

Darren P. Croft · Brett Albanese ·
Bethany J. Arrowsmith · Marc Botham ·
Michael Webster · Jens Krause

Sex-biased movement in the guppy (*Poecilia reticulata*)

Received: 19 September 2002 / Accepted: 4 April 2003 / Published online: 11 July 2003
© Springer-Verlag 2003

Abstract The movement strategies of birds and mammals are often closely linked to their mating system, but few studies have examined the relationship between mating systems and movement in fishes. We examined the movement patterns of the guppy (*Poecilia reticulata*) in the Arima river of Trinidad and predicted that sexual asymmetry in reproductive investment would result in male-biased movement. Since male guppies maximize their reproductive success by mating with as many different females as possible, there should be strong selection for males to move in search of mates. In agreement with our prediction, the percentage of fish that emigrated from release pools was higher for males than females (27.3% vs. 6.9%, respectively). Sex ratio was highly variable among pools and may influence a male's decision to emigrate or continue moving. We also detected a positive relationship between body length and the probability of emigration for males and a significant bias for upstream movement by males. Among the few females that did emigrate, a positive correlation was observed between body length and distance moved. Sex-biased movement appears to be related to mating systems in fishes, but the evidence is very limited. Given the implications for ecology, evolution, and conservation, future studies should explicitly address the influence of sex and mating systems on movement patterns.

Keywords Total length · Dispersal · Emigration · Mating systems · Population structure

Introduction

Identifying ecological factors that trigger movement is necessary to gain a better understanding of animal movement patterns and all of the processes (e.g., colonization, gene flow, etc.) that are directly influenced by movement (Brown and Kodric-Brown 1977; Hansson 1991; Macdonald and Johnson 2001). When the benefits of emigration are high, animals may move from an area. For example, individuals may move to reduce predation risk (Gilliam and Fraser 2001; Schaefer 2001), escape harsh environmental conditions (Railsback et al. 1999; Labbe and Fausch 2000), avoid inbreeding or competition with kin (Gandon and Michalakis 2001), or to increase access to potential mates (Greenwood 1980). In addition, movement allows individuals to exploit spatio-temporal variation in resources, a characteristic of dynamic environments (Schlosser and Angermeier 1995).

Alternatively, when emigration costs are high relative to the benefits of restricted movement, individuals may remain within a local area. Site fidelity may allow individuals to remain within environmentally favourable habitats (Winker et al. 1995; Aparicio and De Sostoa 1999). In addition, individuals remaining in one location may benefit from learning the location of food, refugia, and other resources (Wootton 1998; Perrin and Goudet 2001).

The advantages of movement may not be distributed evenly between the sexes, which has led to the evolution of sex-biased dispersal in many species. Although multiple factors (e.g., avoidance of inbreeding and kin competition) probably play a role, these biases are strongly correlated with mating systems (Greenwood 1980; Lambin et al. 2001; Perrin and Goudet 2001). In monogamous birds, dispersing females benefit by choosing among the best males while philopatric males benefit by defending territories. The opposite pattern occurs in

D. P. Croft (✉) · B. J. Arrowsmith · M. Botham · M. Webster · J. Krause

School of Biology University of Leeds, Leeds, LS2 9JT, UK
e-mail: darren_croft@hotmail.com
Fax: +44-113-2332835

B. Albanese
Department of Zoology, North Carolina State University,
Raleigh, NC 27695-7617, USA

B. Albanese
Georgia Department of Natural Resources,
Georgia Natural Heritage Program, 2117 U.S. Highway 278,
SE Social Circle, GA 30025-4714, USA

polygynous mammals where males maximize their reproductive success by moving among female-defended breeding sites. In contrast to birds and mammals, there is no well-established relationship between dispersal and mating systems in fishes. Indeed, many studies have found no relationship between sex and movement (e.g., Aparicio and De Sostoa 1999).

