**Shape of single and multiple central-place territories in a stream-dwelling fish**

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Territory shape yields important insights into how animals exploit local resources. Territories of stream-dwelling salmonids are typically (i) mapped around a single central-place, (ii) described as circular, elliptical or teardrop-shaped, and (iii) believed to reflect their exploitation of drifting invertebrate prey. In this study, we tested the current view of territory shape by mapping multiple central-place territories for 50 young-of-the-year Atlantic salmon. Multiple central-place areas were more elongated (eccentricity: median = 1.301, range = 1.043-2.784) than the foraging patterns around each central place (eccentricity: median = 1.135, range = 1.014-1.385). In addition, multiple central-place areas were elongated along the stream length (33 of 50 fish), whereas the foraging areas around each station tended to be elongated along the stream width (32 of 50 fish). These findings may be explained by the way that stream salmonids interact with drifting prey. At each central place, a wider foraging area should provide an increased access to prey drifting downstream. Similarly, by regularly patrolling a large multiple central-place area along the stream axis, a territorial fish may increase its access to drifting prey by excluding competitors from upstream areas. Further studies are needed on the ecological factors that determine territory shape in stream fish and multiple central-place foragers.

**Key words:** Home range, space use, foraging, invertebrate drift, rivers, Atlantic salmon**Introduction**

Territory shape provides key insights into how animals exploit and defend local habitats (Covich 1976; Eason 1992; Adams 2001). Early studies of territory shape often focused on single central-place areas, where animals forage from and deliver food to one central location (Anderson 1978; Getty 1981; but see Covich 1976). The optimal shape of central-place areas was often predicted, or assumed, to be circular in homogeneous environments (Andersson 1978; Hixon 1980), or hexagonal in territorial mosaics where a territory holder is surrounded by competitors (Maynard Smith 1974; Adams 1998). To date, irrespective of whether territories or foraging areas have a “central place” or not, numerous studies show that their shape is diverse and affected by various ecological factors (Adams 2001), such as resource distribution (Ford 1983; Davies and Houston 1984), habitat heterogeneity (Reid and Weatherhead 1988; Eason et al. 1999) and defensive cost (Eason 1992).

Drift-feeding stream-dwelling fish provide an interesting model system for investigating territory shape because they typically feed on drifting invertebrate prey, continuously delivered from upstream with the water current (Kalleberg 1956; Noakes and McNicol 1982; Hughes and Dill 1990). Although the shape of space-use patterns in stream-dwelling salmonids has received some attention, it is almost exclusively directed towards fish that sit-and-wait at a single foraging station, from which they attack prey and intruders (e.g., Wankowski 1981; Noakes and McNicol 1982; Hughes et al. 2003). Among salmonids, these central-place territories have been described as cardioid (Noakes and McNicol 1982), teardrop-like (Dill et al. 1981) or elliptical in shape (Kalleberg 1958; Elliott 1990), although the area is often calculated assuming circularity (Grant et al. 1989). Shape of salmonid territories also depends on whether the respective study examines the distribution of foraging or aggressive acts. Foraging effort may be greater along the stream width (Wankowski 1981; Grant et al. 1989), because this increases encounters with prey drifting downstream, whereas individuals may be likelier to attack competitors upstream of their foraging station for similar reasons (Kalleberg 1958; Keeley 2000).

Although some studies show that stream-dwelling fish can **repeatedly switch among a set of foraging stations** within their foraging areas (Bachman 1984; Nakano 1995), called multiple central-place territories (Steingrímsson and Grant 2008), or have no specific central-place (Katano 1996), no study has systematically studied territory shape for fish that do not conform to the central-place territorial model. Because removal of competitors from upstream foraging stations may increase the availability of drifting prey at downstream foraging stations (Elliott 2002a; Steingrímsson and Grant 2011), we suggest that **multiple central-place territories** should be elongated along the stream length rather than the width (e.g., Fig. 3 in Nakano 1995; Fig. 2 in Katano 1996).

In this study, we compare the shape of 50 multiple central-place territories of young-of-the-year (YOY) Atlantic salmon (*Salmo salar*) to the corresponding patterns around their individual foraging stations. We examine two parameters of shape; (*i*) eccentricity, which indicates the degree to which these areas are elongated and (*ii*) the angle of the primary axis, which indicates whether this elongation is parallel or perpendicular to the stream flow. Based on their reliance on drifting prey, we predict that the foraging area at each central-place station will be elongated along the stream width, whereas multiple central-place areas will be elongated along the stream length.

