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| Journal: | *Behavioral Ecology and Sociobiology* |
| Manuscript ID: | BES-10-0066.R1 |
| Manuscript Type: | Original Paper |
| Date Submitted by the Author: | n/a |
| Complete List of Authors: | Steingrímsson, Stefán; Holar University College<br>Grant, James; Concordia University, Department of Biology |
| Keywords: | foraging mode, home range, invertebrate drift, mobility, stream ecology, water current velocity |
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# Determinants of multiple central-place territory use in wild young-of-the-year Atlantic salmon (*Salmo salar*)

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**Abstract** Patterns of space use provide key insights into how animals exploit local resources, and are linked to both the fitness and distribution of individuals. We studied territory size, mobility and foraging behavior of young-of-the-year Atlantic salmon *Salmo salar* in relation to several key environmental factors in Catamaran Brook, New Brunswick, Canada. The 50 study fish were all multiple central-place foragers (i.e. alternated among several sit-and-wait foraging stations) and showed great variability in territory size and the total distance traveled within the territories. Territory size increased with the mean distance traveled between consecutive foraging stations, the number of stations visited and the mean foraging radius. Fish also varied greatly in how much of the total travel distance was associated with foraging at a station (14.8-91.8%) versus switching among stations (4.6-84.3%). As predicted, fish in slow-flowing waters, where drifting prey were scarce, used larger multiple central-place territories than individuals in faster, more productive waters. Interestingly, however, the most mobile fish did not inhabit slow-running waters as predicted, but were found at intermediate (optimal) water current velocities. Hence, our study suggests that among some multiple central-place foragers, increased mobility may not only serve to increase prey encounter rate, but may reflect an attempt to patrol territories in favourable habitats. Further studies are needed to determine the generality and the ultimate benefits of multiple central-place space use among stream-dwelling fish and other animals.

**Keywords** foraging mode, home range, invertebrate drift, mobility, stream ecology, water current velocity

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## Introduction

Animals exhibit great variability in local space-use patterns, which in turn provide important insights into how individuals select, exploit and partition habitats and prey resources (Adams 2001; Helfman 1990; Sutherland 1996). For example, territories vary in size and the degree to which they are defended (Grant 1997), and thus influence food availability (Stamps 1984; Stamps and Eason 1989), the cost of defending an area (Davies and Houston 1984) and local population density (Patterson 1980). Similarly, at local scales, individuals may vary in foraging mode from sit-and-wait foragers, which search for prey from a stationary position, to cruising foragers, which actively search for food (McLaughlin 1989; Pianka 1966; Schoener 1971). In these situations, foraging mobility may affect prey encounter rate (Grant and Noakes 1987) and the cost of exploiting a particular area (De Kerckhove et al. 2006), which together shape habitat use and population distribution (Sutherland 1996). In summary, territoriality, foraging and mobility play a vital role in shaping individual fitness (e.g. growth) and population structure.

Local space-use patterns can be affected by a range of ecological variables (Grant 1997; Helfman 1990). For example, many studies suggest animals occupy smaller and more easily defendable territories when prey is dense and rapidly renewable (Davies and Houston 1984; Grant et al. 1992), the same conditions under which ectothermal animals are expected to adopt a sit-and-wait foraging mode (Helfman 1990; but see Huey and Pianka 1981). In addition, animals are believed to adopt a sit-and-wait foraging mode when prey are mobile or spatially predictable, but cruise for prey when they are sedentary or spatially unpredictable (Helfman 1990; Huey and Pianka 1981). Hence, the literature suggests that territory size and foraging mobility may show a coordinated response to different ecological conditions. However, although cruising foragers are

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often assumed to travel more widely than sit-and-wait foragers (e.g., Huey and Pianka 1981), surprisingly few studies systematically examine how foraging mobility relates to local space-use patterns and territory size (but see e.g., Ford 1983; Katano 1996).