In the current investigation we examine the relationship between sex and movement within the guppy (*Poecilia reticulata*). The guppy is a viviparous shoaling fish with a non-territorial and non-resource based mating system (Liley and Seghers 1975). Reproductive success of female guppies is dependent on their investment in offspring and their selection of high quality mates (Magurran and Seghers 1994) whereas in males it is the total number of successful copulations that determines their reproductive output (Magurran and Seghers 1994). Males have been shown to direct more courtship behaviour toward novel females (Kelley et al. 1999), a phenomena that is reinforced by females being more receptive to mating attempts by novel males (Hughes et al. 1999).

We predict that sexual asymmetry in reproductive strategies will drive male-biased movement within the guppy. Firstly, males should benefit from moving between shoals and pools in search of novel females (Hughes et al. 1999; Kelley et al. 1999). Secondly previous investigations have reported spatial variation in sex ratio in guppies (see Jirotkul 1999a), a phenomenon that is known to affect male movement strategies in other species (e.g., milk weed beetle *Tetraopes tetraophthalmus*, Lawrence 1987; water strider *Aquarius remigis*, Krupa and Sih 1993). If sex ratio varies between pools male guppies could benefit from moving from male-biased locations and remaining stationary in female-biased hotspots. To evaluate our predictions, we conducted a mark-recapture study in the Arima river of Trinidad and tested for relationships between sex and two attributes of movement behaviour: the probability of emigrating from a site and distance moved. To gain a broader understanding of guppy movement patterns, we also examined whether guppy movement occurred more up- or downstream. Finally, the sex composition of several pools within the river was measured to determine the spatial variation in sex ratio.

Materials and methods

The mark-recapture study was conducted in May 2002 (dry season) within a section of the Arima river located in the northern mountain range of Trinidad. Six pools spaced within a 100-m reach of river were designated as mark sites. The pools were of similar size and interconnected by riffles. Guppies were collected by making three passes through each pool with a beach seine (length=2 m, height=1 m, mesh size=3 mm). A 2-mm mesh dipnet was also used in areas that could not be effectively sampled with a seine. To gauge the effectiveness of our sampling, we recorded the number of guppies ≥ 16 mm total length separately for each pass within five of the six pools and estimated population size and catchability using MICROFISH 3.0 (Van Deventer and Platts 1983, 1985).

MICROFISH 3.0 calculates the maximum-likelihood population estimates based on the number of fish captured per sampling pass. The program assumes that no fish move into or out of the area during sampling. To meet this assumption block nets were used where possible to prevent fish from leaving or entering the pool. Although our mesh sizes permitted us to capture smaller guppies, we only included mature fish ≥ 16 mm total length for this and all subsequent analyses because visually sexing fish was not reliable for smaller fish. In a river containing *C. alta*, Rodd and Reznick (1997) found that male and female guppies matured at 13.9 and 16 mm standard length, respectively [standard length, is approximately 80% of total length (percentage of total length represented as standard length: males, $n=15$, mean \pm SD=78.5 \pm 4.4; females, $n=15$, mean \pm SD=81.6 \pm 3.5)]. Thus, our samples consist primarily of adults.

All guppies were anaesthetised with tricaine methanesulfonate (MS-222 Sigma Chemical, St Louis, Mo.) and given a pool-specific mark by injecting different colours of Visible Implant Fluorescent Elastomer (VIE, Northwest Marine Technology) into one or two locations on the dorsal epidermis. Fish were marked streamside and released back into their original pools after a 15-min recovery period. A control group of guppies (males, $n=40$; females, $n=40$) held in aquaria for 8 days, exhibited 1.25% tag loss (one fish) and low mortality (five fish, 6.25%) after they were subjected to the same tagging procedure.

Sampling for recaptures took place 8 days after marked fish were released. A 460-m section of river was sampled by making two passes through each discrete habitat unit (e.g., pool, riffle, and cascade) using the sampling procedure described for the mark sites. The length of stream sampled (180 m) was equal upstream and downstream of the central marking reach, and was determined during an 8-day pilot study (involving 77 males and 74 females) in which the furthest distance moved was 157 m. A tributary entered the river 145 m upstream from the central marking reach. To ensure that any fish moving up to 180 m could be detected, we also extended our sampling 35 m into this tributary. Recaptured fish were returned to the laboratory where their pool-specific mark, sex, total length, and location of capture were recorded. To investigate the degree of variation in the sex ratio between habitat units, we sexed, measured, and counted all mature fish within a 275-m section of river sampled during the recapture event.