**Methods**

*Study sites, population, body size*

We mapped territories of 50 YOY Atlantic salmon at 10 study sites in Catamaran Brook, New Brunswick, Canada, in 2000 (Steingrímsson and Grant 2008). Details on the location of the study sites and the stream biota are found in Steingrímsson and Grant (2003) and Mitchell and Cunjak (2007), respectively. Study fish were originally captured, tagged and measured (fork length = 27.3-40.6 mm) in two snorkeling surveys on 25 June to 4 July, and 12-13 July. Once we finished space-use observations for all focal fish (see below), we caught and measured all tagged fish found in two snorkeling surveys on 20-23 August and 11-12 September, before eventually releasing fish back onto their respective territory. We chose study sites that represented a wide range of habitats (Table 1), which are reflected in the water current velocities ( = 0.159 ms−1, range = 0.012-0.362) and water depths (= 34.4 cm, range = 14.6-78.7) used by the study fish (Steingrímsson and Grant 2011). Body size of each focal fish, on the day of its observation, was estimated by assuming a linear increase in fork length between the preceding and the subsequent capture survey. Earlier, we described the territory size, foraging behavior, mobility and defense for the same focal fish, and how this behavior changed across habitats (Steingrímsson and Grant 2008; 2011).

*Estimates of territory size and shape*

We observed the space use of focal fish via snorkeling from 3 July to 17 August, 2000. Typically, we monitored each fish for four 10-min periods (40-min) dispersed between 1330-1850 h in a single day**;** the only exceptions were three fish where only 30 min of data were obtained and four fish where the last 20-min of data were collected on the subsequent day. After identifying a fish, we waited a minimum of 5 min before each 10-min period to avoid disturbance. For each individual, we noted the location of foraging stations, the direction (1-12 o’clock) and distance (in body lengths) of foraging attempts and aggressive acts, and if the fish was attacked by an intruder. The location of all foraging stations and aggressive acts was recorded consistently throughout the four 10-min periods. However, because the study fish often foraged very frequently, and because we also wanted to estimate foraging rate (see results in Steingrímsson and Grant 2011), we did not record foraging in the same way during all four 10-min periods. More specifically, we recorded the location (i.e., the vector) of as many foraging attempts as possible in the first 30 min, which precluded an accurate estimate of total foraging rate. During the last 10 min, however, we counted all foraging attempts and recorded the station from which they occurred. Spatial mapping of these behaviors was facilitated by creating a simple x-y coordinate system for each study site (Steingrímsson and Grant 2008). All estimates of territory size and shape were obtained via ArcView GIS 3.2 in conjunction with the Animal Movement extension (Hooge and Eichenlaub 2000). More details on the space use measurements can be found in Steingrímsson and Grant (2008; 2011).

For each fish, we mapped areas using both a multiple and a single central-place approach. Multiple central-place areas take into account the relative x-y location of all stations from which foraging occurs, whereas for single central-place estimates, we superimposed all foraging attempts (i.e., direction and distance) onto one station by setting the x and y coordinate for all foraging stations to zero. Because estimates of territory use are usually analyzed separately for aggression and foraging data (Grant et al. 1989; Keeley 2000), and because we observed few aggressive acts per fish (Steingrímsson and Grant 2008), individual estimates of territory size (and shape) were based only on foraging attempts, which represented 97% of all behavioral acts of our fish (Steingrímsson and Grant 2008). For comparison, however, we also estimated the shape of a single central-place “aggressive area” by combining the vectors (in body lengths) of all aggressive acts of all study fish into one estimate. Territory size was estimated via the minimum convex polygon method, based on all foraging attempts (i.e., MCPF100% area)(Schoener 1981). For multiple central-place estimates, these MCPF100% estimates were identical in size to the MCP100%, estimates reported in Steingrímsson & Grant (2008; 2011) on the same fish, which also included aggression (linear regression: log10 MCP100 = 0.026 + 0.964 log10 FMCP100; r2 = 0.986; n = 50; p < 0.001).

We examined and compared the shape of single versus multiple central-place space use patterns by using Jennrich and Turner’s (1969) home range estimates (hereafter, JT estimates), which assume space use follows a bivariate normal distribution. The JT-method has been correctly criticized as a method for estimating territory size (Ford and Krumme 1979; Schoener 1981), but for our purposes it provides two valuable indicators of territory shape: (*i*) eccentricity, which indicates to what degree territories deviate from a circle (i.e., their elongation), and (*ii*) the angle at which territories are elongated. Eccentricity is calculated based on the ratio between the vectors of the major (a) and minor (b) axis of the JT home range (i.e., eccentricity =).

