm SL - dorsal caudal, 65-84 mm SL - ventral caudal, >84 mm SL - anal). The smallest size class was comprised of age 1 individuals, who are not reproductively mature (Johnson et al. 1995). Medium-sized individuals likely were age 2 or 3 and were potentially reproductive (Johnson et al. 1995). Age 4 and older individuals comprised the bulk of the large size class. Color of elastomer mark distinguished original capture segments. Young of the year (< 40 mm SL) were excluded from the study because marking would likely reduce survivorship, and young-of-year SLC are poorly sampled by electroshocking due to their small size.

Follow-up sampling procedures were identical to those used for original capture of the fish; however to assess movement, several 50-m segments up- and downstream were sampled in addition to the original 50-m segments. Downstream segments began at 500, 250, 100 and 50 m below the boundary of the most downstream original segment. Upstream segments began at 0, 100, and 200 m upstream of the boundary of the upstream-most original segment. All SLC captured within the original four 50-m segments and those that had been tagged the preceding year, no matter their recapture location, were remarked with VIE marks. This mark differed from the original tagging scheme in that color no longer indicated capture segment, i.e. all received the same color - blue. Size class of the fish continued to be designated by location of the VIE marks. In 2005, sampling up- and downstream of the original 50-m segments was limited to 150 m in each direction in 50-m increments and occurred at all sites. Individuals from all original 50-m segments not previously encountered and previously tagged were marked with

the color green. Sampling was restricted to Salina Creek in 2006, and the area sampled was extended to include areas further from the original tagging segments (up to 1 km) to assess long-distance movement.

Probability of movement by size in Salina and Lost Creeks (i.e. 2003) was examined using Chi-squared analysis ([Table 4](#)). To adjust for low expected values (e.g. < 5 individuals) for large individuals at Salina Creek the analysis was performed with large and medium sized individuals pooled. Low recapture rates at San Pitch River and Soldier and Mammoth Creeks prevented their inclusion in this analysis.

Results

Movement patterns varied greatly among streams. After one year (2004 – 2005), recaptures within San Pitch River (n = 30), Mammoth Creek (n = 9) and Soldier Creek (n = 8) were extremely low, yielding recapture rates of about 4% at each site. In contrast, Lost Creek (2 years) and Salina Creek (3 years) averaged much higher year-to-year recapture rates, 20% and 36%, respectively. Average turnover rates, i.e. proportion of new immigrants into a tagging segment, approached 100% in Soldier Creek and San Pitch River. Salina Creek segments had slightly lower average turnover rates (i.e. new immigrants) from 2003 to 2004 than Lost Creek, 69% and 77%, respectively. In Mammoth Creek, density of southern leatherside chub declined to zero individuals within the tagging segments ([Figure 5](#)). All recaptures for Mammoth Creek were located in a single large backwater area within 50 m upstream of the original tagging segments. Distribution of recaptures was spread throughout the sampling area for Soldier Creek and San Pitch River, and year-to-year population density trends were similar to the other streams in the study, suggesting that the paucity of recaptures was not due to localized mortality.

After one year, 66% of recaptured individuals in Salina Creek were captured in the same segment in which they were marked, and 95% were recaptured within 100 m. These values were slightly less for Lost Creek (45% and 88%, respectively). After three years in Salina Creek, sixteen percent of recaptured individuals originally marked in 2003 were recaptured in the segment in which they were tagged, and 58% percent had moved to the segment immediately upstream. Of the individuals that moved in Salina Creek, 44% were recaptured upstream after one year, 90% after two years, and 93% after three years. Within Lost Creek, 71% and 86% of individuals that moved were recaptured upstream, one and two years post-marking, respectively.

In sampling that occurred in 2006, we captured 24 individuals from 450 - 750 m upstream of the last marking segment ([Figure 6](#)). These individuals were tagged within the four tagging sections in 2003 (n = 1), 2004 (n = 3), and 2005 (n = 20). We also encountered two individuals that were marked in 2005 nearly 2 km upstream.

Size was not significantly related to the probability of movement one year after tagging (2003-2004) in either Salina Creek ($\chi^2 = 0.193$, d.f. = 1, p = 0.66) or Lost Creek ($\chi^2 = 0.411$, d.f. = 2, p = 0.81).

Discussion

An understanding of the underlying movement patterns of a species provides information on the ecology and adaptive environment, enabling managers and conservationists to make informed decisions for recovery and further protection of species (Albanese et al. 2004; Bach et al. 2007). In exploring the sources of variation in movement patterns for southern leatherside chub we found that habitat quality and individual level traits appear to contribute to diversity in movement patterns of this species. Populations in poor quality habitat or in areas with high

levels of disturbance appear to become highly mobile and exhibit greater spatial and temporal variation than populations occurring in better habitat (Bates et al. 2006; Bowler and Benton 2005).

We conclude that movement within San Pitch River and Soldier Creek, both poor habitat environments for southern leatherside chub, is on a scale broader than that covered by the sampling scheme. Movement of individuals in these streams contrasts with streams of relatively better habitat, Salina and Lost Creek, in which individuals tend to be more stationary and remain in the area over longer periods. Given the habitat homogeneity of the poor quality streams, movement may be required to exploit broader areas in order to obtain sufficient food or habitat resources (Gowan and Fausch 2002; Smithson and Johnston 1999) and habitats for year-round requirements (Gowan and Fausch 2002; Smithson and Johnston 1999). Movement can also be an important behavior for individuals in high quality streams (McMahon and Matter 2006); however, the difference is that the temporal scale is much shorter (e.g. weekly or daily) in poorer habitats. Populations occurring in less complex habitats can be less resistant and less resilient to disturbance (Pearsons et al. 1992). Long-term instability may contribute to population fragmentation and patchiness as a negative feedback loop, and further expose populations to greater possibilities of local extinction (Fagan et al. 2002; Pimm et al. 1988; Shaffer 1981). For management and conservation this pattern has significant implications. Sampling schemes should be adaptive and tailored to the type of stream. Sampling broader areas in better quality streams will be potentially inefficient, and sampling narrower areas in poor quality streams will lead to inaccurate estimates which may fluctuate broadly from year to year given the ephemeral nature of population densities in certain areas (Fausch et al. 1995; Van Dyck and Baguette 2005).

Population parameters as a whole may be relatively stable, but our ability to accurately detect trends is greatly diminished.

Those streams within our study that were qualitatively characterized as poor southern leatherside chub habitat, specifically San Pitch River and Soldier Creek, yielded very few recaptures, which may be due to either high mortality, tag loss, or high movement and turnover rates. High mortality is an unlikely factor in this case because we should have observed abnormal declines in densities and extremely rapid growth rates of remaining individuals. Data are lacking to assess growth rates, but the possibility that unequal mortality of marked fish or that tag loss led to poor recapture rates is not supported by the fact that VIE tags have been shown to perform well in this species, with 96% retention rates and 93% survival rates six months after tagging (J. Rasmussen, *unpublished data*). Furthermore, comparisons with other streams in the study suggest high retention of tags and survival of tagged fish, e.g. recapture rates after three years were as high as 7% in some instances ([Table 3](#)). Similarly, size distributions in 2005 for both creeks are comparable to those encountered in 2004 (J. Rasmussen, *unpublished data*), suggesting that low recapture rates are not a result of loss of larger individuals because of tagging-related mortality and a subsequent recruitment of younger individuals into the population.

Variation of individual movement within populations is intricately linked with scale (Curry et al. 2002; Fausch et al. 1995). By increasing the scale of our observations we were able to detect greater variation within the population. The presence of a distinct group, albeit a small one, that moved significantly farther distances than the main body of the sample population indicates that variation may also occur among individuals within populations. Rodriguez (2002)

found that distributions of recaptures in 17 out of 28 salmonid populations provided evidence for two distinct movement “morphs” in the population with differing median distances moved and turnover rates. The underlying causes of this variation in our study are not clear, but size is apparently not a strong predictor of membership in movement group. Fraser (2001) suggests that movement differences are linked to behavioral traits such as boldness.

The importance of habitat quality to dispersal is evident in that nearly all long-distance movers by-passed poorer habitat (i.e. riffles or shallow pools) and settled in relatively better habitat. When temporal and/or spatial variation in habitat quality is present, divergent dispersal morphs may assist a population in maintaining stability (Bowler and Benton 2005). Poorer habitat may function as an incomplete barrier, but may be of little consequence to populations if sufficient numbers are able to move beyond such areas depending on the scale of movement and patchiness of habitat (Fraser et al. 1995; Gilliam and Fraser 2001; Gresswell and Hendricks 2007). Permanent barriers are likely to affect movement patterns over longer time periods and may cause local extinction if habitat is poor and access to other habitats is blocked.

Brown trout were present at three of the five sites in this study; however, poor recapture rates preclude this factor from rigorous comparison. The two sites with sufficient recapture rates, Salina and Lost Creeks, differed in predator environment and slightly in general movement patterns. Salina Creek had higher recaptures rates ([Table 3](#)) and less apparent movement, as indicated by the lower turnover rates. Similarly, Gilliam and Fraser (2001) found that predators promoted dispersal and movement through areas. However, further replicated experiments are necessary to assess the validity of these trends.

An understanding of the spatial and temporal variation of these components of variation of movement patterns of southern leatherside chub provides information not only on the ecology of the species, but can facilitate management decisions and assessment of actions (McMahon and Matter 2006). Further investigation into the underlying causes of intra-population variation should be undertaken to clarify the variability that exists in those cases. Likewise, finer assessment of the role habitat performs in affecting southern leatherside chub movement patterns will aid in understanding the variation in this important ecological process.