Freshwater fishes and salmonids in particular, are an excellent model system for studying the effects of environmental factors on local space use, because they exhibit great variability in territorial and foraging behavior in the wild (Grant and Noakes 1987; Katano 1996; Nakano et al. 1999). In fast-running waters, where drifting invertebrates provide a spatially predictable, rapidly renewing and abundant prey resource, stream-dwelling salmonids typically sit-and-wait and intercept mobile prey from a centrally-placed foraging station (Grant et al. 1989; Kalleberg 1958). Intuitively, because the space use of these fish is constrained by repeated returns to the same central-place location, they are often viewed as sedentary and as using small territories (but see Steingrímsson and Grant 2008). In slow-running waters and lakes, however, fish may cruise over large areas, as they specialize on sedentary or patchy food, such as benthic or planktonic invertebrates (Biro et al. 1997; Katano 1996; McLaughlin et al. 1992; Minns 1995). Social status can also influence local space use of stream-salmonids. Dominant individuals adopt sit-and-wait foraging as they defend the best feeding positions where fast water flow provides abundant drifting prey, whereas subordinate fish travel widely where less prey are available (Grant and Noakes 1988; Nakano 1995; but see Martin-Smith and Armstrong 2002).

To date, several studies show that salmonid territories tend to be smaller in faster waters where drifting prey is more abundant (Keeley and Grant 1995; McNicol and Noakes 1984; but see Dill et al.1981). Similarly, foraging mode has been demonstrated to vary between species (Ferguson and Noakes 1983; Nakano et al. 1999), between lake and stream populations of the same species (Biro and Ridgway 1995), and between conspecific individuals found in slow- and

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faster-running waters of the same stream (Grant and Noakes 1987; McLaughlin et al. 1992). To date, however, studies on salmonids rarely examine how territory size relates to foraging mode and mobility; in part because estimates of territory size are typically confined to sit-and-wait individuals that forage from a single central-place (see Steingrímsson and Grant 2008). This is especially true for young-of-the-year (YOY) fish, which can be difficult to tag and follow in natural settings (see Bachman 1984; Nakano 1995 for studies on older fish).

In this paper, we adapt general predictions on how space use relates to water current velocity and prey abundance and apply them to YOY Atlantic salmon, which typically sit-and-wait for prey, but can be defined as multiple central-place (MCP) foragers because they rotate among several foraging stations (Steingrímsson and Grant 2008; see Chapman et al. 1989; Covich 1976; McLaughlin and Montgomerie 1989 for other MCP animals). We predict that fish will (*i*) use smaller territories, (*ii*) visit fewer foraging stations, and (*iii*) be less mobile, as current velocity and the abundance of drifting prey increase. Second, with increasing current velocity and drift abundance, fish will (*i*) travel shorter distances on each foraging attempt, (*ii*) forage more frequently, and (*iii*) be less likely to attack benthic prey. Finally, we expect YOY found at the most preferred current velocity (6-24 $cm \cdot s^{-1}$; Girard et al. 2004) to be the most aggressive and grow fastest (Grant and Noakes 1988; but see Martin-Smith and Armstrong 2002).

To test these predictions, we observed the local space use of 50 tagged YOY Atlantic salmon in a natural stream, and measured habitat features of their territories. Below, we first describe the variability in space use found among our study fish, and then examine whether and how territory size relates to foraging behavior and mobility. Finally, we test if, and how space use is associated with water current velocity, prey availability and other key ecological variables.

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## Materials and methods

### Study population, sampling surveys, body size and growth

We studied YOY Atlantic salmon at 10 study sites in Catamaran Brook in New Brunswick in 2000 (see Cunjak et al. 1993 and Steingrímsson and Grant 2003 for details on the stream biota and the location of the study sites, respectively). Initially, 90 fish were captured, tagged and measured for fork length (range: 27.3-40.6 mm) in two snorkeling surveys on 25 June to 4 July, and 12-13 July. Once we finished the space-use observations for all focal fish (see below), we measured all tagged fish found in the study sites in two final snorkeling surveys on 20-23 August and 11-12 September. In general, we tried to tag and observe fish in the complete range of habitats used by YOY salmon in terms of water current velocity and depth. We described the patterns of MCP territory size and defense for the same fish in Steingrímsson and Grant (2008).

Because we did not measure fish on the exact day of their space-use observation, we estimated fork length of each fish on the day of observation by assuming a linear increase in fork length between the capture surveys closest in time; one preceding and the other subsequent to the observation date (Steingrímsson and Grant 2008). Growth rate was measured as (Fork $\text{length}_{\text{final}}$ - Fork $\text{length}_{\text{initial}}$) · (Day of $\text{year}_{\text{final}}$ - Day of $\text{year}_{\text{initial}})^{-1}$ (unit = $\text{mm}\cdot\text{day}^{-1}$). Because most fish were observed between the second (12-13 July) and the third (20-23 August) survey, and because growth rate varied slightly between different time periods, only fish found in both these surveys were used to test if and how growth changed across current velocities.