Hence, the length of the major (a) and the minor (b) axis represent the length and width of the JT estimate, and are statistically identical to the first and second eigenvectors of a bivariate normal distribution, respectively (Sokal and Rohlf 1981). Consequently, eccentricity = 1, when home ranges are circular (i.e., a = b), and then increases in value as the shape becomes more elliptical (i.e., a >> b). We used the angle of the major axis of the JT-estimate to determine (via a simple G-test) whether home ranges were elongated along the stream length (absolute value of the angle = 45-90°; where 90° represents the up- vs. downstream direction) or along the stream width (absolute value of the angle = 0-45°, where 0° is perpendicular to the water flow) (Hooge and Eichenlaub 2000).

**Results**

YOY Atlantic salmon in Catamaran Brook defend multiple-central place territories (number of foraging stations; = 12.5, range = 3-26) within which they travel long distances ( = 39.3 m·40min-1, range = 15.7 - 95.0) primarily devoted to attacking prey ( = 48.9%) and switching between foraging stations ( = 47.8%) (Steingrímsson and Grant 2008; 2011). Based on foraging data, the multiple central-place areas were 19.1 times larger (, back-transformed from log10 = 0.859 m2; range = 0.218 - 4.182 m2) than the single central-place areas calculated for the same data when superimposed onto one station for the respective fish (, back-transformed from log10 = 0.045 m2; range = 0.013 - 0.364 m2).

Shape of multiple central-place areas clearly **differs** from the shape that emerges when the same spatial data are superimposed onto a single central-place (Fig. 1). More specifically, multiple central place areas are significantly more elongated (eccentricity: = 1.301, range = 1.043-2.784) than the patterns of foraging around each central place station (Wilcoxon signed-ranks test: Z = 4.619, n = 50, p < 0.001), which are much closer to circular in shape (eccentricity: = 1.135, range = 1.014-1.385) (Fig. 2a). Moreover, multiple central-place areas had significantly higher primary angles ( = 60.1) than single central-place areas ( = 23.8) (Wilcoxon signed-ranks test: Z = 2.935, n = 50, p = 0.003). More specifically, multiple central-place areas were elongated along the stream length (i.e., absolute angle > 45°) for 33 of the 50 fish, whereas 32 of the foraging areas around each station were elongated along the stream width (i.e., absolute angle < 45°) (Fig. 2b) (*G*-test of independence, Williams correction: Gadj = 4.504, df = 1, p < 0.05). For comparison, a single central-place “aggressive area” based on all aggressive acts across individuals was similar in shape as those based on only foraging data; i.e., it was nearly circular in shape (eccentricity = 1.023) with minor elongation occurring along the stream width (angle = 6.1). In summary, a typical YOY Atlantic salmon in this study used a multiple central-place area, which was elongated along the stream length and was 68% longer than wide, whereas the foraging area around each focal point was elongated parallel to the water flow and was 29% wider than it was long. Finally, for the multiple central-place areas, neither eccentricity nor the angle was related to any habitat features measured for each territory (see Steingrímsson and Grant 2011), such as water depth, current velocity or distance from shore (Spearman´s rank correlation: p > 0.05 in all cases).

**Discussion**

*Shape of single central-place areas*

In general, our study agrees with previous studies on the shape of single central-place territories in stream salmonids. First, in spite of the slight elongation of the foraging area, and the fact that the shape of central-place territories may sometimes be more accurately described as cardioid (Noakes and McNicol 1982), teardrop-like (Dill et al. 1981) or elliptical (Kalleberg 1958; Elliott 1990), these areas typically do not deviate much from circularity (see also Grant et al. 1989; Keeley 2000). Second, similar to our study, the slight elongation of the foraging effort tends to occur along the stream width (Wankowski 1981; Grant et al. 1989). The size and shape of single central-place foraging areas used by salmonids are likely related to their reliance on drifting invertebrates (91.2% of the prey items in this study; Steingrímsson and Grant 2011). As fish grow, their foraging radius increases, allowing them to intercept a greater number of prey drifting downstream (Grant et al. 1989; Keeley and Grant 1994; Keeley and McPhail 1998). Similarly, a wider foraging area at each central-place may enhance prey encounter rate by increasing the number of available prey drifting over each foraging station (Grant et al. 1989).

