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Factors triggering floodplain fish emigration: Importance of fish density and food availability

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Abstract

Emigration is a widespread phenomenon among fish species in seasonal habitats, but little is known about the factors which trigger this behaviour. In controlled experiments using *Tilapia guineensis*, a species widely occurring in the seasonal floodplains of West Africa, density of fish played a significant role in triggering fish migration, whereas a lack of food available caused an increase in exploratory behaviour but with no impact on successful emigration. The impact of fish density and subsequently interactions between individuals on emigration suggests that this may be an important causal factor of emigration in fish species exhibiting social interactions.

Keywords

Emigration; *Tilapia guineensis*; seasonal movement; floodplains; food availability; density

Introduction

Migration is one of the commonest behavioural adaptations of animals living in seasonal environments and occurs in a variety of taxa including mammals, insects, birds and fish (Kennedy 1951; Wolff 1994; Lucas & Baras 2001; Makrakis et al. 2007; Castello 2008), but surprisingly little is known of the factors which trigger individuals to emigrate to new habitats (Taylor & Norris 2007). Emigration is defined as a one-way movement from the home area (Lidicker & Stenseth 1992; Dingle & Drake 2007) and suggested cues that trigger this exploratory behaviour include unfavourable environmental conditions, lack of resources, predation pressure and intra- and interspecific competition (Bell 1991).

The relative strength of the different factors which trigger emigration may vary between species and particular environments. The proximate food limitation hypothesis assumes that territories are only important as a mechanism of capturing food (Marschall & Crowder 1995), suggesting that only food availability truly determines the individual's decision to migrate. By contrast other studies suggest that a wider range of factors such as water temperature, flow and cover availability can trigger fish emigration (McMahon & Hartman 1989; Keeley 2001). Under controlled conditions McMahon & Tash (1988) recorded increased emigration rates of the desert pupfish, *Cyprinodon macularius*, in response to a doubling in densities and a consequent halving of available food and cover. Keeley (2001) found both food and density, rather than either exclusively, to be important components of demographic changes (emigration and mortality) in steelhead trout, *Oncorhynchus mykiss*. It is important to tease apart individual factors that influence fish migratory behaviour so that their relative influence can be assessed. Due to difficulties in isolating causal factors for emigration in the field, it has been suggested that only well-controlled laboratory studies can

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identify the truly significant factors (McMahon & Tash 1988; Matter et al. 1989; McMahon & Matter 2006). Yet, these same experiments, on fish and non-fish taxa, have mostly been carried out on species which do not exhibit well-defined seasonal migration patterns (McMahon & Tash 1988; Matter et al. 1989; McMahon & Matter 2006). Emigration behaviour is considered to be at least partly genetically determined (Dingle 1980; Lidicker & Stenseth 1992) and therefore experiments testing factors that influence emigration should also consider species adapted to seasonal environments.

Floodplain habitats are highly seasonal and provide dynamic conditions, some of which may present threats to fish and in other cases, advantages. Whilst fish may become concentrated into isolated pools or channels as water levels recede, floodwater also provides access to new habitat, which can be important for reproduction and/or feeding. Exploitation of seasonal floodplains by fishes may, therefore, be triggered by specific environmental conditions. The Guinea tilapia, *Tilapia guineensis*, is widely distributed on West African floodplains (Campbell 1987). It is the commonest fish species encountered on the highly seasonal Gambia River floodplains, and readily colonises new habitats which become available during the rainy season (V. Louca, unpublished data). Although most cichlids have very limited migratory habits (Hert 1992; Lucas & Baras 2001), this is not the case in cichlids living in seasonal floodplains habitat (Benech & Penaz 1995). While average Guinea tilapia densities in inundated floodplain have been recorded as 11 fish m⁻², densities of 40–70 fish m⁻² are not uncommon and in floodplain pools densities of 500 fish m⁻² can occur (V. Louca, unpublished data). In this species, the strongest territorial behaviour is exhibited by adult reproductive individuals which defend small areas from conspecifics (Campbell 1987), and this is consistent with cichlid behaviour in general in which social interactions between siblings of juvenile cichlids start as simple physical encounters and avoidance and progress to elaborate lateral posturing and finally to strong sexual and dominance interactions (Valerio & Barlow 1986; Keenleyside 1991).

This study examined, under controlled conditions, the role of food availability and fish density in emigratory behaviour of the tropical floodplain fish, the Guinea tilapia. We hypothesised that exploratory behaviour leading to emigration would increase with elevated density and reduced food, due to increased competition for space and food resources.