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Tables

Table 3 Numbers of southern leatherside chub marked and recaptured each year within each of the five study sites. Two sites (Salina and Lost Creeks) were started in 2003; whereas the other three were started in 2004.

| Stream | Year | Marked | 2004 | 2005 | 2006 | Total |
|-----------------|------|--------|------|------|------|-------|
| Lost Creek | | | | | | |
| | 2003 | 645 | 128 | 5 | - | 133 |
| | 2004 | 669 | - | 137 | - | 137 |
| | 2005 | 309 | - | - | - | - |
| Mammoth Creek | | | | | | |
| | 2004 | 237 | - | 9 | - | 3 |
| | 2005 | 3 | - | - | - | - |
| Salina Creek | | | | | | |
| | 2003 | 715 | 275 | 25 | 9 | 309 |
| | 2004 | 911 | - | 284 | 68 | 352 |
| | 2005 | 623 | - | - | 244 | 244 |
| San Pitch River | | | | | | |
| | 2004 | 673 | - | 30 | - | 30 |
| | 2005 | 288 | - | - | - | - |
| Soldier Creek | | | | | | |
| | 2004 | 169 | - | 8 | - | 8 |
| | 2005 | 222 | - | - | - | - |

Table 4 Cross tabulation tables for (A) Salina Creek and (B) Lost Creek recaptures of the original 2003 cohort in 2004 by size. For Chi-squared analysis*, Salina Creek large and medium individuals were pooled due to low expected values.

| (A) | Moved | Large | Medium | Small | Total |
|-------|-------|-------|--------|-------|-------|
| No | | 4 | 114 | 63 | 181 |
| Yes | | 6 | 52 | 36 | 94 |
| Total | | 10 | 166 | 99 | 275 |

* $\chi^2 = 0.193$, d.f. = 1, p = 0.66

| (B) | Moved | Large | Medium | Small | Total |
|-------|-------|-------|--------|-------|-------|
| No | | 11 | 21 | 26 | 58 |
| Yes | | 16 | 26 | 28 | 70 |
| Total | | 27 | 47 | 54 | 128 |

* $\chi^2 = 0.411$, d.f. = 2, p = 0.81

Figures

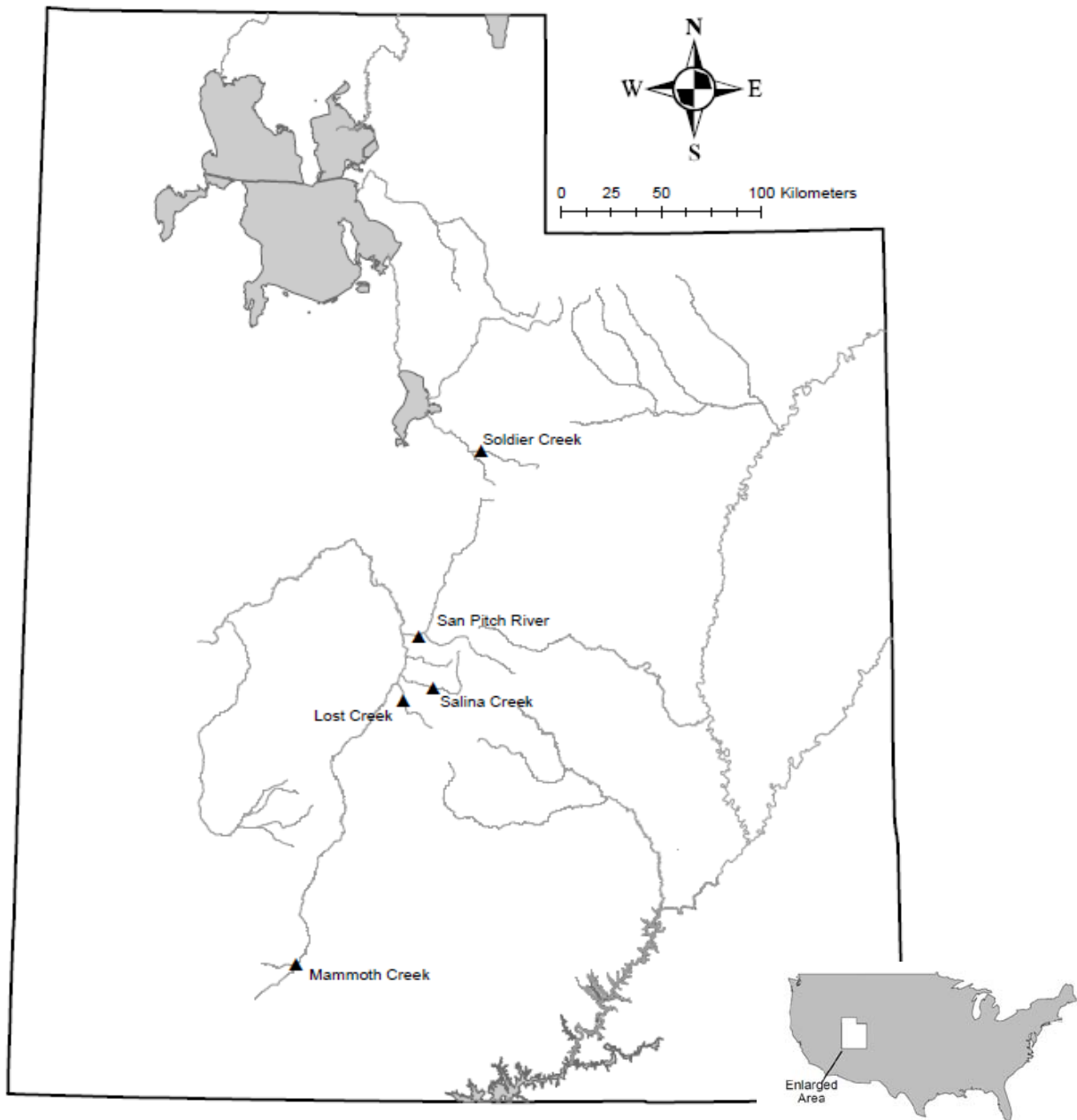


Figure 4 Sites included in this study. Southern leatherside chub co-occurred with predators at three sites (Lost, Mammoth, and Soldier Creeks). Salina and Lost Creeks exhibit high quality habitat for southern leatherside chub.

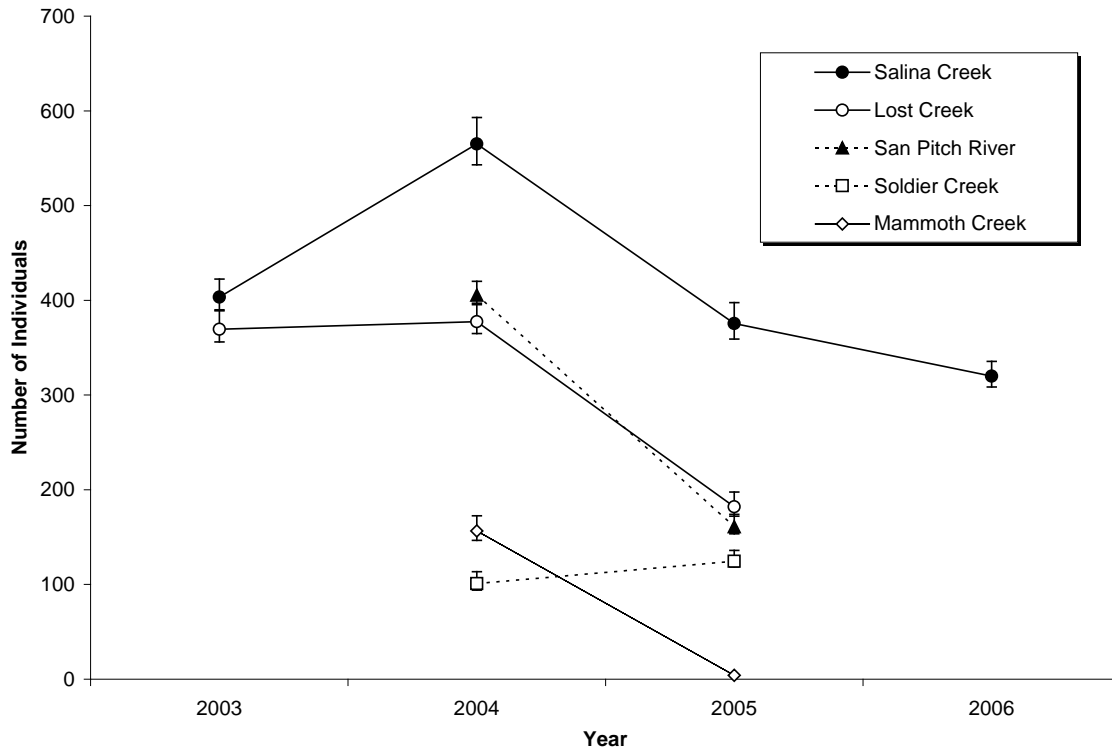


Figure 5 Average density estimates of southern leatherside chub per 100 m calculated by year for each of the five streams using Program CAPTURE. Bars represent 95% confidence intervals.

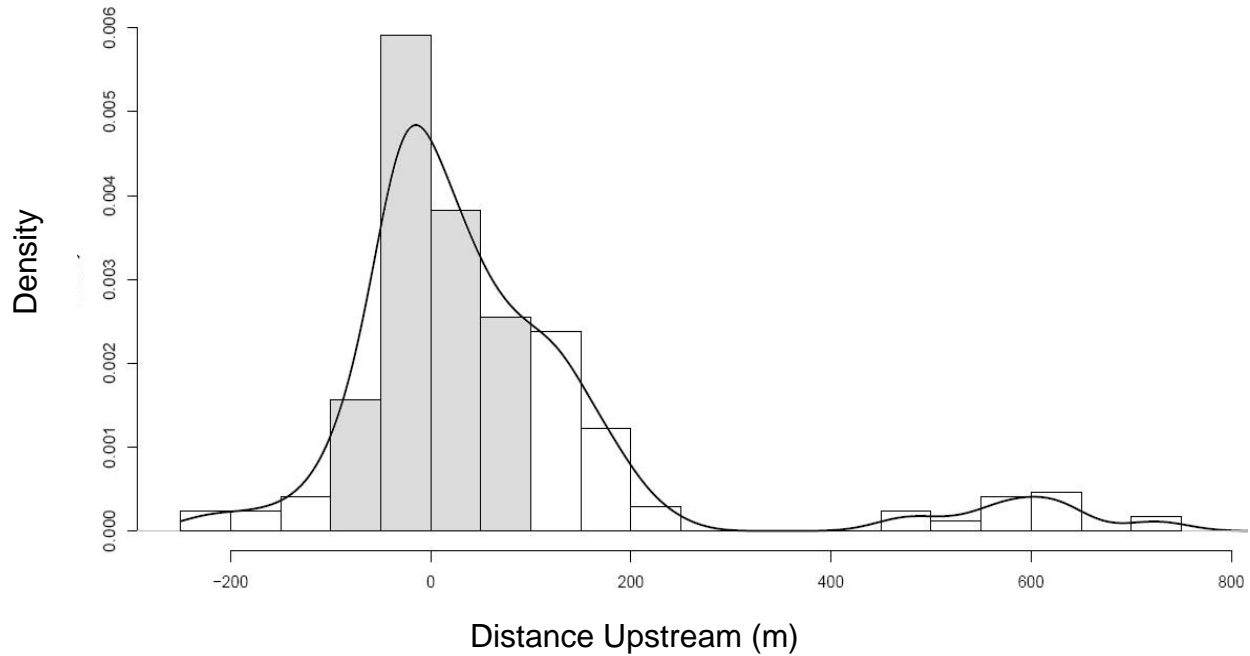


Figure 6 Kernel density estimate (using *density* function in R [R Core Development team, 2008]) overlaid on proportions of marked individuals captured in the final re-sampling event (i.e. 2006) in Salina Creek, centered on the mid-point of the tagging segments. Tagging segments indicated by shaded bars. Stream segments represent 50 m of stream. Estimates exclude two individuals marked in 2005 and recaptured in 2006 approximately 1 km further upstream.