The frequency at which guppies of both sexes were captured externally to their release pool, and the frequency that they moved both up and downstream was compared using χ^2 tests. Factors associated with the probability that an individual left its mark site were identified using a logistic regression. Within the model, sex and total length were included as predictor variables. Movement distances were calculated as the difference between midpoints of mark and recapture sites. The distance moved by males and females was not normally distributed, so we compared movement distance distributions with a Mann-Whitney *U*-test.

Results

Our sampling technique was highly effective. Population estimates using MICROFISH 3.0, (Van Deventer and Platts 1983, 1985) did not differ from the total catch within the mark and release pools ($n=5$) after three sampling passes. Furthermore, guppies within all pools had a high capture probability (defined as the proportion of fish captured on a given sampling pass, capture probability \pm SE for individual pools=0.77 \pm 0.07, 0.83 \pm 0.03, 0.92 \pm 0.06, 0.76 \pm 0.09, 0.82 \pm 0.05). Within the first two sampling passes, a mean (\pm SD) of 95.4 \pm 4.6% of the estimated population size was captured (Table 1).

We marked 156 male and 245 female guppies and recaptured 99 males (63%) and 154 females (63%)

Table 1 The number of fish captured per sampling pass

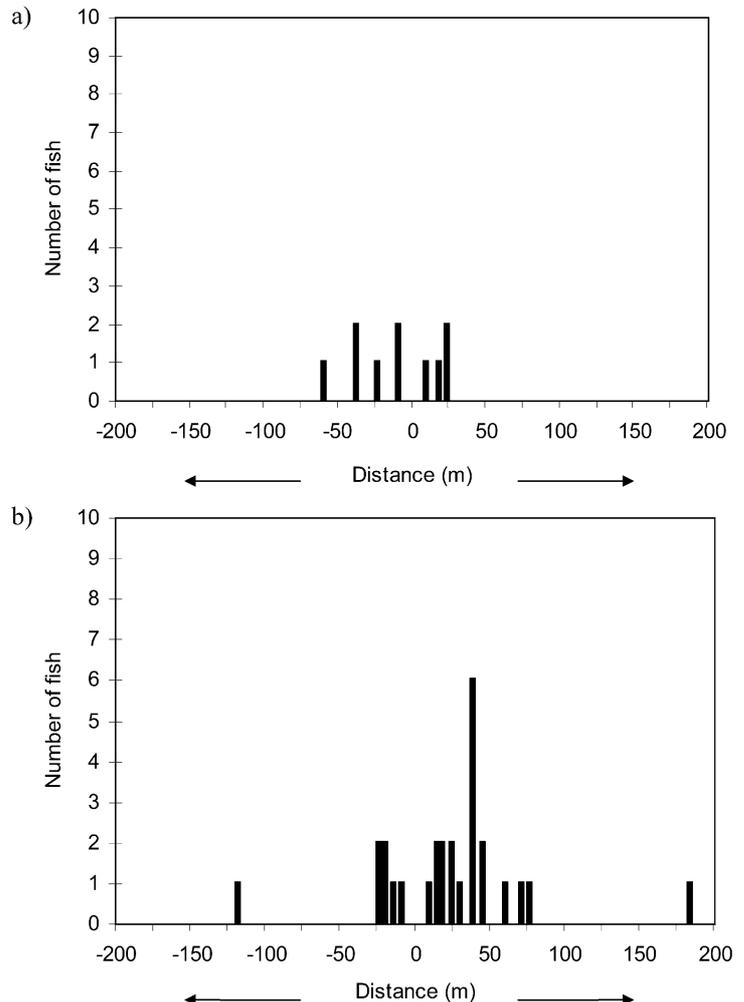
Sampling pass	Pool no.				
	1	2	3	4	5
1	34	121	20	18	41
2	2	22	2	5	7
3	2	4	0	1	2
Total	38	147	22	24	50