Methodology

Study site and test fish

The study was carried out at the Medical Research Council's field station at Farafenni town (UTM coordinates: 1500200N, 435500E), The Gambia, located in the southern Sahel region and characterised by a single rainy season from June to October. It lies in an open flat Sudan savannah dominated by the Gambia River and the highly seasonal floodplains which border it (Svensson 1933; Pages & Citeau 1990).

Juvenile Guinea tilapia were collected from local floodplains using cast nets in 2007. Specimens were kept in large holding tanks for a minimum of 2 weeks to acclimatise the fish and accustom them to being fed on aquarium dried flake food (Tetramin, fed *ad libitum*). The total length of the fish collected varied from 5 to 7cm, a range which represents non-breeding individuals (V. Louca, unpublished data). Young Guinea tilapia do not show any sexual dimorphism (Paugy et al. 2003), so sexes were not differentiated in the study.

Emigration experiments

Six cement tanks were constructed under a shed with open sides so that the tanks would be exposed to the natural day/night variations in shade temperature and light, but prevent any

changes in the water level of the tanks due to rainfall. Each tank was divided into two parts, each 1.0 m long and 1.0 m wide, with a water depth of 0.75m, and a connecting ramp in the middle (Fig. 1). Fish were placed on one side of the tank (A) and a clear tube (length, 7cm, diameter, 3cm) connected to the narrowing ramp (length, 15cm) (Fig. 1), prevented return of fish which moved to the opposite side of the tank. Following introduction of fish into the holding tank, the water level was raised using a hose pipe and kept constant at 0.5 cm at the ramp (about one third of fish body depth), so as to make fish movement across the ramp challenging, so that only those individuals with sufficiently strong motivation to emigrate would do so (McMahon & Matter 2006). Preliminary observations showed that tilapia readily approached and accessed the ramp and those which successfully traversed it did not return to the holding tank (cumulative increase in numbers in receiving compartment B and no recorded incidences of fish accessing the ramp via the tube). The effect of fish density on emigration was tested with high (40 fish m⁻²), medium (25 fish m⁻²) and low (10 fish m⁻²) density treatments, densities naturally encountered in the wild, all of which were fed standard aquarium flake at a ration of 5% of fish biomass/day (Legendre & Ecoutin 1989). Experiments lasted 7 days and comprised 12 tank replicates per treatment. For the food treatment, 25 fish per tank were used for treatment and control groups. Food (standard aquarium flake, 5% of average fish biomass/day) was provided for the control group and no food was given to the treated group for the whole 7-day duration of each experimental round. There were 12 tank replicates each for the food and control treatments.

Preliminary observations showed that fish approached and traversed the ramp throughout the day, but the lack of light prevented night-time observations. Behavioural observations were therefore carried out daily between 14:00 and 17:00, for 90 minutes in one randomly selected tank per treatment and the exploratory behaviour of the fish in that tank was assessed by counting the number of times fish moved onto the ramp (an individual fish exposing its whole body on the ramp). As the ramp was the area of the tank that became newly available at the start of the experiment, we consider an individual fish's effort to move onto the ramp as a good indicator of increased exploratory behaviour. The total number of fish that crossed into the emigration section over 24 hours was recorded daily at 17:00 from counts of fish in the emigration section of each tank. No mortality or loss of fish was recorded during the study. Individual fish were used only once to avoid problems related to learned behaviour.

Statistical analysis

The impacts of the density and food treatments on the number of fish which migrated and the number of attempted crossings were analysed using General Estimating Equations (GEE). This analysis extends generalized linear models (GLMs) to account for repeated measures and clustering of samples as well as allowing for linear and non-linear models (Horton & Lipsitz 1999). Since tanks were repeatedly sampled daily, it was important to select a method which accounts for repeated measures. Tank number was incorporated into the model as a repeated measures variable assuming an exchangeable correlations matrix. Data were fitted to a negative binomial distribution with a negative binomial link function as untransformed data followed a negative binomial distribution. All analysis was performed in SPSS version 15.

Results

The starting fish density in the holding tank had a highly significant effect on the proportion of fish which migrated ($P < 0.01$, Table 1) with the highest emigration rate observed with an initial density of 40 fish/m², with a relative odd's ratio (O.R., the proportional change relative to the reference group of 20 fish m⁻²) of 1.48, whereas there was no significant difference between medium and low densities (Table 1). By contrast, food availability had

no impact on the proportion of fish emigrating (Table 1). Both food availability (O.R. = 1.22) and the highest fish density (40 fish m⁻²; O.R. = 1.13) caused a significant increase in the relative level of exploratory behaviour (Table 1). Relative levels of exploratory behaviour per fish, both for fish kept with and without food did not vary significantly over time (Table 1), but there was a significant decrease in the daily proportion of fish migrating for the medium (25 fish m⁻²) fish density.