Chapter 3: Behavioural Assay Predicts Probability of Movement in Southern

Leatherside Chub, *Lepidomeda aliciae*

Abstract

Movement of organisms from one locality to another is an ecological process determined by the interaction of individual (intrinsic) traits and environmental (extrinsic) factors. Although many studies have addressed and quantified movement, few have evaluated both intrinsic and extrinsic factors. We test the relative importance of extrinsic (density and habitat quality) factors and intrinsic (behavioural tendencies and size) characteristics on movement by a medium-sized western United States minnow, southern leatherside chub (*Lepidomeda aliciae*). We assessed variable density and habitat quality by manipulating densities and including study segments in disparate habitat types, and we assayed behavioural movement tendency (mover or non-mover). We used a generalized linear mixed model with a binomial response to determine the probability of movement of marked individuals one year after tagging. Individuals with open habitat within 50 m were 4.9 times as likely to move as individuals without open habitat or individuals with open habitat > 50 m away. Similarly, southern leatherside chub in areas with less suitable habitat (steep gradient with large substrate) had much higher probabilities of movement (3 – 40 times higher). Individuals behaviourally classified as movers were 3.6 times more likely to move compared to behavioural non-movers. Size was not significantly related to movement probabilities. Our results suggest that both extrinsic and intrinsic factors can play a role in movement. Recognition of behavioural movement phenotypes may facilitate understanding of patterns and drivers of movement within and among populations.

Keywords: *Lepidomeda*, behavioural phenotype, habitat heterogeneity, population density

Introduction

Movement of organisms, or their propagules, is an important ecological process that occurs at the individual level; however, movement also has important ecological and evolutionary implications at higher levels of organization, such as population (Hassel and Nay 1985; Gresswell and Hendricks 2007) or community (Bohonak 1999; Hanski and Gaggiotti 2004; Bowler and Benton 2005; Ronce 2007). Movement of individuals decreases population density in one location and increases it in another (Dieckmann et al. 1999). It may mitigate negative interactions between ontogenetic stages or close relatives (Stenseth and Lidicker 1992), or significantly alter the genetic dynamics of metapopulations (e.g. genetic rescue or by reducing local genetic adaptation) (Tallmon et al. 2004).

Given the broad ramifications of movement (Dieckmann et al. 1999; Tallmon et al. 2004), we can expect that causes or drivers of movement are many and complex (Ewers and Didham 2006). Proximate causes of animal movement are often ecological in nature, including such things as resource availability, the presence of predators, and environmental conditions (Fraser et al. 1999; Bowler and Benton 2005); however, forces acting on long-term, evolutionary time scales may ultimately determine the reaction of organisms to ecological conditions, and thereby drive movement patterns within and among populations (Dodson 1997; Dieckmann et al. 1999; Bowler and Benton 2005).

Individuals perceive and process information about themselves (e.g. fat stores, hunger levels, and fear levels) and their environment (e.g. predation risk, population densities, and resource levels) either directly through exploratory behaviour or indirectly through social interactions (Valone and Templeton 2002; Danchin et al. 2004; Dall et al. 2005; Cote and

Clobert 2007b). Information can provide feedback to movement through prompts or suppression (Gowan and Fausch 2002). External sources of information may include the presence of predators (Fraser et al. 1999), habitat (Fausch et al. 1995), or resources (Belanger and Rodriguez 2002), such as food, space, or potential mates (Lawrence 1987). Information may be important in assessing an individual's current home range, and may enable an organism to compare its current occupied area with surrounding areas such that residency or movement behaviour is based on relative site optimality. However, it is often unclear how much area individuals are able to sample through either private or public information (Danchin et al. 2001).

An individual's intrinsic characteristics or traits certainly interact with these extrinsic factors, and therefore can also perform a significant function in affecting movement behaviour (Bowler and Benton 2005). Traits typically considered in movement analysis include age (Downs et al. 2006; Ekman 2007), sex (Croft et al. 2003; Eikenaar et al. 2008), and reproductive status (Andreu and Barba 2006). However, lesser studied intrinsic traits may also contribute notably to movement, such as behavioural tendencies (Cote and Clobert 2007a), morphology (O'Rian et al. 1996) or social status (Aragon et al. 2006). Expression of movement behaviour may therefore depend on extrinsic and intrinsic factors.

Different innate predilections to move or disperse may exist among individuals of a population, a phenotype we call behavioural movement tendencies. Evidence for behavioural movement tendencies has been observed in several species (Knaepkens et al. 2005; Godinho et al. 2007; Gresswell and Hendricks 2007). Southern leatherside chub (*Lepidomeda aliciae*) from one stream displayed dimorphism in movement behaviour with the majority moving < 50 m

from year to year (Chapter 2), but a small group of individuals moved significantly longer distances (0.5 – 1 km).

Here we test the influence of extrinsic factors (variable density and habitat quality) and intrinsic factors (individual behavioural tendency and size) on the probability of movement in the southern leatherside chub. We specifically test the hypotheses that 1) local variability in patch density and quality will promote movement behaviour and 2) quantifiable behavioural tendencies and size predict long-term movement probabilities of individuals.

Methods

Southern leatherside chub is a medium-sized cyprinid species (maximum standard length [SL] approximately 145 mm) that historically inhabited streams and lakes within the Bonneville Basin of western United States. Individuals can live up to 8 years (Johnson et al. 1995; Johnson et al. 2004). This species can be locally abundant in some areas, occurring in densities up to 600 individuals per 100 m of stream (Chapter 2), providing a system with sufficient individuals to conduct an informative mark-recapture study. In addition, southern leatherside chub populations exhibit mainly short-distance movement in some locations, with a small number of individuals undertaking extreme long-distance movement events (Chapter 2).

This study was conducted with southern leatherside chub in Salina Creek (located in Salina Canyon near Salina, Utah, USA) from August 2005 through November 2006. Salina creek is a third order stream which runs roughly parallel to Interstate 70 through much of the canyon. Average annual stream flow during the study was $4.9 \text{ m}^3\text{s}^{-1}$, as measured at United States Geological Survey water gauge 10205030. High flows are primarily driven by spring runoff, with peak flows (approximately $19.5 \text{ m}^3\text{s}^{-1}$) occurring during May and June. Many

portions of the stream are channelized and straightened or have been modified by the addition of large culverts that pass beneath the interstate. A delineation of habitat variability occurring along a longitudinal gradient allows for assessment of influences on movement by habitat on several levels, i.e. reach and segment scales. Upstream segments are comprised predominantly of large boulders, high gradient, and modest amounts of slack water. In contrast, downstream segments lack large structure in the channel, substrate materials are typically sand and gravel, and flows are relatively slower. This lower habitat type is typically utilized to a greater extent by southern leatherside chub (Wilson and Belk 2001).

Native fish assemblage in Salina Creek is comprised of southern leatherside chub, mottled sculpin (*Cottus bairdi*), speckled dace (*Rhinichthys osculus*), and mountain sucker (*Catostomus platyrhynchus*). Non-native rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) have been introduced into the stream, but occur only in upstream segments of the creek, which were not utilized in this study, to avoid confounding with portions unoccupied by predators. Competition for food resources between southern leatherside chub and non-predaceous species is probably an insignificant factor on leatherside chub movement behavior, given that the chub typically feed in the drift and the others are primarily demersal or benthic feeders.

Twelve 1-km sections of the stream were randomly selected spanning approximately 15 km of stream ([Figure 7](#)). At the centre of each 1-km segment a 25-m segment (i.e. target segment) of stream was delineated to which one of three density manipulations was applied. Density manipulations consisted of the following, 1) control – no density manipulations made, 2) adjacent - a 50 m stretch immediately upstream of target segment was depopulated of all

southern leatherside chub, and 3) skip – the portion of stream 50 – 100 m upstream of the target segment was depopulated of all southern leatherside chub, i.e. densities of the 50-m stretch immediately upstream of the target segment were left intact.

Sampling and marking were conducted from August – November 2005; re-sampling took place from August to October 2006. Original sampling consisted of a three-pass depletion procedure using a backpack electro-shocker within each 25-m target segment and associated 50-m segments, where appropriate. However, for re-sampling the original 25-m target segments, as well as 100 m up- and downstream, were sampled with two passes in 10-m increments. Beyond this, 50 m downstream and 200 m upstream were sampled in 10-m increments using only one pass. Therefore, we re-sampled upstream farther distances than downstream, 300 m and 150 m respectively. Capture efficiency with one and two passes is relatively high in this system, on average 79% and 86%, respectively (Belk et al. 2009). Southern leatherside chub have been shown to move predominantly upstream (Belk et al. 2009); however, the vast majority of recaptured individuals (95%) from a separate mark-recapture study were observed to have moved < 100 m, with the remaining small fraction found in the adjoining 1-km sections up- and downstream (Chapter 2).

Captured fish were held (typically < 1 hr) in aerated tanks with approximately 85 L of clean water. Fish from the removal segments were quickly transported in aerated tanks to other sites within Salina Creek but to a portion beyond the bounds of the study (> 2 km upstream of the uppermost segment) to prevent potential confounding due to homing behaviour, which has been often recorded for stream fish (Lucas and Baras 2001).

Behaviour of southern leatherside chub > 40 mm SL ($n = 1,041$) from the 25 m target segments was assayed using a portable swim chamber in the field ([Table 5](#)). This minimum length (~ 40 mm) represents most age-1 individuals and is the smallest size which could be captured reliably with the methods employed. Each swim chamber was constructed from a white, five-gallon bucket with a bowl weighted with a cobble-sized rock from the stream and positioned in the centre thereby creating a circular swim track approximately 100 mm in depth with a minimum (e.g. interior) circumference of 440 mm and a maximum (e.g. exterior) circumference of 839 mm. Inconspicuous hash marks were placed around the swim chamber to facilitate estimation of distance swum during the test. Individuals were placed inside the swim chamber and allowed to acclimate for two minutes. Following the acclimation period, we tallied the distance swum by the fish during one minute, based on the hash marks. Distance measurements consisted of units relative to the swim chamber, i.e. measured in terms of laps around the swim chamber. Based on preliminary tests, the fish were binned into two groups: 1) non-movers - less than 1 lap swum (86%) and 2) movers – greater than or equal to 1 lap (14%).

Standard length (SL) was measured and fish were binned into three size classes, small (< 65 mm; 21%), medium (64 – 84 mm; 55%) and large (≥ 84 mm; 24%). Prior to tagging, small groups (i.e. 10 individuals or less) were anesthetized in a bath containing a non-lethal dose of MS-222 (Argent Chemical Laboratories Inc., Redmond WA). Each individual was then given an identifying batch mark of visible implant elastomer (Northwest Marine Technologies Inc., Shaw Island, Washington, USA) reflecting size bin (by location of mark) and behavioural tendency (by colour). Fish were then allowed to recover in a holding tank with aeration until all individuals

recuperated, typically 30 min, before being replaced near the midpoint of the 25-m target segment.

We used a generalized-linear mixed model (GLMM) and model selection procedures to relate the probability of movement from the original 25-m target segment (response: recapture outside 25-m target segment = 1 and recapture within 25-m target segment = 0) to intrinsic and extrinsic predictors. Overall, 271 marked individuals (26%) were recaptured after one year; of these 52% ([Figure 8](#)) had emigrated from the original 25-m target segment where they had been captured and marked.