(Table 2). A higher proportion of males (27.3% vs. 6.9%) were captured outside of their original mark sites (χ^2 test, $\chi^2=18.9$, $P<0.001$). The overall logistic regression model was significant (likelihood ratio test, $n=244$, $df=2$, $P<0.001$) and males were more likely to emigrate from mark sites ($P<0.001$) than females when total length was controlled for statistically. Fish of greater total length were also more likely to emigrate from their mark sites than small ones ($P=0.009$). Separate logistic regression analyses for males and females indicated that total length was a significant predictor of emigration only in males (males, median body length of emigrating fish=23, lower quartile=22.75, upper quartile=24, non-emigrating

Table 2 The number of males and females marked, released, and recaptured within and outside the pool of release after 8 days

		Pool no.					
		1	2	3	4	5	6
Males	No. released	25	46	46	7	7	25
	Recaptured within the pool of release	8	38	13	1	2	10
	Recaptured outside the pool of release	8	1	3	3	2	10
Females	No. released	15	96	77	15	17	25
	Recaptured within the pool of release	10	72	15	11	15	21
	Recaptured outside the pool of release	1	1	3	2	3	0

Fig. 1 Movement distribution for emigrating females (a) and males (b) showing the distance travelled up and down stream by individuals after an 8-day period



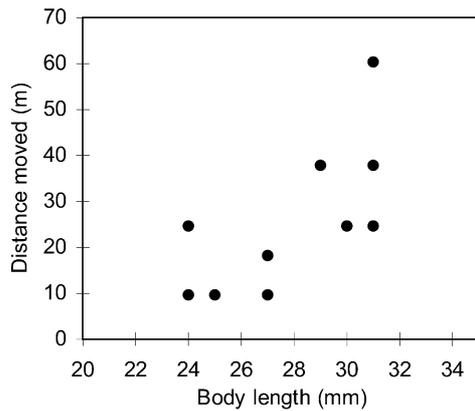


Fig. 2 Female dispersal as function of body length after an 8-day period ($n=10$, Spearman's $r=0.71$, $P=0.021$)

fish=22, lower quartile=21, upper quartile=23, $n=99$, $df=1$, $P=0.006$; females, median body length of emigrating fish=23, lower quartile=22.75, upper quartile=24, non-emigrating fish=22, lower quartile=21, upper quartile=23, $n=145$, $df=1$, $P=0.178$).

We recorded movements up to 184 m for males but females never moved >60 m (Fig. 1a, b). However, there was no significant difference in median distance moved by dispersing males and females (males, 31 m; females, 25 m; Mann Whitney U -test, $P=0.22$ $U=150.5$). Distance moved was positively correlated with total length in females ($n=10$, Spearman's $r=0.71$, $P=0.021$; Fig. 2), but not males ($n=27$, Spearman's $r=0.08$, $P=0.687$).

Males moved upstream more frequently than downstream (χ^2 test, $\chi^2=5.34$, $df=1$, $P=0.021$; upstream, $n=20$; downstream, $n=7$). In contrast, we did not detect a bias in the direction of female movement (χ^2 test, $\chi^2=0.1$, $df=1$, $P=0.751$; upstream, $n=4$; downstream, $n=6$). No marked guppies were recaptured within the lower 35 m of the tributary stream.

Sex ratio (expressed as number of females/males) varied significantly between pools, with the observed number of males differing from the expect, assuming an even distribution of males relative to females (χ^2 test, $n=17$, $\chi^2=52.8$, $P<0.01$). A mean (\pm SD) sex ratio of 2.18 ± 1.24 was observed with a maximum value of 5 and a minimum value of 0.5 within the 17 habitat units (275 m of river) sampled.

Discussion

Very few investigations have quantified the effects of sex on movement patterns in fish (see below), and this is the first investigation to quantify sex-biased movement in the guppy. In agreement with our predictions, male guppies were found to move from their pool of initial capture more frequently than females. In addition, the probability of emigration by males was positively related to total length, and there was a significant bias for upstream movement by male guppies. Within the emigrating

females, the distance moved was positively correlated with total length.

Why is movement male-biased in the guppy?