Discussion

For animals exhibiting social interactions, recent models based on emigration behaviour argue against resource availability as a driving force for emigration, but suggest social interaction to be a far more important factor (Wolff 1994). However, others argue that resource availability, habitat use and social interactions and their effects on emigration are closely intertwined (McMahon & Matter 2006). Cichlid fish are known to exhibit complex behavioural patterns with a variety of different interactions between individuals including juveniles (Keenleyside 1991). In this study high fish density was shown to be a primary factor triggering emigration. During the dry season, the floodplains of the Gambia River are reduced to small water bodies with high densities of fish taking refuge in them (Svensson 1933; V. Louca, unpublished data). Interactions between tilapias with established territories within those shrinking habitats and other individuals that find refuge in them during the dry season is likely to be a major factor driving fish out on to newly flooded areas at the beginning of the rainy season.

These results show that a lack of food induces increased exploration (Table 1), probably to find food, but there is no indication in our experimental set-up that it triggers them to make the extra effort needed to negotiate a shallow-water conduit and emigrate to a new habitat (Table 1). This finding is also in accordance with Mesick (1988) who concluded that food is not a strong trigger of emigration in stream-dwelling trout. These processes may be considered in the context of a mechanistic model whereby the availability of resources (e.g. food, cover, territorial space) affects the exploratory behaviour of individuals, such that elevated motivation of individuals and increased exploratory behaviour will lead eventually to emigration (Sale 1969; McMahon & Matter 2006). In this study the exploratory behaviour for fish with and without food did not vary over time suggesting that food availability is a relatively weak motivation for fish to emigrate. Emigration patterns in fish which occupy more permanent habitats, for example salmonids in streams and tropical fish in coral reefs are mostly well understood. Dominant fish hold territories and subordinate individuals exhibit increased exploratory behaviour and emigration, with subsequent high costs for the emigrating individuals, which often move to areas of poor quality habitat where energy gain may be low and predation risk high (Clarke 1970; Larson 1980; Marschall & Crowder 1995; Keeley 2001). However, if local resource availability is low, substantial costs can also be involved for fish that do not emigrate (McMahon & Tash 1988), so there is a potential trade off of fitness costs and benefits to emigration. In the case of species such as the Guinea tilapia, which utilise seasonally flooded areas, emigrating into newly flooded, high-quality habitat unoccupied by other fish and with few aquatic predators can be expected to increase their survival chances (Welcomme 1979; Lowe-McConnell 1987; Lucas & Baras 2001). In these habitats emigration may, therefore, be a characteristic of strong fitness benefit.

Acknowledgments

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Figure 1.

Experimental setup of the emigration test tanks. Fish were introduced on side A (75 cm deep), and emigrating individuals moved across the ramp (water depth at the ramp, 0.5 cm) to side B. The clear tube at the end of the ramp stopped fish from moving back to side A.

Comparisons of the proportion of Guinea tilapia that successfully migrated across the ramp and relative frequency of exploratory movements onto the ramp per fish in relation to fish density and food availability. C.I. is 95% confidence interval. Significant values are given in bold.

Table 1

Factors	Median	Range		Odds' ratio	95% Wald C.I.		P
		Min.	Max.		Low	High	
Emigration (proportion of fish over 7-day experimental period)	High density	0.54	0.02	0.92	1.48	1.24	1.75
	Med. density	0.02	0.00	0.76	1.23	0.97	1.55
	Low density	0.00	0.00	0.20	1.00	-	-
	No food	0.20	0.00	0.92	1.04	0.84	1.31
Change in emigration over time (Days)	Food supplied	0.02	0.00	0.76	1.00	-	-
	High density	0.03	0.00	0.63	0.99	0.99	1.00
	Med. density	0.00	0.00	0.62	0.98	0.97	0.99
	Low density	0.00	0.00	0.20	0.99	0.98	1.01
Ramp explorations (during 90-minute observation period)	High density	0.09	0.00	2.60	1.13	1.00	1.28
	Med. density	0.00	0.00	0.29	0.95	0.79	1.19
	Low density	0.00	0.00	0.60	1.00	-	-
	No food	0.15	0.00	5.50	1.22	1.05	1.41
Change in ramp explorations over time (Days)	Food supplied	0.00	0.00	0.29	1.00	-	-
	No food	0.15	0.00	5.50	0.99	0.99	0.98
	Food supplied	0.00	0.00	0.29	0.98	0.94	1.02
							0.34