*Shape of multiple central-place territories*

Although home ranges of stream-dwelling fish, whose foraging activity is not confined to a single central place, are often depicted (e.g., Bachman 1984; Nakano 1995; Katano 1996), their shape, according to our knowledge, has not been analysed systematically. This study shows that multiple central-place territories of YOY Atlantic salmon (*i*) deviate much more from a circular shape than single central-place foraging areas, and (*ii*) are elongated along the stream length rather than the stream width. The former finding is not surprising; by switching from exploiting one central place to many, the shape may become more irregular (Chapman et al. 1989), in part because space use is no longer constrained by repeated returns to the same central place.

Why multiple central-place territories of stream-dwelling fish are elongated along the stream length is less obvious. Sometimes, the shape of the foraging area may simply be constrained by the stream width; i.e., in narrow streams, a larger area can only be achieved by increasing its length along the stream axis (Katano 1996). A similar elongation along the stream length may also arise when space use is measured over a longer time; eventually, larger-scale relocation or habitat exploration will primarily occur along the stream length (e.g., Armstrong et al. 1999). Neither explanation, however, applies to our results as the side-to-side diameter of these multiple central-place foraging areas is very small (maximum side-to-side diameter of the median territory = 1.03 m) relative to the width of our study stream ( = 5.9 m, range = 4.2-8.8), and because these territories are measured over a single day, over which larger scale exploration is unlikely (Steingrímsson and Grant 2003).

One potential explanation of the shape of multiple central-place areas in YOY Atlantic salmon emerges from the way that stream salmonids interact with drifting prey. In some situations, a competitor immediately upstream from a territorial fish may reduce the availability of drifting prey via “shadow competition” (*sensu* Elliott 2002a; see also Nakano 1995). Because a significant portion of invertebrates drift distances short enough to originate from within a multiple central-place territory (McIntosh and Townsend 1998; Elliott 2002b), the prey encounter rate may be greater if these areas are patrolled to exclude competitors immediately upstream of many foraging stations (see Steingrímsson and Grant 2011). If true, this idea may help explain why multiple central-place territories tend to be elongated along the stream length, a shape for which any local increase in drifting prey would affect more stations in the downstream direction.

Given the great variability in the shape of the multiple central-place territories, it is likely that habitat heterogeneity and the landscape of the local habitat also play a role (*sensu* Eason and Stamps 1992; Eason et al. 1999). For example, if fish actively select foraging stations in habitats of optimal current velocity or water depths, an elongation along the stream length may be expected because these variables are typically more uniform in the up-downstream direction (e.g., Nakano 1995). Alternatively, if fish benefit from having access to a wide range in water current velocity, water depth and substrate size within a territory, e.g., for feeding and sheltering at different hours of the day (Metcalfe et al. 1997; Bardonnet et al. 2006), these areas should rather be elongated along the stream width to include diverse habitats that vary in proximity to the shore.

*General implication for territory shape in animals*

In many ways, stream-dwelling salmonids mirror the literature on territory shape in mobile animals. Early studies typically predict that central-place areas should be circular, assuming that food resources are distributed homogeneously and that this shape minimizes defense costs (Anderson 1978; Getty 1981). Although a directional downstream delivery of prey to drift-feeding salmonids (Noakes and McNicol 1982; Hughes et al. 2003) likely violates the former assumption, their single central-place foraging area is near-circular in shape because fish constantly return to one location from which shorter foraging and aggressive bouts are more frequent and less costly (Grant et al. 1989; Keeley 2000). Hence, stream salmonids confined to a single central-place show that territories in mobile animals may remain close to circular in shape even if food resources are not homogeneously distributed.

Similarly, when salmonid territories are mapped in a multi-central manner, their shape becomes more diverse and thus resembles home ranges of animals observed under more natural conditions where shape may be affected by resource distribution (Ford 1983; Davies and Houston 1984), competitors and landscape (Eason 1992; Eason et al. 1999). For example, the variability in eccentricity reported for multiple central-place areas in our study (range = 1.043-2.784) is similar to that reported by Ford (1983) in an early review of home range shape among mammals and bird (square-root transformed values, range = 1.05-2.53).