### Observations of space use

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We observed the space use of 50 tagged individuals via snorkeling from 3 July to 17 August, 2000. Typically, fish were monitored for two 10-min periods in the early afternoon, and another two 10-min periods later that same afternoon, yielding 40-min of data for each fish collected between 1330-1850 h. After identifying the focal fish, we waited at least 5 min before each 10-min period to avoid disturbance. For each territory, we recorded the location of foraging stations, the direction (1-12 o'clock) and the estimated distance (in body lengths) of foraging attempts, the location of aggressive acts, and if the focal fish was chased by an intruder. We estimated various aspects of space use by creating a simple x-y coordinate system for each study site, and mapping each territory using ArcView GIS 3.2 in conjunction with the Animal Movement extension (Hooge and Eichenlaub 2000). Territory size was estimated via the minimum convex polygon method based on all spatial coordinates ($MCP_{100\%}$) (Schoener 1981). More details on the measurement and estimation of space use are reported in Steingrímsson and Grant (2008).

Because of rapid changes in the behavior of the study fish, we could not record every behavioral event for all 50 fish. We thus gave priority to recording the location of all foraging stations visited (because these greatly affect estimates of territory size), and the location of all aggressive acts (because these events are rare); these variables were recorded consistently over the 40-min observation. We estimated the distance and direction of as many foraging attempts as possible during the first 30 minutes, whereas during the last 10-min period we only estimated foraging rate. Finally, we counted switches between foraging sites and estimated the mean and total distance allocated toward switching for fish using only those 10-min periods in which we recorded all switches between stations.

Movement within territories was associated with four activities; (*i*) foraging at a station,

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(*ii*) switching between foraging stations, (*iii*) attacking intruding fish, and (*iv*) fleeing from an intruder. First, the distance traveled while foraging at a station was calculated as the number of foraging attempts × 2 × the mean foraging radius; hence, each foraging bout included a direct return to the same station. Second, we estimated the distance traveled while switching based on the number of switches × the mean distance traveled between consecutive stations. Finally, the distance traveled while chasing and fleeing from an intruder was calculated as the frequency of these events × 2 × the mean aggressive radius. Because focal fish rarely fled from an intruder and because we did not estimate the mean fleeing distance, we assumed it equaled the mean aggressive radius.

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## Habitat and food abundance

For each fish, current velocity and water column depth were measured at, and averaged across the five stations where most foraging attempts were recorded. If a fish visited fewer than five stations, we measured the habitat at all stations visited. We measured current velocity at 40% of the total depth (measured from the bottom) with a Marsh-McBirney meter (Model 201D; Marsh-McBirney, 4539 Metropolitan Ct., Frederick, MD 21704, U.S.A.). Water temperature was measured before and after the 20 min of observation in the early and late afternoon, respectively.

Because of time constraints, we did not sample invertebrate drift at each of the 50 territories, but predicted drift abundance at each territory using a multiple regression model established for 30 drift samples, collected in the 10 study sites on three occasions (22-23 July, 8-9 August, and 4-5 September) over the season. We sampled drift by placing a 1-m long drift net (mesh size = 300 µm) with a metal frame opening (15.2 × 23 cm), haphazardly at the initial location of one of the 90 tagged YOY salmon; no location was sampled more than once. We varied the sampling time depending on how fast drift accumulated in the net (mean = 49 min, range = 15-120 min). For each sample, we recorded the time and day of sampling, water temperature, current velocity (measured in the center of the net opening) and water depth at the sampling location. Samples were only collected during daylight hours (from1325h to 1845h).