Model estimation was performed using SAS 9.2 PROC NLMIXED (SAS Institute 2006), which utilizes full maximum likelihood for parameter estimation. Our full additive model includes as fixed effect variables, manipulation (control, adjacent, skip), size class (small, medium or large) and behavioural movement category (yes or no), as well as a fourth fixed effect variable (position) created by grouping segments relative to position within the stream, i.e. downstream, midstream, and upstream (as a test of habitat quality given the longitudinal differences of quality in the stream). Two-way interactions between behaviour and the manipulation and position factors each were also included. Density estimates for each 25 m target segment based on three-pass depletion methods and using Program CAPTURE (White et al. 1978; Pollock and Otto 1983) were calculated and included in the model as a covariate as a measure of habitat quality. Finally, sites ($n = 12$) were included in the model as a random effect, assuming that the log odds of movement among sites was normally distributed with a mean of zero. Given the binomial distribution of the response, the logit was used as the link-function giving the form of the full model as

$$\begin{aligned} \text{logit}(P) = & \beta_0 + \beta_1 \times \text{Manipulation(Adjacent)} + \beta_2 \times \text{Manipulation(Skip)} + \beta_3 \times \\ & \text{Size(Medium)} + \beta_4 \times \text{Size(Large)} + \beta_5 \times \text{Mover(Yes)} + \beta_6 \times \text{Density} + \\ & \beta_7 \times \text{Position(Midstream)} + \beta_8 \times \text{Position(Upstream)} + \beta_9 \times \\ & \text{Manipulation(Adjacent)} \times \text{Mover(Yes)} + \beta_{10} \times \text{Manipulation(Skip)} \times \\ & \text{Mover(Yes)} + \beta_{11} \times \text{Position(Midstream)} \times \text{Mover(Yes)} + \beta_{12} \times \\ & \text{Position(Upstream)} \times \text{Mover(Yes)} + u \end{aligned}$$

where P is the probability of emigrating from the original 25-m target segment in one year and u is the variance of the random effect. Probability values can be calculated by

$$P = 1/[1 + e^{\text{logit}(P)}]$$

where e is the base of the natural logarithm.

Fit of the full model was assessed by comparing the deviance ($-2 \times$ Negative Log Likelihood) of the full model to that of the saturated model assuming a chi-squared (χ^2) distribution of deviances, i.e. drop-in-deviance test. The full model fit sufficiently well ($\chi^2 = 22.2$, d.f. = 30, $p = 0.85$) to continue with model selection. Reduced model selection was based on drop-in-deviance tests and Akaike's Information Criterion (AIC), which evaluates model performance based on the number of parameters in addition to the amount of variance explained ([Table 6](#)). Based on these tests, models including the variables of size and density did not explain significantly more variation than models excluding these variables; therefore a reduced model, including manipulation, behavioural tendency, and position within the stream was preferred as it was more parsimonious ([Table 8](#)). Similarly, all included interactions among the terms were non-significant and not included in the final, reduced model.

Discrimination of the preferred reduced model was assessed using area under the receiver operator curve (ROC) and the Hosmer-Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow 2000). Based on ROC assessment, model discrimination is acceptable (74.9%), indicating that this model will perform (i.e. correctly discriminate response outcome among individuals) approximately 75% as well on a separate dataset. Likewise, the null hypothesis that the reduced model sufficiently discriminates cannot be rejected based on the Hosmer-Lemeshow goodness-of-fit statistic ($\chi^2 = 12.29$, d.f. = 8, $p = 0.13$).

Results

No significant differences were detected among size classes in proportions of movers and non-movers ($\chi^2 = 2.75$, d.f. = 2, $p = 0.25$). However, our preferred GLMM assessing the relationship between the probability of emigration from the original 25-m target segment and manipulations did reveal significant differences among manipulations. Individuals were 4.9 (95% Confidence Interval [CI]: 2.0 – 12.4) times as likely to disperse when an open patch was created within 50 m upstream compared to when no segments manipulations were made. In contrast, segment density manipulations creating open habitat > 50 m upstream produced no differences in the odds of dispersing (odds ratio [OR] = 0.9; 95% CI: 0.5 – 1.9) with individuals at control sites. In addition, individuals classified by our field behavioural assay of movement phenotype as expressing higher tendencies towards movement were 3.6 times (1.5 – 9.0) as likely to have dispersed after one year than individuals categorized as not tending to movement.

Assessment of movement based on relative location of the target reach within the stream, i.e. upstream, midstream and downstream, indicated significant differences among these areas. There is a definite positive relationship linking odds of dispersing and distance from the lowest

portion of the study; however, poor representation among upstream ($n = 28$) compared to downstream ($n = 172$) and midstream ($n = 71$) sites produced broad ranges in confidence intervals. Fish within the middle third of the study reach are 3.0 (1.5 – 6.3) times as likely to have moved as an individual with similar characteristics downstream. The odds ratio increases in the upstream third to 40.8 (4.6 – 362) times as likely relative to downstream third.

Discussion

Movement behaviour of organisms is a measurable phenotypic trait variably expressed by individuals within and among populations (Brown and Braithwaite 2004). Expression of movement behaviour is a product of interactions between environmental conditions and genetically-based traits (Murren et al. 2001; Bowler and Benton 2005; Templeton 2006). Our results provide experimental evidence of the role of intrinsic and extrinsic factors in determining movement.

The utility of being able to assess short-term behavioural phenotype and subsequently link this with long-term patterns provides a unique and powerful tool to understand evolutionary dynamics. In a recent review of behavioural syndromes Sih et al. (2004) noted that correlated behaviours within individuals consistently occur for activity, shy/boldness, and fearfulness, all of which may be related to movement phenotypes. Our results clearly indicate that a behavioural movement phenotype exists and can be assessed sufficiently well to provide information on the prevalence and expression of the phenotype within a population, even using somewhat coarse techniques. More importantly, this assessment can then be translated to naturally occurring patterns, such that individuals classified as expressing a movement phenotype were more likely to have moved after one year. Using these techniques produces the potential to identify

evolutionary syndromes (e.g. the suite of traits associated with important evolutionary processes) and make comparisons among and within populations and species.

Prevalence of the expression of the movement phenotype by individuals within a population may vary depending on conditions at several levels. Ecological factors directly impact costs and benefits of movement behaviour (Soulsbury et al. 2008), but long-term evolutionary effects may also drive the prominence of such behaviour in population, e.g. kin competition or inbreeding avoidance. For instance, catastrophic events, e.g. flooding, are directly tied to re-invasion events which may foster higher mobility rates given the increased probability of considerable payoffs for movement (Chapman and Kramer 1991). In stable periods costs of moving may tend to promote sedentary behaviour in a population. The recurrence rate and severity of catastrophic events then become very important factors driving the expression of this phenotype within and among populations. Within this study, variation in habitat quality – upstream vs. downstream sites – was linked to variation in movement patterns, which may be indicative of varying disturbance regimes among the reaches.

Movement can be a very costly behaviour, especially if surrounding habitat conditions are unsuitable (Clobert et al. 2001; Cote and Clobert 2007b). However, information about surrounding areas can greatly decrease costs and risks of movement (Dall et al. 2005). This information can be “personal”, i.e. directly gathered through experience by the individual, perhaps in the course of exploratory excursions, or the information may be acquired through social interactions with other individuals (Brown and Laland 2003; Danchin et al. 2004; Dall et al. 2005). The area about and from which an individual may reasonably gather and process information, known as neighbourhood size, may be an important characteristic of populations

with evolutionary implications. It makes sense that upstream movement is more prevalent in fish since the directional nature of flowing water creates a bias in available information. This area appears to be relatively small for southern leatherside chub. Open habitat > 50 m upstream exerted little evident pressure on movement. Individuals with this manipulation dispersed with the same probability as individuals that had no open habitat. In contrast, when open habitat was nearer (< 50 m), fish were much more likely to move. This indicates that the fish are able in some way to assess at least this much territory, whether by exploratory expeditions or some form of public information (Danchin et al. 2001; Gowan and Fausch 2002).

Similarly, habitat quality significantly influenced movement probabilities. The distinction of habitat types among the downstream, midstream, and upstream portions of the study reach can be inferred to produce the marked differences in the probabilities of movement among individuals from those sites. Areas, i.e. upstream segments, with “poorer” habitat (Wilson and Belk 2001) exhibited much higher movement rates, possibly suggesting that movement is an adaptive tactic in “fringe” patches, or in other words, much more extensive home ranges are required to supply needs than that required in more suitable areas, in this case downstream areas (Lucas and Baras 2001; Mikheev 2005). The related factor of discrete segment density within the original 25-m segments can also be considered a measure of habitat quality. We assume that areas with higher densities are more suitable for supporting southern leatherside chub. While it is possible that this factor is explaining the same variation as the stream position factor, it is also a possibility that each factor is explaining separate data and that density is simply relatively unimportant (Heggenes 1988; Natsumeda 2003).

Individual body size has often been found to be correlated with movement (Clobert et al. 2001; Bowler and Benton 2005); however, these measurements are likely confounded with other more difficult to measure phenotypic traits that may also be correlated with size and movement. Size, in reality, is a surrogate for many other potential factors such as age, ontogenetic stage, reproductive status or possibly segment quality. We found no differences among the size classes in the relative proportions of movers and non-movers in this system. Size might correlate with movement in the short-term, as in the case of *Brachyrhaphis episcopi* juveniles that were quicker to move from refuge than adults, attributed to higher metabolisms and energy needs (Brown and Braithwaite 2004). However, when viewed over longer intervals, differences in size more likely reflect ontogenetic shifts, but may also be affected by size-preferences of predators.

This research provides further clarification of the factors influencing the movement of stream fish. Individuals may have unique probabilities of expressing movement behaviour, which of course will influence the dynamics of the population or ecological group to which they belong as well as surrounding groups. This knowledge can be useful on many levels, such as evaluation of management options given population characteristics and environment, and illumination of evolutionary pressures within diverse habitats or species. Likewise, understanding how a movement phenotype correlates with other behavioural traits will extend our ability to assess the development of behavioural syndromes and the social pressures that influence them.