There are two mechanisms that may select for male-biased movement in the guppy. First, females have been shown to demonstrate a preference for unusual/unfamiliar males (Farr 1977; Hughes et al. 1999) and males have been shown to express a preference for mating with novel partners (Kelley et al. 1999). Therefore, male guppies that move between shoals and pools will not only increase the total number of potential mates encountered, but will also encounter females that are more receptive to their mating attempts. In accordance with this Croft et al. (2002) found that male guppies moved between shoals more frequently than females. Similarly, in polygynous mammals male-biased dispersal is the common trend. As in the guppy, females invest heavily in offspring and are the limiting sex. Males, in comparison invest relatively little and compete for access to females. Thus there is strong selection for males to move among females to maximize their reproductive success (Greenwood 1980).

Secondly, the mating success of a male will be dependent on the operational sex ratio (OSR) it encounters. The OSR is influenced by the overall adult sex ratio and represents the proportion of sexually reproductive adults within the population. Within guppies the OSR is strongly male biased due to females only being receptive when virginal or directly after giving birth, which occurs approximately once a month (Houde 1997). This strong male-biased OSR increases male-male competition for access to females (Jirotkul 1999a, 1999b). The sex ratio within the Arima river varied spatially from male biased (0.5) to highly female biased (5). This finding is in accordance with previous observations where sex ratios have been reported to vary spatially and temporally within guppy populations (see Jirotkul 1999a). Spatial fluctuations in the sex ratio will result in fluctuations in the OSR, thus males in an area with a male-biased sex ratio will benefit from dispersing into areas with more females. Further evidence that the sex ratio can affect the movement strategies in males comes from studies in the milk weed beetle (*Tetraopes tetraophthalmus*), and the water strider (*A. remigis*), where males remain stationary in female-biased hot spots or move from male-biased locations (Lawrence 1987; Krupa and Sih 1993, respectively). Additional field studies and experiments are needed to more closely examine the effect of sex ratio on movement patterns in guppies.

In addition to the probability of emigrating from a site, it is also important to consider distance moved; these factors together determine the distribution of individuals within the environment in time and space (Clarke et al. 1997). Although some male guppies moved further than any of the females (maximum=183.6 m vs. 60.4 m, respectively), no significant difference was found in their movement-distance distributions. We found a similar

pattern in a pilot study conducted in the Arima river. A single male fish moved 157 m in 8 days but females were not detected moving >90 m during this period (D. P. Croft, unpublished data). We expect that male guppies may move longer distances than females but the low number of female emigrants will make it difficult to detect such differences.

Why do females exhibit high site fidelity?

In the current investigation only a small number (6.5%) of females within the population moved. High levels of site fidelity have been reported previously in the guppy, but without regard to sex (Haskins et al. 1961; Magurran et al. 1994; Reznick et al. 1996). Becher and Magurran (2000) compared mitochondrial haplotypes between upstream and downstream locations and found that female guppies were responsible for some of the gene flow, but the frequency at which females moved within the population was not quantified. In addition to the benefits of restricted movement mentioned in the Introduction, local site fidelity by females may facilitate the development and maintenance of familiarity between conspecifics. Preference for familiar individuals has been shown to exist in free ranging female guppies (Griffiths and Magurran 1997a), and familiar recognition has been shown to take 12 days to acquire (Griffiths and Magurran 1997b). Associations between familiar individuals may reduce the risk of predation (Chivers et al. 1995), facilitate foraging (Metcalfe and Thomson 1995) and enhance social learning (Swaney et al. 2001).

Other factors influencing movement

Sex is obviously not the only cause of movement and studies that address a suite of ecological factors (e.g., food availability, habitat complexity, predator density) will contribute to a better understanding of movement patterns (Gandon and Michalakis 2001). In this study, the probability of emigrating from a pool was positively correlated with total length in males. This could result from greater resource requirements of larger fish (Gowan and Fausch 1996), and/or an interaction between body size and reproductive strategy in male guppies (Gandolfi 1971). We also found a positive relationship between distance moved and total length in females, despite the small number of females that emigrated from pools. This finding is in accordance with Brown (1985), who observed a positive relationship between female body length and distance travelled in the mosquitofish (*Gambusia affinis*). Brown (1985) suggested that dispersal of large female poeciliids (who are longer and thus capable of carrying more foetuses) would be advantageous, allowing them to colonise and utilise ephemeral habitats.