Each drift sample was preserved in 10% buffered formalin and processed at Concordia University. First, we separated intact organisms from other drifting material and counted all organisms within the size range of edible prey (>99% of the total number) for YOY Atlantic salmon (Keeley and Grant 1997). Second, we obtained the dry weight of each sample by placing it in an oven at 50ºC for 72 h (Merritt and Cummins 1978), then moving it to a desiccator, and weighing it once on three consecutive days until the weight was stable (± 0.0001 g). The number and dry weight of drifting prey were prorated to the area of the drift net frame (if not completely submerged) and to a fixed time of 20 minutes. Because the numbers and dry weights of drift samples were highly correlated [linear regression: $\log_{10}$ drift dry weight ($\mathrm{mg \cdot 20min^{-1}}$) = -1.710 + 1.032 $\log_{10}$ drift number ($\mathrm{no. \cdot 20min^{-1}}$), $r^2 = 0.881$, $n = 30$, $p < 0.001$], we only report numbers hereafter. Finally, we established a multiple regression model based on the sampling date and measured habitat features to predict the invertebrate drift rate at the 50 territories. Overall, the number of prey increased with current velocity, but decreased as the summer progressed [multiple regression: $\log_{10}$ invertebrate drift (no. organisms·area of drift net opening$^{-1}$·20min$^{-1}$) = 4.431 + 1.345 $\log_{10}$ current velocity ($\mathrm{ms^{-1}}$) - 0.009 day of year, $r^2 = 0.918$, $n = 30$, $p < 0.001$]. Neither water temperature (partial $p = 0.231$), water depth (partial $p = 0.727$), nor time of day (partial $p = 0.300$) added significantly to this model. Hence, we predicted the drift rate at each territory based on the mean current velocity at the territory and the Julian date of the observation.

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### Statistical analysis

To facilitate the analysis, we applied a few general rules. First, because drift rate was derived from, and strongly related to current velocity (see above), and because space use changed in an identical manner in response to both variables, we only report on current velocity as a predictor hereafter. Second, because we did not always expect current velocity to associate with space use in a linear manner, we tested for it´s effect both via a simple linear regression, and by adding a quadratic component to the model; the best model (with the lowest $AIC_c$ value) was selected using the Akaike´s information criteria (Motulsky and Christopoulos 2004). Third, because water depth, water temperature and fork length may also influence space use, we tested for their effect along with current velocity via multiple regression. Overall, these additional variables had minor effects on the *p*-value obtained for current velocity, and never altered whether current velocity was better associated with space use in a linear or curvilinear manner. Because we do not put forward a priori hypotheses on the effect of water depth, water temperature and fork length on space use in stream-salmonids, we compared partial *p*-values for these variables to a Bonferroni corrected significance level ($\alpha$-value) of 0.005 (unplanned tests for eleven space use variables for each correlate = 0.05/11). Where necessary, variables were $\log_{10}$- or square-root transformed.

## Results

### Variability in territory use

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The 50 YOY Atlantic salmon monitored in this study (mean fork length = 4.30 cm, range = 2.99-5.24) exhibited great variability in local space-use patterns. Over the 40-min observation, focal fish used territories ($MCP_{100\%}$), which ranged from 0.268 $m^2$ to 4.469 $m^2$ (mean, back-transformed from $\log_{10}$ = 0.932 $m^2$) (Fig. 1abc), visited as few as 3, and as many as 26 foraging stations (median = 12.5 stations) (Fig. 2 in Steingrímsson and Grant 2008), and traveled within their territory, a total distance ranging from 15.7 to 95.0 m (median = 39.3 m) (Fig. 1def).

Further variability is revealed when the distance traveled by each fish is classified into different behavioral activities (Table 1; Fig. 2). The distance traveled during foraging attempts varied 6.0 fold, from 8.2 m to 49.6 m over 40 minutes. More impressively, the distance traveled while switching between stations ranged 33.7 fold from 2.4 m to 79.2 m (Table 1). In terms of frequency, YOY Atlantic salmon foraged, on average, 0.85 to 48 times at each station before switching, which occurred as rarely as once every 10 minutes, and as often as once every 12.9 seconds (Table 1). Together, foraging (mean = 48.9%, range = 14.8-91.4%) and switching stations (mean = 47.8%, range = 4.6-84.3%), accounted for 96.6% of the total distance traveled, whereas only limited distances were allocated towards chasing (mean = 3.0%, range = 0-20.3%) or fleeing from (mean = 0.4%, range = 0-1.8%) intruders (Fig. 2).