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Tables

Table 5 Summary of data for each study segment beginning at the most downstream. Mover classification based on field behavioral assay. Individuals recaptured outside of the original 25-m tagging section were assumed to have dispersed.

| Manipulation | Density* | Marked | # Classified Mover | Recaptured | Dispersed |
|--------------|----------|--------|-----------------------|------------|-----------|
| Control | 118 | 107 | 5 | 44 | 12 |
| Adjacent | 135 | 105 | 1 | 23 | 15 |
| Control | 241 | 178 | 14 | 53 | 20 |
| Skip | 291 | 215 | 4 | 52 | 21 |
| Adjacent | 25 | 55 | 3 | 23 | 22 |
| Control | 26 | 24 | 2 | 5 | 4 |
| Skip | 194 | 175 | 6 | 33 | 17 |
| Adjacent | 53 | 25 | 0 | 6 | 6 |
| Control | 45 | 41 | 0 | 10 | 4 |
| Skip | 34 | 34 | 1 | 12 | 10 |
| Adjacent | 53 | 46 | 0 | 7 | 7 |
| Skip | 38 | 36 | 0 | 3 | 3 |
| | | 1041 | 36 | 271 | 141 |

Table 6 A summary of generalized linear mixed model analysis using logit link function. Models listed chosen *a priori*, including the saturated model. Model parameters have been abbreviated: manipulation (M), behavior (B), density (D), stream position (SP), size (S). Chi-squared values are based on drop-in-deviance tests.

| Model | -LogLik | Deviance. | Parameters | AIC |
|--------------------|---------|-----------|------------|-------|
| M + B + SP | -153.0 | 306.1 | 7 | 320.1 |
| M * B + SP | -151.7 | 303.4 | 9 | 321.4 |
| M + S + B + SP | -152.1 | 304.2 | 9 | 322.2 |
| M + B + D + SP | -153.1 | 306.3 | 8 | 322.3 |
| M + B * SP | -152.3 | 304.5 | 9 | 322.5 |
| M + S * B + D + SP | -150.7 | 301.4 | 12 | 325.4 |
| M + S + B + D + SP | -152.9 | 305.8 | 10 | 325.8 |
| M + S + B + D * SP | -151.4 | 302.8 | 12 | 326.8 |
| M + SP | -158.0 | 316.0 | 6 | 328.0 |
| B + P | -159.5 | 318.9 | 5 | 328.9 |
| M * S + B + D + SP | -150.7 | 301.4 | 14 | 329.4 |
| M + B | -160.5 | 321.0 | 5 | 331.0 |
| M * B + S + D + SP | -153.6 | 307.2 | 12 | 331.2 |
| Saturated | -141.8 | 283.6 | 40 | 363.6 |

Table 7 Statistical significance of effects included in generalized linear mixed model based on a drop-in-deviance test.

| Effect | Chi-square | DF | <i>P-value</i> |
|--------------------------|------------|----|----------------|
| Behaviour | 9.9 | 1 | 0.002 |
| Density | 1.6 | 1 | 0.206 |
| Manipulation | 12.8 | 2 | 0.002 |
| Stream Position | 14.9 | 2 | 0.001 |
| Size | 0.5 | 2 | 0.779 |
| Behaviour x Position | 1.6 | 2 | 0.449 |
| Behaviour x Manipulation | 2.7 | 2 | 0.259 |
| Behaviour x Size | 4.4 | 2 | 0.111 |
| Manipulation x Size | 4.4 | 4 | 0.355 |
| Position x Density | 3.0 | 2 | 0.223 |

Figures

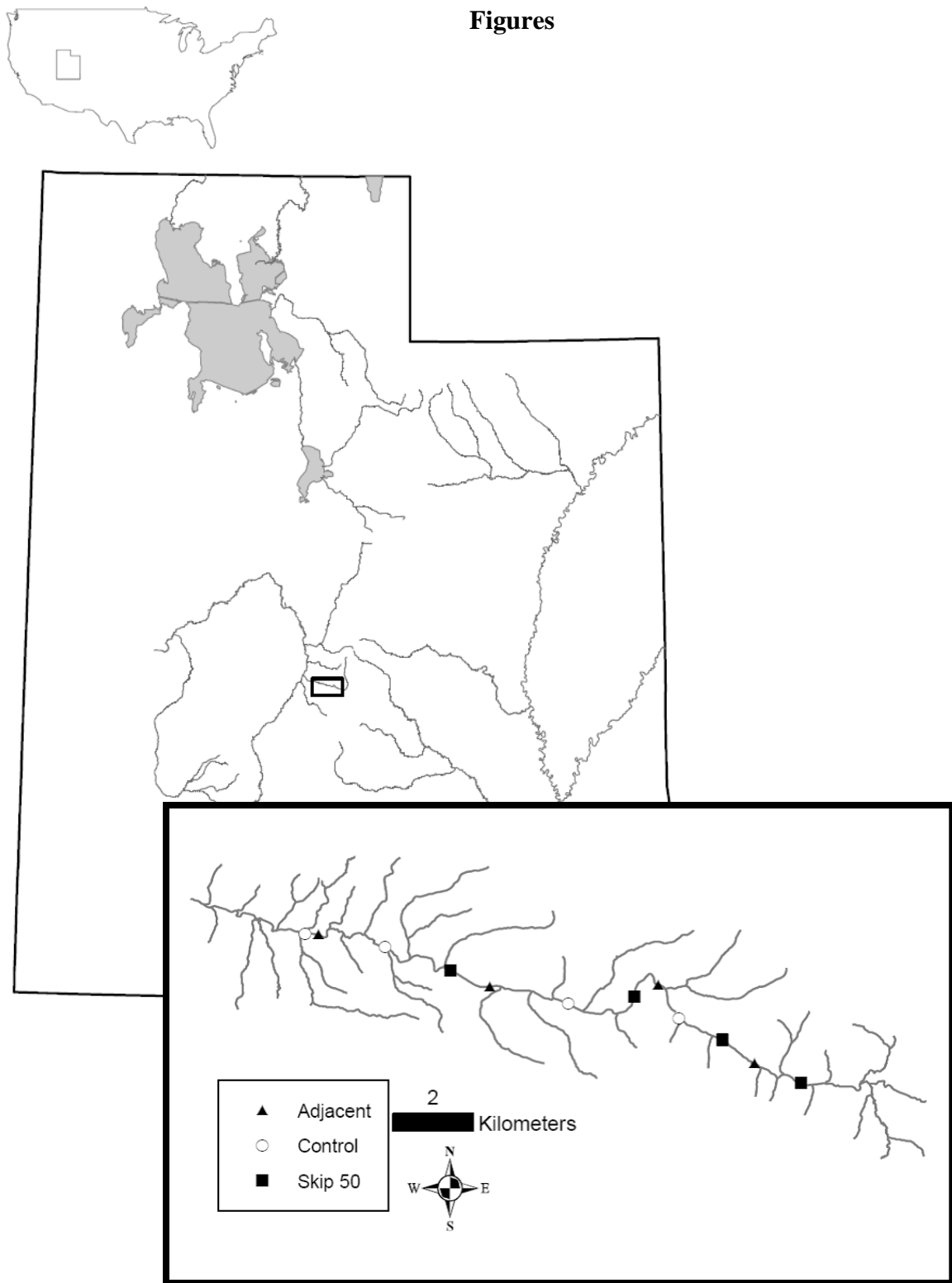


Figure 7 Locations of the 12 study segments along Salina Creek in central Utah.

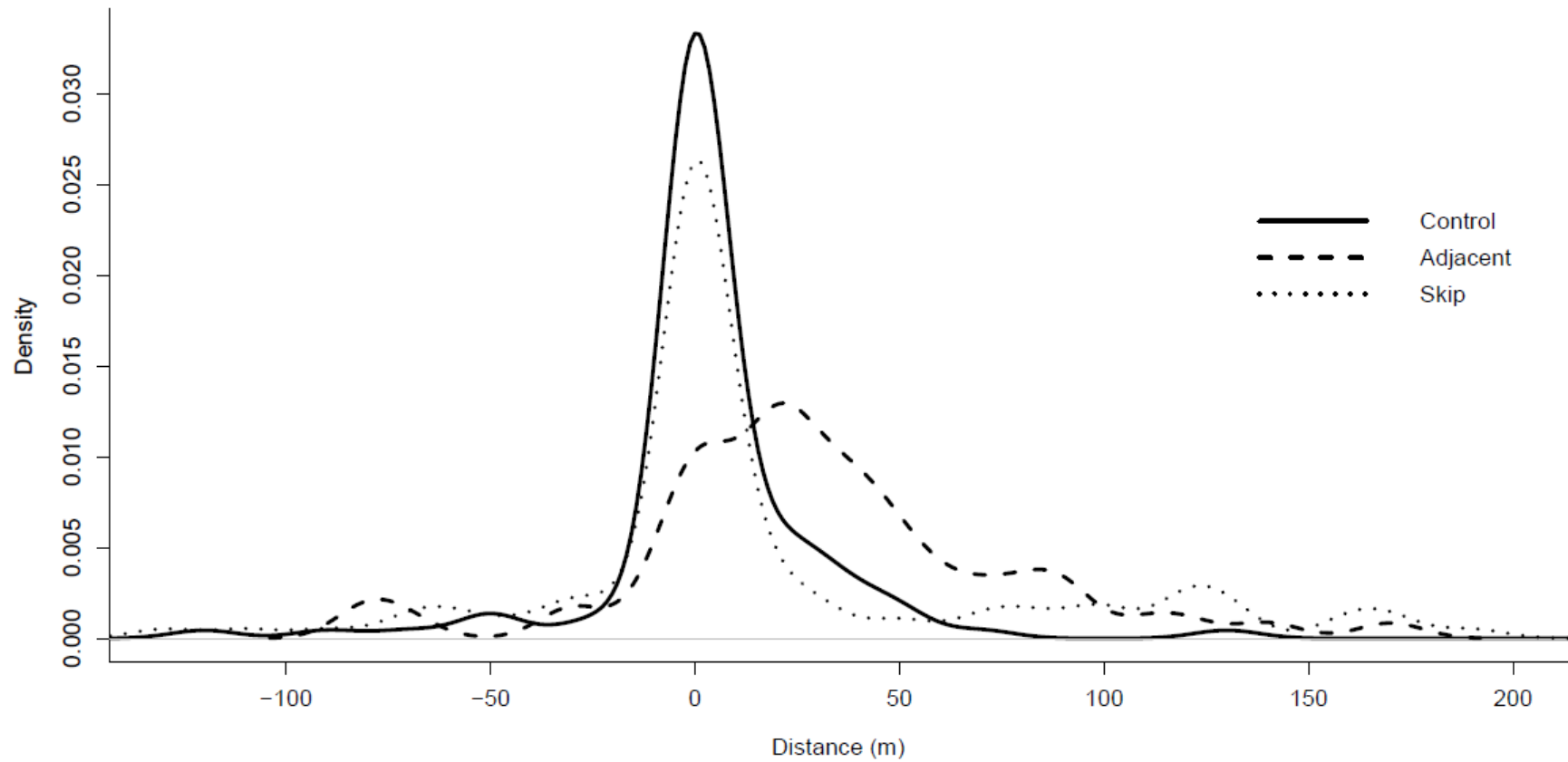


Figure 8 Kernel density estimates (using *density* function in R [R Core Development team, 2008]) of counts of recaptured individuals pooled by manipulation type. Distance is measured in meters from the original 25-m marking segment.

Chapter 4: Predation Environment Affects Body Shape Variation and Behavioral Phenotypes of a Neotropical Livebearer

Abstract

Diversity of expression of phenotypic traits within and among populations is central to evolutionary ecological research. Behavioral traits of individuals are important phenotypes that can potentially interact with many other phenotypic traits, and may be important components of behavioral syndromes that can advance understanding of the suite of evolutionary forces affecting populations. To determine the interactive effect of predator environment on movement phenotype and body shape of *Brachyrhaphis rhabdophora* at predator-free ($n = 6$) and predator sites ($n = 4$), we assessed movement in a portable swim chamber. Predator environment is significantly associated with proportion of mobile and sedentary individuals within populations ($\chi^2 = 8.2$, d.f. = 1, $P = 0.004$). Geometric morphometric analysis was performed on digital images of the fish ($n = 633$), and the resulting relative warps were used as repeated measures in a linear mixed model analysis including fixed effects (predation environment, sex, and behavioral classification) and random effects (locations). All fixed effects included in the model were significantly related to variation in body shape statistically. Fish co-occurring with predators possessed slightly longer caudal peduncles, which can increase burst speed and thus escape ability.