Male guppies displayed significant bias for upstream movement. It has been suggested that upstream movement may allow riverine populations to maintain positions

within a stream (Kaya 1991). Chapman and Kramer (1991) found that male and juvenile *P. gilli* were more likely to disperse downstream after floods (via flushing and/or active movements). Thus an upstream bias by male guppies could compensate for downstream displacement during flooding. An alternative explanation is that males move upstream to reduce predation pressure. The species richness of rivers in the northern mountain range of Trinidad follow the common pattern of a decrease in richness as one moves from the larger rivers up to the head waters (Haskins et al. 1961; Seghers 1973; Liley and Seghers 1975). This decrease in species richness is associated with a reduction in the richness and density of the major predators of the guppy (Gilliam et al. 1993).

Mating systems and sex-biased movement in fishes

Unfortunately, there are only a handful of species where the relationships among movement, mating systems and sex have been examined. This information gap occurs because it is not always possible to sex fish in the field and because movement behaviour and/or mating systems are unknown for so many species. However, the few studies that have been done seem to suggest a link between sex-biased movement and mating systems in fishes.

First, there is some evidence for male-biased movement in live-bearing species where females invest substantial resources into the nourishment of young (e.g., *P. gillii* Chapman and Kramer 1991, *G. affinis* Brown 1985, *P. reticulata*, this study). However, this trend is not universal: Congdon (1994) found that movement by female *Gambusia holbrooki* was greater than that of males at high but not low water velocity in an experimental stream. Thus, environmental conditions may modify or even reverse relationships between sex and movement.

Secondly, movement may be female-biased in species where males invest more in parental care than females. For example, in a cardinalfish (*Apogon niger*) males mouth-brood an egg mass received from one female at a time. Okuda (1999) found that females dispersed more frequently during the breeding season than males. Similarly, in the shell-dwelling cichlid (*Neolamprologus multifasciatus*), where several reproductive males and females defend a territory, Schradin and Lamprecht (2000) found that females exhibited a higher tendency than males to migrate. However, once again, the trend is not universal. Schleusner and Maughan (1999) found no differential rate of movement between male and female largemouth bass (*Micropterus salmoides*), a species where the male guards a nest in which multiple females deposit their eggs.

Finally, species with external fertilization and little or no post-spawning parental investment may not exhibit sex-biased movement. For example, Gilliam and Fraser (2001) found no difference in movement-distance distributions for male and female Hart's *Rivulus* (*Rivulus*

hartii). Similarly, Aparicio and Sostoa (1999) found no difference in movement patterns for male and female *Barbus haasi*. Both of these species are egg-layers and exhibit no post-spawning parental care (E. Aparicio and D. F. Fraser, personal communication).

Implications

An understanding of the dynamics of sex-biased movement is of great importance, and has both ecological and evolutionary implications. For example, high rates of male movement could be a major source of gene flow, and could be the key to understanding why guppies have not undergone isolation and speciation (Magurran 1996, 1998). An understanding of fish movement patterns is also essential when considering the conservation of a species (Kramer and Chapman 1999; Meyer et al. 2000), and sex-biased dispersal may add an additional layer of complexity to such considerations. Despite this importance, sex-biased movement is a relatively unexplored area for fish ecology and future studies should address the influence of sex and mating systems on movement patterns.

Acknowledgements D. P. C. was supported by a Frank Parkinson Scholarship from the University of Leeds. We would also like to thank James Gilliam and the Asa Wright Nature Centre for access to equipment and laboratory space, Anne Magurran for valuable discussions and Graeme Ruxton and two anonymous referees for valuable comments on the manuscript.