Finally, the focal fish directed most of their foraging attempts toward prey drifting in the water column (mean = 91.2%: range = 75.0-99.1%), and only few attempts towards the benthos (mean = 7.5%; range = 0.0-25.0%) or the water surface (mean = 1.3%; range = 0.0-12.1%).

## Behavioral determinants of territory size

The size of the multiple central-place territories of YOY Atlantic salmon increased with the

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mean distance traveled between consecutive foraging stations ($p < 0.001$), the number of stations visited within the territory ($p < 0.001$) and the mean foraging radius around these stations ($p = 0.019$) (Table 2). Neither foraging rate nor the rate at which individuals switched stations was related to territory size (partial $p > 0.05$). Finally, in two univariate analyses, territory size increased with the distance traveled while switching stations (Pearson's $r = 0.308$, $n = 50$, $p = 0.030$; both variables $\log_{10}$ transformed) but not with the total distance traveled (Pearson's $r = 0.206$, $n = 50$, $p = 0.151$; both variables $\log_{10}$ transformed). Hence, whether territory size is significantly associated with fish mobility depends on our measure of mobility.

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Ecological determinants of space use and growth

The 50 study fish were observed over a wide range of current velocities (mean = $0.159\ \mathrm{m \cdot s^{-1}}$, range = 0.012-0.362) and water depths (mean = 34.4 cm, range = 14.6-78.7), but at a narrow range in water temperatures (mean = 19.8 ºC, range = 17.5-22.5). Predicted drift rate at the 50 territories varied 99.7 fold from 0.9 to 89.7 invertebrates (mean = 30.0) drifting through an area equal to the drift net frame ($15.2 \times 23\ \mathrm{cm} = 349.6\ \mathrm{cm}^2$) in 20 minutes.

Water current velocity was related to several components of space use in YOY Atlantic salmon, but not always as expected (Fig. 3). First, as predicted, territory size decreased with increasing current velocity ($\log_{10}$ territory size $\mathrm{m}^2 = 0.301 - 0.886$ current velocity$^{1/2}$ $\mathrm{m \cdot s^{-1}}$, $r^2 = 0.119$, $n = 50$, $p = 0.014$) (Fig. 3a). Second, contrary to predictions, the number of stations visited within a territory did not increase as current velocity decreased (no. of foraging stations = 9.516 + 8.573 current velocity$^{1/2}$ $\mathrm{m \cdot s^{-1}}$, $r^2 = 0.034$, $n = 50$, $p = 0.202$) (Fig. 3b). Third, the total distance traveled within territories was best described by a curvilinear relationship, where fish traveled most at intermediate water current velocities ($\log_{10}$ total distance traveled m = 0.547 + 6.010 current velocity$^{1/2}$ - 7.907 current velocity m·s$^{-1}$, $r^2 = 0.298$, $n = 50$, $p < 0.001$) (Fig 3c); this contradicts the prediction that mobility should be greater in slow waters where drifting prey is scarce. Overall, the results above were supported when the effects of current velocity on space use were examined via multiple regression analysis. In no case did the inclusion of water depth, water temperature and fork length, affect whether current velocity was significantly associated with a given space-use component, or whether this relationship was better described in a linear or curvilinear manner. Water depth was the only other correlate that was related to the components of space use; fish in deep waters used significantly larger territories than those found in shallow waters (partial $p = 0.005$). Interestingly, the total distance traveled was not related to the size of the focal fish (partial $p = 0.315$).

The influence of current velocity on space use was explored further by examining the foraging and switching behavior of the study fish (Fig. 4). Overall, these two components of behavior showed a similar response to current velocity, although these results were not always predicted from MCP theory. First, as expected from the increased availability of drifting prey and increased swimming costs, the mean foraging radius and the mean distance traveled between consecutive stations decreased as current velocity increased ($\log_{10}$ mean foraging radius cm = 0.828 - 0.306 current velocity$^{1/2}$ m·s$^{-1}$, $r^2 = 0.102$, $n = 50$, $p = 0.023$; $\log_{10}$ mean switching distance cm = 1.916 - 0.804 current velocity$^{1/2}$ m·s$^{-1}$, $r^2 = 0.370$, $n = 50$, $p < 0.001$) (Fig. 4ad). Second, as current velocity increased, both the foraging rate and the rate at which fish switched between stations, increased initially and then leveled off and decreased slightly ($\log_{10}$ foraging attempts no.·10 min$^{-1}$ = 0.809 + 4.355 current velocity$^{1/2}$ - 5.359 current velocity m·s$^{-1}$, $r^2$ = 0.348, $n = 50$, $p < 0.001$; $\log_{10}$ station switches no.·10 min$^{-1}$ = -0.409 + 6.980 current velocity$^{1/2}$ -