Keywords: *Brachyrhaphis*, Poeciliidae; morphometrics, behavioral syndromes

Introduction

Phenotypic diversity among and within populations is an important foundation of evolutionary ecological research (Adams and Collyer 2009). Variation arises from genetic diversity and phenotypic plasticity, both of which often result from dissimilar evolutionary pressures among locations in space or time (Reznick and Yang 1993; Robinson and Wilson 1994). Patterns in adaptive responses to extrinsic evolutionary pressures, such as competition (Schluter 1994; Adams and Rohlf 2000; Strelman and Danley 2003) and predation (Reznick and Endler 1982; Johnson and Belk 2001; Jennions and Telford 2002; Langerhans et al. 2004), have been shown to affect phenotypic expression. Likewise, intrinsic factors, including sexual dimorphism or ontogenetic changes (Brown and Braithwaite 2004), also cause apparent phenotypic differences among individuals. Understanding the relative strengths of extrinsic environmental pressures and intrinsic traits of the individual on phenotypes is important in furthering knowledge of phenotypic diversity (Endler 1995).

Expression of behavioral phenotypes is an important component of within-species diversity (Magurran 1995; Sutherland 1996). Differences in such behaviors as schooling (Magurran and Seghers 1990a, 1991), predator inspection (Magurran and Seghers 1990b; Huntingford et al. 1994), and courtship (Magurran and Seghers 1994) have been documented among populations in response to predation regime. A behavioral movement phenotype, i.e. tendency to move or be active, has received relatively little attention (Sih et al. 2004). However, diversity within and covariance among phenotypic traits that relate to movement, such as body shape and movement tendencies may be important in understanding key ecological processes, including dispersal, foraging, and inter-specific interactions (Fraser et al. 2001).

Aquatic environments are a source of strong evolutionary pressure on traits related to movement (Vogel 1994). Selection for efficient movement within a relatively viscous material (i.e. water compared to air) has been a major evolutionary force, especially for highly motile organisms such as fish. However, opposing extrinsic and intrinsic forces may produce negative interactions within individuals leading to tradeoffs (DeWitt et al. 2000). For instance, different swimming behaviors (e.g. escape and sustained swimming) are maximized by distinctive body shape phenotypes. Escape ability is certainly important when predators are present, but sustained swimming ability may be equally important in optimizing foraging or dispersal. Body plans in fish selected for maximization of sustained swimming ability have reduced maximum burst speeds and decreased escape ability, and vice versa (O'Steen et al. 2002); and therefore evolutionary tradeoffs arise such that phenotypes are a product of these interactions.

We test the hypotheses that movement phenotype frequency varies between predator and non-predator sites and that body shape is related to movement phenotype using *Brachyrhaphis rhabdophora*, a tropical member of the livebearing fish family Poeciliidae endemic to the continental northwestern Costa Rica (Bussing 1987). This species provides an excellent subject for this research because they are locally abundant, small-bodied, mature rapidly, and inhabit streams with varying degrees of predation (Johnson and Belk 2001) providing opportunity for individual replication at several levels, i.e. population and individual. Specifically, we examined differences in the body shape in relation to movement phenotype of both males and females from sites with differing predation environments.

Study Sites

Brachyrhaphis rhabdophora were collected during the dry season at nine separate locations on the western versant of Costa Rica ([Figure 9](#)). Sites were classified as having the native piscivorous cichlid guapote (*Parachromis dovii*; n = 4) or without guapote (n = 6; Table 7). Native fish communities also included mollies (*Poecilia gillii*), convict cichlids (*Amatitlania nigrofasciatus*), and banded tetra (*Astyanax aeneus*). One site, Rio Chiquito, also had an herbivorous characin (*Brycon behreae*) which was probably introduced by local residents. Predation environment classification may represent differences in habitats, of which the presence of predators is one trait, albeit an important one. Competition for food resources between *B. rhabdophora* and the other species may occur; however, as *B. rhabdophora* primarily consumes insects and the others are more generalists or herbivorous (the molly and characin, especially), this probably produces low selective pressure. Habitat characteristics differed markedly between predator and non-predator sites, but were relatively uniform within classifications for attributes such as gradient, discharge, riparian cover and elevation.

Methods

We collected approximately 150 adults from each of ten locations using a handheld seine net (0.5 cm mesh). Sexually mature males were identified by the presence of a fully-developed gonopodium. Females greater than 27 mm (standard length; SL) were assumed to be sexually mature and were included in the analysis (Johnson and Belk 2001).

Behavior of all sexually mature individuals (n = 1,088) was assayed in a portable swim chamber constructed from a five-gallon bucket. A smaller bucket was placed in the center to create a circular swim track approximately 100 mm in depth with a minimum (i.e. interior)

circumference of 440 mm and a maximum (i.e. exterior) circumference of 839 mm.

Inconspicuous marks were placed around the swim chamber to facilitate estimation of distance during the test. Individuals were placed inside the swim chamber and allowed to acclimate for two minutes. After the acclimation period, we tallied the distance swum by the fish during one minute. Distance measurements consisted of units relative to the swim chamber, i.e. measured in terms of laps around the swim chamber. We then categorized all individuals into one of two groups, 0 laps = non-movers, ≥ 1 lap = movers and separated them into appropriate holding tanks.

After completion of the behavioral assay, small groups of *B. rhabdophora* (i.e. 10 individuals or less) were anesthetized in a bath containing a non-lethal dose of Fiquel (Argent Chemical Laboratories Inc., Redmond, Washington, USA) and subsequently photographed laterally (left side) using a Kodak Z-650 digital camera (6.1 mega pixels). Individuals were recovered in fresh water prior to replacement into the stream. All individuals tested were photographed; however, images of 433 individuals were excluded from morphometric analyses due to insufficient image quality. Apparent statistical outliers were examined and also removed from the analysis for males and females, 10 and 11 respectively. The remaining 633 included in the analyses consisted of 199 males, 79 from predator sites, and 434 females, 173 from predator sites ([Table 8](#)).

Statistical Analysis

To assess differences in movement phenotype frequencies due to predator environment and sex we used a generalized linear mixed model including all behaviorally assayed individuals (n=1,088). Analysis was performed using SAS PROC GLIMMIX (SAS v.9.2, SAS Institute,

Cary, North Carolina, USA) which uses full maximum likelihood methods. The response was a binomial factor designating whether each individual fish was classified as active (1) or inactive (0), and thus the logit link function was used. Individuals completing at least one lap in the behavioral assay (55%) were classified as active. Predator environment and sex were included as fixed effects in the model, with location as a random effect. Sex was subsequently excluded from the model given insignificant main effects ($\chi^2 = 0.05$, d.f. = 1, $p = 0.82$) and interaction ($\chi^2 = 1.5$, d.f. = 1, $p = 0.22$).

Analysis of the relationship of shape to intrinsic and extrinsic variables of interest was conducted with geometric morphometrics using, in part, the Thin-plate Spline (Tps) software series (F. James Rohlf, Ecology and Evolution, SUNY at Stony Brook, Stony Brook, New York, USA). TpsDig2 (v. 2.10) was used to digitize 12 biologically homologous landmarks on digital images ([Figure 10](#)): 1) snout, 2) insertion of dorsal fin, 3) semi-landmark near the nape or posterior edge of the head, 4) dorsal insertion of the caudal fin, 5) ventral insertion of the caudal fin, 6) semi-landmark midway between landmarks 2 and 4, 7) insertion of the anal fin (or gonopodium in the case of males), 8) semi-landmark midway between landmarks 5 and 7, 9) intersection of the insertion of the of the pelvic fin with the ventral outline of the body, 10) intersection of the operculum with the ventral outline of the body, 11) semi-landmark midway between landmarks 9 and 10, and 12) center of the eye. Three other landmarks were digitized to facilitate digital unbending of the specimens using TpsUtil (v. 1.38), but were not included in the final analysis. These landmarks were placed directly under landmarks 2 and 6 and on the furthest posterior point of the caudal peduncle centered on the fourth row of scales as counted from the dorsal outline.

Non-shape variation, i.e. variation due to the position, orientation and scale of the specimen in each image, was removed using Generalized Procrustes Analysis (GPA: (Rohlf and Slice 1990) with TpsRelw (v. 1.45), and the resultant data were then superimposed producing aligned specimens. Partial warp scores (Bookstein 1991) and standard uniform components (Rohlf and Bookstein 2003) were calculated from the aligned specimens using the same software. Relative warp scores (RWS), (i.e., principal component scores) were outputted from TpsRelw for inclusion as response variables in a multivariate mixed analysis of variance. Only the first 10 RWS of a possible 16, accounting for 96.6% of the variation, were included in the analysis because four of the landmarks were considered semi-landmarks and were considered mathematically fixed in one direction.

Our full model included predation environment, sex, and a dichotomous grouping factor based on behavioral assay results (behavior); individuals swimming more than one lap were classified as a “active” and those swimming less than one lap as a “inactive.” Additionally, a categorical factor analogous to the univariate general mean termed “trait” was created and included in the model. Levels within this factor were given the names of the RWS in the model. This factor permits accurate estimation of the main effects such that the interaction between a main effect and trait is actually the correct estimation of the main effect due to the covariance among multivariate response data (Rencher 2002). Additionally, all possible interactions among factors were considered. Given that the digitized landmarks, and the resultant RWS, are repeated measurements on individuals, a random factor, individuals, was included in the model nested within a second random variable, location. To properly account for ordering and covariance among RWS, a heterogeneous general correlation variance matrix was specified allowing a

unique estimation of correlation for each experimental unit within the trait factor, i.e. each relative warp score. Similarly, correlations among RWS were allowed to vary within and among locations. Calculations were performed using ASReml-R version 2.00 (VSN International Ltd., Hemel Hempstead, United Kingdom) within R (R v.2.8.1, R Foundation for Statistical Computing, Vienna, Austria). The multivariate analysis with mixed effects revealed that only the interaction between predator environment and sex, and of course including trait to properly estimate values, was statistically significant ([Table 9](#)); therefore all other interactions, including the three-way among the fixed effects of interest were removed from the model. We then proceeded with the analysis including all main fixed effects and an interaction between predator environment and sex.

A measurement of size was not included in the model due to the confounding of size with both predator environment and sex (Johnson and Belk 2001). A univariate linear mixed model of the log standard length of sexually mature individuals revealed that sex ($F_{1,621} = 134.9, P < 0.001$) and predation environment ($F_{1,8} = 13.79, P < 0.0001$), as well as their interaction ($F_{1,621} = 4.87, P = 0.03$), were significantly related to differences in size. Growth in this species follows the typical pattern of livebearer growth (Magurran 1995). Females, as indeterminate growers, are generally longer than males, which are determinant growers. Likewise, individuals co-occurring with piscivorous predators are typically smaller than at non-predator sites, with the difference between females slightly greater. Size as a factor was also undesirable because in females it was confounded with stage of pregnancy.