References

- Aparicio E, De Sostoa A (1999) Pattern of movements of adult *Barbus haasi* in a small Mediterranean stream. *J Fish Biol* 55:1086–1095
- Becher SA, Magurran AE (2000) Gene flow in Trinidadian guppies. *J Fish Biol* 56:241–249
- Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449
- Brown KL (1985) Demographic and genetic characteristics of dispersal in the mosquitofish, *Gambusia-Affinis* (Pisces, Poeciliidae). *Copeia* 1985:597–612
- Chapman LJ, Kramer DL (1991) The consequences of flooding for the dispersal and fate of Poeciliid fish in an intermittent tropical stream. *Oecologia* 87:299–306
- Chivers DP, Brown GE, Smith RJF (1995) Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*) - implications for antipredator behaviour. *Can J Zool* 73:955–960
- Clarke AL, Saether BE, Roskaft E (1997) Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429–438
- Congdon BC (1994) Characteristics of dispersal in the eastern mosquitofish *Gambusia-Holbrooki*. *J Fish Biol* 45:943–952
- Croft DP, Arrowsmith BJ, Bielby J, Skinner K, White E, Couzin ID, Magurran AE, Ramnarine I, Krause J (2003) Mechanisms underlying shoal composition in the Trinidadian guppy (*Poecilia reticulata*). *Oikos* 100:429–438
- Farr JA (1977) Male rarity of novelty, female choice behaviour, and sexual selection in the guppy *Poecilia reticulata* (Pisces: Poeciliidae). *Evolution* 31:162–168
- Gandolfi G (1971) Sexual selection in relation to the social status of males in *Poecilia reticulata* (Teleostei: Poeciliidae). *Boll Zool* 38:35–48
- Gandon S, Michalakis Y (2001) Multiple causes of the evolution of dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) *Dispersal*. Oxford University Press, New York, pp 155–167
- Gilliam JF, Fraser DF (2001) Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. *Ecology* 82:258–273
- Gilliam JF, Fraser DF, Alkinkoo M (1993) Structure of a tropical stream fish community — a role for biotic interactions. *Ecology* 74:1856–1870
- Gowan C, Fausch KD (1996) Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. *Can J Fish Aquat Sci* 53:1370–1381
- Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162
- Griffiths SW, Magurran AE (1997) Schooling preferences for familiar fish vary with group size in a wild guppy population. *Proc R Soc Lond Ser B* 264:547–551
- Griffiths SW, Magurran AE (1997b) Familiarity in schooling fish: how long does it take to acquire? *Anim Behav* 53:945–949
- Hansson L (1991) Dispersal and connectivity in metapopulations. *Biol J Linn Soc* 42:89–103
- Haskins CP, Haskins EF, McLaughlin JJA, Hewitt RE (1961) Polymorphism and population structure in *Lebistes reticulatus*, an ecological study. In: Blair WF (ed) *Vertebrate speciation*. University of Texas Press, Austin, Tex., pp 320–395
- Houde AE (1997) Sex, color, and mate choice in guppies. Princeton University Press, Princeton, N.J.
- Hughes KA, Du L, Rodd FH, Reznick DN (1999) Familiarity leads to female mate preference for novel males in the guppy, *Poecilia reticulata*. *Anim Behav* 58:907–916
- Jirotkul M (1999a) Operational sex ratio influences female preference and male-male competition in guppies. *Anim Behav* 58:287–294
- Jirotkul M (1999b) Population density influences male-male competition in guppies. *Anim Behav* 58:1169–1175
- Kaya CM (1991) Rheotactic differentiation between fluvial and lacustrine populations of Arctic grayling (*Thymallus-Arcticus*), and Implications for the only remaining indigenous population of fluvial Montana grayling. *Can J Fish Aquat Sci* 48:53–59
- Kelley JL, Graves JA, Magurran AE (1999) Familiarity breeds contempt in guppies. *Nature* 401:661–662
- Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. *Environ Biol Fishes* 55:65–79
- Krupa JJ, Sih A (1993) Experimental studies on water strider mating dynamics — spatial variation in density and sex-ratio. *Behav Ecol Sociobiol* 33:107–120
- Labbe TR, Fausch KD (2000) Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecol Appl* 10:1774–1791
- Lambin X, Aars J, Pieltney SB (2001) Dispersal, intraspecific competition, kin competition, and kin facilitation: a review of the empirical evidence. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) *Dispersal*. Oxford University Press, New York, pp 110–122
- Lawrence WS (1987) Effects of sex-ratio on milkweed beetle emigration from host plant patches. *Ecology* 68:539–546
- Liley NR, Seghers BH (1975) Factors affecting the morphology and behaviour of the guppy (*Poecilia reticulata*) in Trinidad. In: Baerands G, Manning A (eds), *Function and behaviour in evolution*. Oxford University Press, Oxford, pp 92–118
- Macdonald DW, Johnson DDP (2001) Dispersal in theory and practice: consequences for conservation biology. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) *Dispersal*. Oxford University Press, New York, pp 358–372
- Magurran AE (1996) Battle of the sexes. *Nature* 383:307–307
- Magurran AE (1998) Population differentiation without speciation. *Philos Trans R Soc Lond Ser B* 353:275–286