In summary, animals exhibit a great variability in territory shape, which is believed to reflect their disposition to maximize individual fitness while interacting with and being constrained by local environment and neighbors (Adams 2001). In this context, stream fish may provide a good example of how territory shape may relate to the delivery and renewal rate of aquatic prey resources. However, a more detailed study is necessary to determine the relative roles of ecological factors such as competition, prey delivery and landscape on the shape of territories in stream salmonids, and other multiple central-place animals.

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**Table 1.** Habitat characteristics for the 10 study sites in Catamaran Brook, New Brunswick.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| site | site dimensions | |  | habitat characteristics, (range) | | | |
|  | length, m | width, m |  | water velocity, ms-1 | water depth, cm | substrate size | n |
| 1 | 10.0 | 5.0 **(4.0 - 5.9)** |  | 0.086 (0 - 0.18) | 32.3 (1 - 59) | 4.5 (1 - 6) | 30 |
| 2 | 9.0 | 5.3 **(4.4 - 6.1)** |  | 0.088 (0 - 0.35) | 22.1 (1 - 47) | 3.9 (1 - 6) | 27 |
| 3 | 8.5 | 8.8 **(8.3 - 9.2)** |  | 0.045 (0 - 0.14) | 34.5 (1 - 76) | 4.8 (2 - 6) | 44 |
| 4 | 10.0 | 4.2 **(3.1 - 5.8)** |  | 0.155 (0 - 0.66) | 23.4 (2 - 52) | 5.0 (3 - 6) | 27 |
| 5 | 10.0 | 5.4 **(4.4 - 6.5)** |  | 0.063 (0 - 0.17) | 33.0 (2 - 66) | 4.4 (1 - 6) | 32 |
| 6 | 9.0 | 4.8 **(4.3 - 5.0)** |  | 0.178 (0 - 0.42) | 18.4 (1 - 43) | 5.1 (4 - 6) | 22 |
| 7 | 6.0 | 4.9 **(4.4 - 5.5)** |  | 0.058 (0 - 0.11) | 47.1 (3 -105) | 4.7 (4 - 6) | 19 |
| 8 | 11.0 | 5.4 **(5.0 - 6.0)** |  | 0.070 (0 - 0.34) | 34.4 (1 - 69) | 4.5 (2 - 6) | 32 |
| 9 | 11.0 | 8.6 **(5.6 - 10.5)** |  | 0.054 (0 - 0.21) | 28.5 (1 - 82) | 4.8 (2 - 6) | 50 |
| 10 | 11.0 | 6.7 **(5.7 – 7.6)** |  | 0.078 (0 - 0.38) | 22.6 (2 - 47) | 4.7 (1 - 6) | 39 |

Site width is an average based on 4-6 transects located at every 2 m along the stream length for each site. Habitat variables were measured across each transect on 18-19 August, 2000. Water current velocity was measured at 40% depth (from the substrate), using a Marsh-McBirney meter (model 201D; Marsh-McBirney Inc., 4539 Metropolitan Ct., Frederick, MD 21704, U.S.A.). Substrate size is based on a modified Wentworth scale from DeGraaf and Bain (1986) [1, < 0.004 mm (plant detritus, clay); 2, 0.004-2.0 mm (silt, sand); 3, 2-16 mm (gravel); 4, 17-64 mm (pebble); 5, 65-256 mm (cobble); 6, > 256 mm (boulder); 7 (bedrock)].

**Figure legends**

**Fig. 1.** Territory shape of a typical young-of-the-year Atlantic salmon in Catamaran brook, New Brunswick, mapped via a (a) single and (b) multiple central-place approach, resulting in areas elongated along the stream width (absolute angle = 21°, eccentricity = 1.306; see Fig. 2) and length (angle = 77°, eccentricity = 1.284), respectively. The solid lines represent the boundaries of the minimum convex polygon, which here includes foraging attempts (black circles), foraging stations (crossed circles) and aggressive acts (stars). The arrow shows the direction of the water flow.

**Fig. 2.** Shape of single (black) and multiple (grey) central-place areas for 50 young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick. Eccentricity (a) indicates to what degree home ranges are elongated (1 = circular), and (b) the absolute value of the angle along which territories are elongated. The angle indicates if the areas are elongated along the stream length (absolute angle = 45-90°; where 90° is the up-downstream direction) or along the stream width (absolute angle = 0-45°, where 0° is perpendicular to the water flow). The shapes corresponding to the extreme x-axes values for eccentricity and angle are depicted in the top corners of the two graphs.