Results

Predator environment was significantly ($\chi^2 = 8.2$, d.f. = 1, $P = 0.004$) related to movement phenotype. Individuals from predator environments are about half as likely to be classified as “active” compared to fish from non-predator sites, odds ratio = 0.65 (95% C.I.: 0.39 – 1.09).

The first relative warp explained 61.3% of the variation in the data and was primarily related to the difference in body shape between males and females. Differences of body shape between predator and predator-free sites were most strongly associated with the second relative warp, which explained 8.32%. In addition to these significant main effects, a significant interaction between sex and predator environment was also detected ([Table 10](#)). Based on our permutation tests, this interaction is due to the angle (84.6°) of shape trajectories through multivariate space ($P = 0.001$; [Figure 11](#)). The magnitude of the differences (0.0005 on a scale relative to the RWS) of the trajectories through shape space is not significant ($P = 0.78$). Examination of thin-plate spline deformation grids reveals that both males and females in predator sites exhibit an increase in the caudal peduncle region ([Figure 12](#)) relative to predator-free sites. At predator sites males also have a slightly smaller head and females are slightly less robust in the abdomen.

The dichotomous factor of behavioral movement tendencies was statistically significant ($\chi^2 = 25.26$, d.f. = 9, $P = 0.002$) in our analysis ([Table 10](#)). However, comparisons of shape differences on the two strongest RWS, i.e. one and two, revealed no distinguishable differences between the groupings. Scrutiny of the model coefficients revealed the strongest relationship with body shape occurred with relative warp 7 and relative warp 10, neither of which contributes

markedly to the amount of variation explained, 2.8% and 0.9% respectively. *Post hoc* analysis of the behavioral movement phenotype effect on body morphology revealed no distinguishable differences between active and inactive fish, even under reasonable magnification (e.g. 3X).

Discussion

Phenotypic diversity is an important component of ecology typically resulting from the complex interplay of extrinsic and intrinsic factors affecting individuals. In this study, we show that certain phenotypic traits, behavior and body shape, are affected by interspecific interactions. This diversity has the potential to have a trickle-down effect, influencing other broadly important processes such as dispersal and speciation.

We can not fully separate the predation effect from the suite of confounding habitat differences between predator and non-predator sites. Nonetheless, it is apparent that this predation environment reduces or limits the activity level of individuals of *Brachyrhaphis rhabdophora*. Abnormal appearance or behavior, such as higher activity levels, will often attract the unwanted attention of a predator (Ohguchi 1981; Theodarkis 1989; Martin et al. 2000; Almany et al. 2007). It is unclear as to whether this behavior has a genetic basis or if it is learned after having been attacked unsuccessfully or through social learning (Brown and Laland 2002). However, Johnson (2001) showed that divergence in isolated drainages with predators induced differences in age and size at maturity, which is maintained genetically. Consequences of lower activity levels may be that individuals sympatric with predators may have less opportunity to forage for food or mates leading to divergent feeding and possibly mating behaviors (Gilliam and Fraser 1987; Sih 1997; Skalski and Gilliam 2002). Interestingly, we found no differences between the sexes with this effect, as we had predicted males would be

affected to a larger degree given their method of maximizing fitness, which is maximizing the number of reproductive partners. Brown and Braithwaite (2004) found differing rates of boldness, e.g. time until exiting refuge habitat, of *Brachyrhaphis episcopi* to be size based; a phenomenon they attributed to relatively higher metabolic requirements of smaller fish. They also found, however, that predation risk was related to decreased boldness, assuming that smaller fish were at a higher risk.

Behavioral differences were also found to be statistically significant in predicting body shape of the fish, even after having accounted for sex and predator effects; however, there were no tangible morphological differences between the groupings of active and inactive fish. This suggests that the statistical significance of this factor may not represent biological significance. However, given the multivariate nature of the analysis, it is difficult to isolate changes due to secondary effects, i.e. potentially important effects with a background role compared to the much stronger primary factors, in this case sex and predator environment. The total effect size of each factor in this case was spread across 10 different measurements rendering visualization inefficient, at best. Nevertheless, had behavioral movement tendencies been more strongly related to morphological differences it would have surely comprised a larger portion of the variation explained by the principle RWS.

The effect on body shape of *B. rhabdophora* by predators is very similar to that found with other species. Langerhans et al. (2004) found that western mosquitofish (*Gambusia affinis*) occurring with predators also had increased caudal peduncles, smaller heads, and more elongate bodies. These same differences were found in this study, albeit not to the same strength or extent across both sexes. Langerhans et al. (2004) also described a posterior, ventral shift in the

placement of the eye, an effect not detected in this study. These changes are consistent with an increased burst speed and therefore escape ability.

The topic of co-evolution of behavioral and morphometric traits across broader taxa and suites of environmental conditions remains to be addressed. We may view these adaptations of behavioral shifts and morphometric differences as components of a broader syndrome of co-evolved traits (Sih et al. 2004). Traits which respond to the selective pressures of complex environments, of which predation is a significant element, in much the same manner as other life history traits (Reznick and Endler 1982; Johnson 2001; Johnson and Belk 2001).

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Tables

Table 8 Numbers of individuals used for analysis by location. Number of active individuals indicates the number swimming greater than one lap in the field behavioral assay. Heading "GM" indicates the number of individuals used for the geometric morphometric analysis.

| Stream | Type | Females | | | Males | | |
|--------------------|---------------|---------|--------|----|-------|--------|----|
| | | Total | Active | GM | Total | Active | GM |
| Quebrada Azul | Predator-Free | 148 | 84 | 60 | 38 | 25 | 21 |
| Rio Chiquito | Predator-Free | 64 | 30 | 33 | 29 | 15 | 18 |
| Quebrada Grande | Predator-Free | 87 | 57 | 44 | 43 | 27 | 35 |
| Rio Higueron | Predator | 109 | 53 | 42 | 44 | 31 | 24 |
| Rio Javilla | Predator | 51 | 30 | 12 | 19 | 6 | 9 |
| Rio Lajas | Predator | 60 | 34 | 22 | 25 | 14 | 17 |
| Quebrada Maravilla | Predator-Free | 58 | 27 | 26 | 27 | 21 | 20 |
| Rio Nosara | Predator | 101 | 31 | 35 | 38 | 10 | 19 |
| Rio Santa Rosa | Predator-Free | 52 | 33 | 11 | 26 | 20 | 12 |
| Rio Sucio | Predator-Free | 56 | 40 | 19 | 13 | 11 | 6 |

Table 9 Summary results of multivariate mixed model on 10 relative warp scores of digitized landmarks of body shape. Trait variable is equivalent to a univariate general mean and is included to facilitate proper estimates of fixed effects. *P*-values are based on a Chi-squared distribution.

| Term | DF | Sum of Squares | Wald Statistic | P-Value |
|----------------------|----|----------------|----------------|---------|
| Trait | 10 | 1.34 | 1.34 | 0.999 |
| Pred | 1 | 1.49 | 1.49 | 0.222 |
| Sex | 1 | 10.39 | 10.39 | 0.001 |
| Mover | 1 | 1.28 | 1.28 | 0.259 |
| Pred:Sex | 1 | 0.07 | 0.07 | 0.794 |
| Pred:Mover | 1 | 0.14 | 0.14 | 0.711 |
| Sex:Mover | 1 | 1.04 | 1.04 | 0.308 |
| Pred:Sex:Mover | 1 | 1.13 | 1.13 | 0.288 |
| Trait:Pred | 9 | 19.72 | 19.72 | 0.020 |
| Trait:Sex | 9 | 1961.42 | 1961.42 | 0.000 |
| Trait:Mover | 9 | 25.23 | 25.23 | 0.003 |
| Trait:Pred:Sex | 9 | 34.03 | 34.03 | 0.000 |
| Trait:Pred:Mover | 9 | 10.39 | 10.39 | 0.320 |
| Trait:Sex:Mover | 9 | 3.29 | 3.29 | 0.952 |
| Trait:Pred:Sex:Mover | 9 | 7.77 | 7.77 | 0.557 |

Table 10 Summary results of reduced multivariate mixed model on 10 relative warp scores of digitized landmarks of body shape. Trait variable is equivalent to a univariate general mean and is included to facilitate proper estimates of fixed effects. *P*-values are based on a Chi-squared distribution.

| Term | DF | Sum of Squares | Wald Statistic | P-Value |
|----------------|----|----------------|----------------|---------|
| Trait | 10 | 1.33 | 1.33 | 0.999 |
| Pred | 1 | 1.41 | 1.41 | 0.235 |
| Sex | 1 | 10.26 | 10.26 | 0.001 |
| Mover | 1 | 1.26 | 1.26 | 0.262 |
| Pred:Sex | 1 | 0.07 | 0.07 | 0.797 |
| Trait:Pred | 9 | 19.86 | 19.86 | 0.019 |
| Trait:Sex | 9 | 1963.52 | 1963.52 | 0.000 |
| Trait:Mover | 9 | 25.26 | 25.26 | 0.003 |
| Trait:Pred:Sex | 9 | 34.07 | 34.07 | 0.000 |