- Magurran AE, Seghers BH (1994) Sexual conflict as a consequence of ecology — evidence from guppy, *Poecilia-Reticulata*, populations in Trinidad. *Proc R Soc Lond Ser B* 255:31–36
- Magurran AE, Seghers BH, Shaw PW, Carvalho GR (1994) Schooling preferences for familial fish in the Guppy, *Poecilia-reticulata*. *J Fish Biol* 45:401–406
- Metcalf NB, Thomson BC (1995) Fish recognise and prefer to shoal with poor competitors. *Proc R Soc Lond B* 259:207–210
- Meyer CG, Holland KN, Wetherbee BM, Lowe CG (2000) Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. *Environ Biol Fish* 59:235–242
- Okuda N (1999) Female mating strategy and male brood cannibalism in a sand-dwelling cardinalfish. *Anim Behav* 58:273–279
- Perrin N, Goudet J (2001) Inbreeding, kinship, and the evolution of natal dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) *Dispersal*. Oxford University Press, New York, pp 123–142
- Railsback SF, Lamberson RH, Harvey BC, Duffy WE (1999) Movement rules for individual-based models of stream fish. *Ecol Model* 123:73–89
- Reznick DN, Butler MJ, Rodd FH, Ross P (1996) Life-history evolution in guppies (*Poecilia reticulata*). 6. Differential mortality as a mechanism for natural selection. *Evolution* 50:1651–1660
- Rodd FH, Reznick DN (1997) Variation in the demography of guppy populations: the importance of predation and life histories. *Ecology* 78:405–418
- Schaefer J (2001) Riffles as barriers to interpool movement by three cyprinids (*Notropis boops*, *Campostoma anomalum* and *Cyprinella venusta*). *Freshwater Biol* 46:379–388
- Schleusner CJ, Maughan OE (1999) Mobility of largemouth bass in a desert lake in Arizona. *Fish Res* 44:175–178
- Schlosser IJ, Angermeier PL (1995) Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. In: Nielsen JL (ed) *Evolution and the aquatic ecosystem: defining unique units in population conservation*. American Fisheries Society symposium 17. American Fisheries Society, Bethesda, Md., pp 392–401
- Schradin C, Lamprecht J (2000) Female-biased immigration and male peace-keeping in groups of the shell-dwelling cichlid fish *Neolamprologus multifasciatus*. *Behav Ecol Sociobiol* 48:236–242
- Seghers BH (1973) An analysis of geographic variation in the antipredator adaptations of the Guppy, *Poecilia reticulata*. PhD thesis. University of British Columbia, B.C.
- Swaney W, Kendal J, Capon H, Brown C, Laland KN (2001) Familiarity facilitates social learning of foraging behaviour in the guppy. *Anim Behav* 62:591–598
- Van Deventer JS, Platts WS (1983) Sampling and estimating fish populations from streams. *Trans Nat Am Wild Nat Res* 48:349–354
- Van Deventer JS, Platts WS (1985) A computer software system for entering, managing, and analyzing fish capture data from streams. Research note INT-352. Intermountain Forest and Range Experimental Station, US Department of Agriculture, Forest Service, Ogden, Utah
- Winker K, Rappole JH, Ramos MA (1995) The use of movement data as an assay of habitat quality. *Oecologia* 101:211–216
- Wootton RJ (1998) *Ecology of Teleost fishes*. Kluwer, Dordrecht