Figures

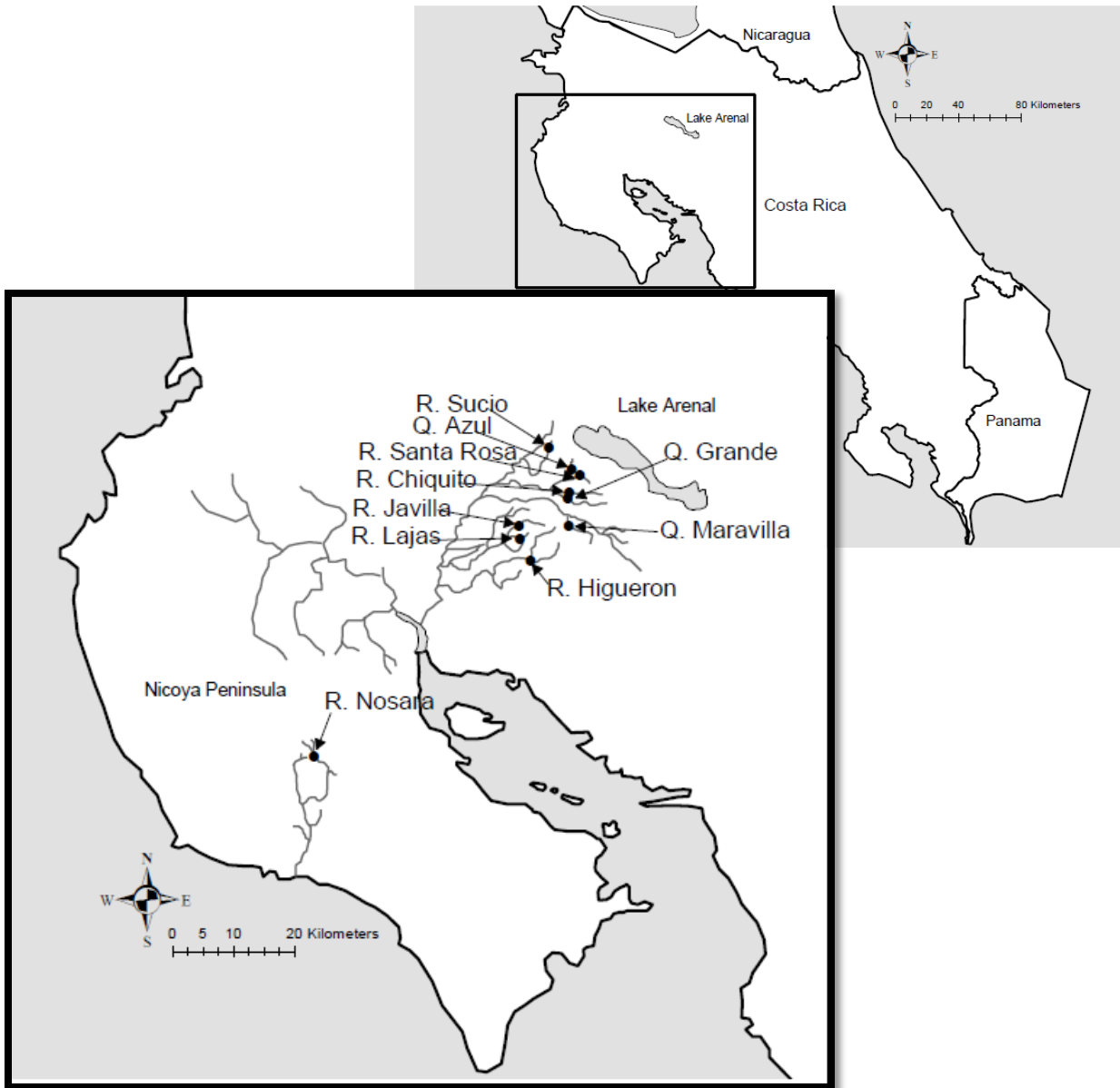


Figure 9 Location of nine sites in Costa Rica (four predator, five non-predator) where fish were sampled for behavioral and morphometric analysis. Rivers Higueron, Javilla, Lajas, and Nosara were classified as predator sites given the presence of guapote (*Parachromis dovii*).

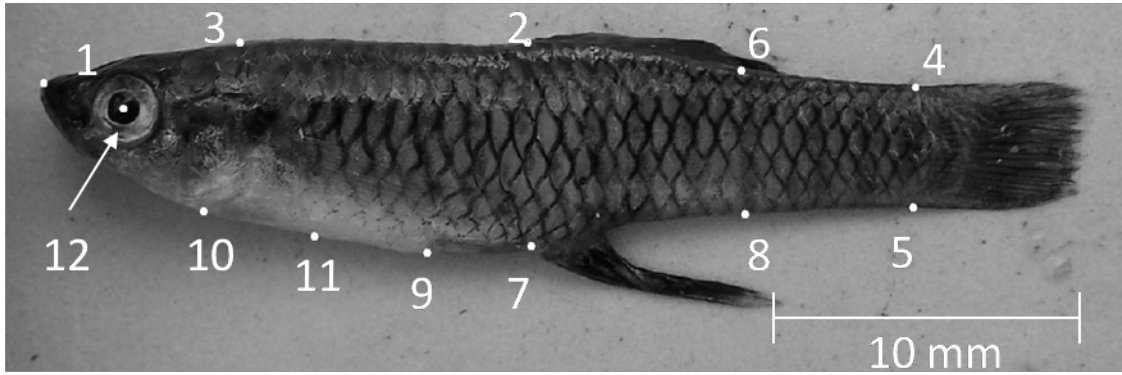


Figure 10 Representative mature male *Brachyrhaphis rhabdophora* and the locations of 12 digitized landmarks used in morphometric analysis.

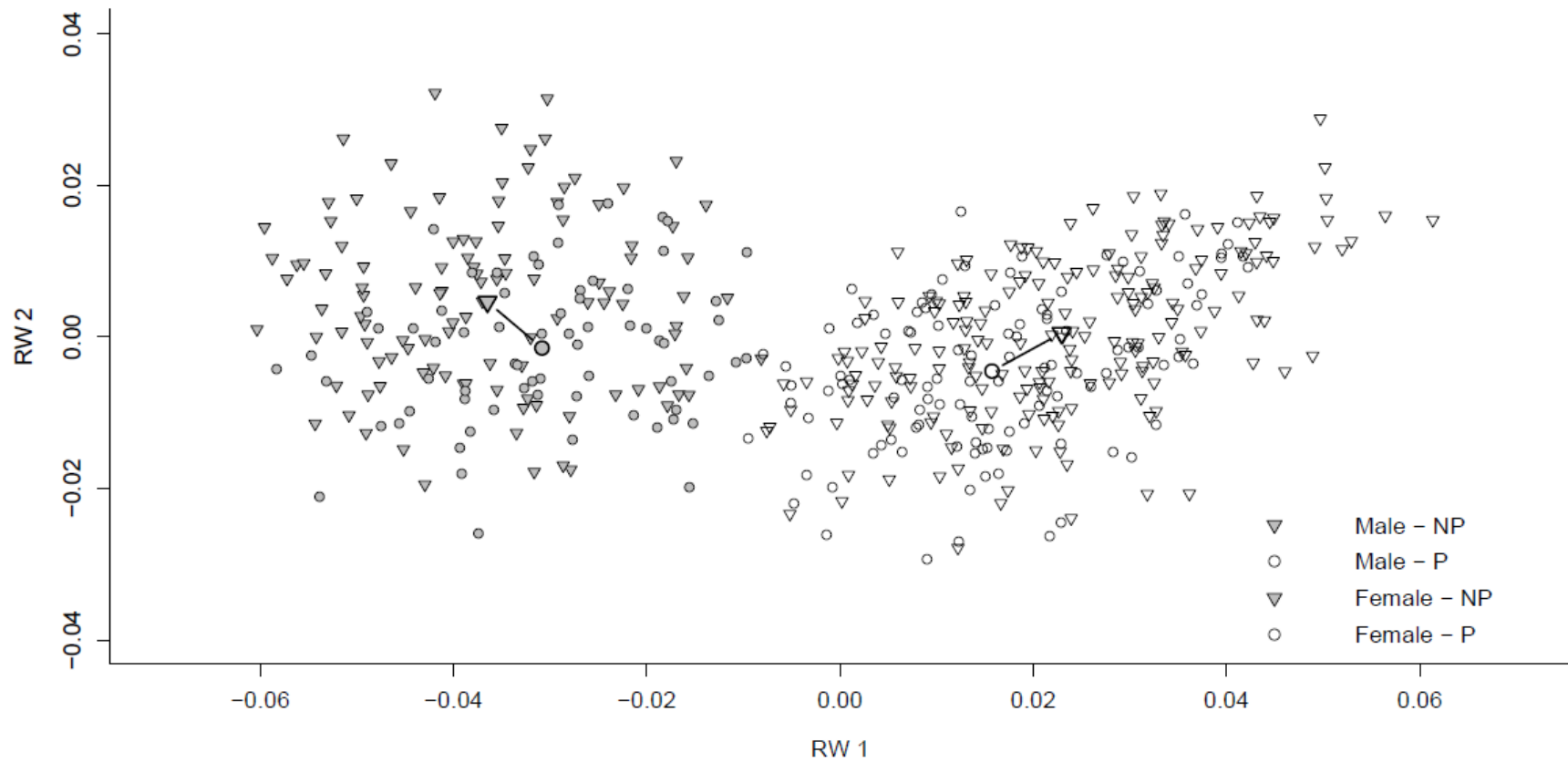


Figure 11 Relative warps 1 and 2 (explaining 61.3% and 8.3% of the shape variation, respectively). Enlarged symbols are the least-squares means for each group. Significant statistical interaction between the sex and predator environment main effects is a result of the diverging angle of the difference and not the magnitude as determined by a permutation procedure.

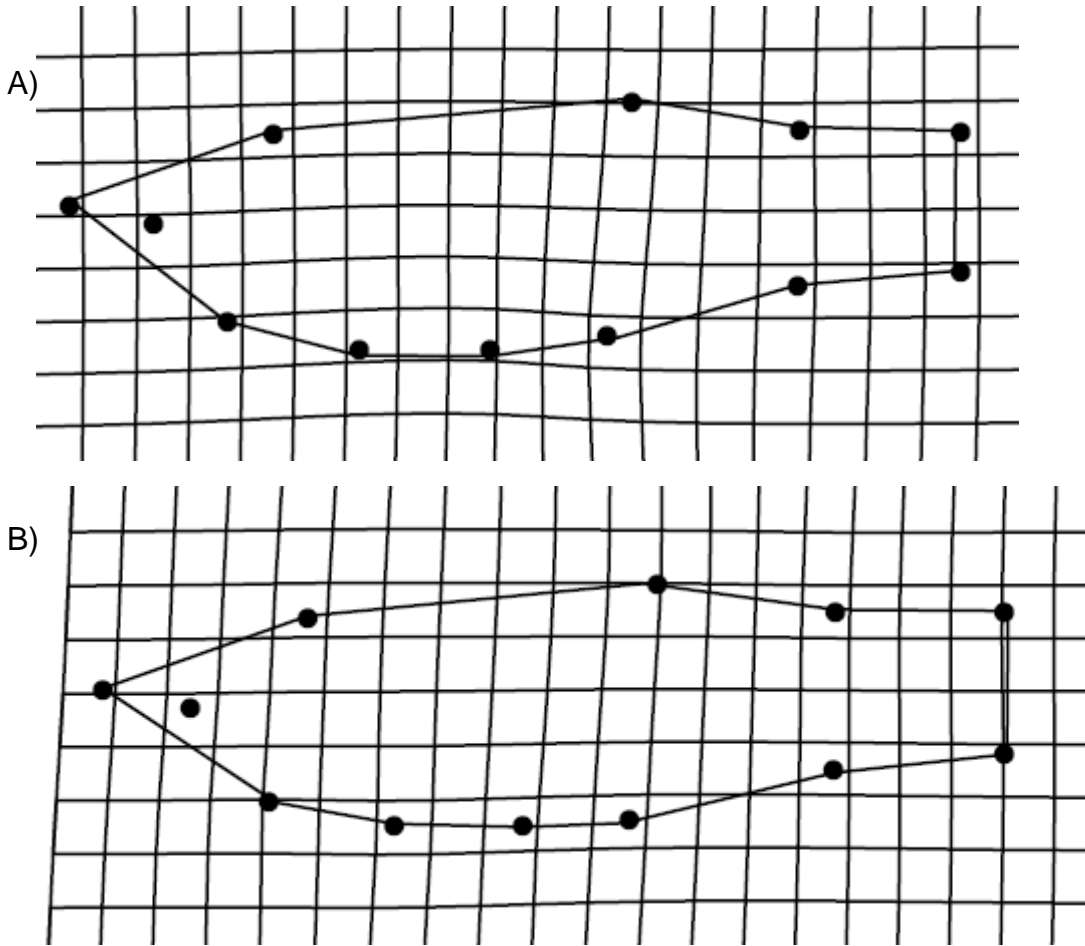


Figure 12 Thin-plate spline deformation plots showing the bending energy (magnified 3x) required to produce the average body shape at predator sites from the average body shape at non-predator sites for A) females and B) males. In both cases, a shift towards greater area in the caudal peduncle region is observed.