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7.966 current velocity m·s$^{-1}$, $r^2 = 0.174$, $n = 50$, $p = 0.011$) (Fig. 4be). These findings were unexpected for the switching frequency because drift-feeding fish are predicted to be less mobile in fast waters where prey is abundant. Third, the distance traveled during foraging attempts was greatest at intermediate current velocities ($\log_{10}$ distance traveled foraging m·40 min$^{-1}$ = 0.342 + 5.215 current velocity$^{1/2}$ - 6.928 current velocity m·s$^{-1}$, $r^2 = 0.262$, $n = 50$, $p < 0.001$) (Fig. 4c). Similarly, the total distance moved between stations fit better to current velocity in a curvilinear manner, although not significantly ($\log_{10}$ distance traveled switching m·40 min$^{-1}$ = 0.251 + 5.323 current velocity$^{1/2}$ - 6.752 current velocity m·s$^{-1}$, $r^2 = 0.078$, $n = 50$, $p = 0.147$) (Fig. 4f). A multivariate approach did not alter how foraging and switching behavior was associated with current velocity and only revealed one significant association with another potential predictor; i.e., larger fish attacked prey at a greater distance (partial $p < 0.001$). Finally, fish did not switch to benthos in slow running waters as no association, neither linear ($p = 0.780$) nor curvilinear ($p = 0.293$), was detected between the percent of benthic foraging and current velocity.

Our results were equivocal regarding the hypothesis that more aggressive individuals, with greater growth potential, inhabit and defend territories in faster waters where drifting prey is more abundant. Based on few aggressive acts per fish, aggression toward intruders was more common at intermediate current velocities than in slow-running waters, but decreased again as current velocity increased further ($\log_{10}$ chase frequency no.+1·40min$^{-1}$ = -0.390 + 5.843 current velocity$^{1/2}$ - 8.189 current velocity m·s$^{-1}$, $r^2 = 0.128$, $n = 50$, $p = 0.041$) (Fig. 5a). Interestingly, fish inhabiting fast water grew more slowly than those found in slow water (growth rate mm·day$^{-1}$ = 0.448 - 0.184 current velocity$^{1/2}$ m·s$^{-1}$, $r^2 = 0.191$, n = 38, $p = 0.006$) (Fig. 5b). The respective multivariate analyses for aggression and growth found no significant effect of water temperature, water depth and fork length (partial $p > 0.3$ in all cases).

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## Discussion

### Patterns of territory use

Many stream fish adopt alternative foraging tactics as they either actively cruise for benthic or patchy prey items (movers), or are relatively sedentary and ambush drifting prey via sit-and-wait foraging tactics (stayers) (Grant and Noakes 1987; Katano 1996; McLaughlin et al. 1999). In this study, however, YOY Atlantic salmon were best described as multiple central-place foragers, which sit-and-wait for prey, rotate among several foraging stations, but rarely attack their prey while moving (Steingrímsson and Grant 2008). Importantly, although our study fish do not appear to be able to switch from sit-and-wait to cruising foraging, they exhibit considerable and often unexpected variability in their territory use patterns.

First, YOY Atlantic salmon in Catamaran Brook use MCP territories that are very large compared to typical single central-place territories defended by other YOY stream-dwelling salmonids, and are also highly variable in size (0.268 - 4.469 $m^2$) (see Steingrímsson and Grant 2008). Second, our study shows that stream salmonids can vary greatly in the number of foraging stations visited within their territories (3-26 stations) (see Nakano 1995). Finally, in spite of being predominately sit-and-wait foragers, the study fish were very mobile, traveling a total distance of 15.7 to 95.0 m (median = 39.3 m = 914 body lengths·40 $min^{-1}$), of which 47.8% (4.6-84.3%) was due to switching between foraging stations. In comparison, based on the mean radii and the frequency of aggressive acts and foraging attempts initiated by a territorial stream-fish from one foraging station (*sensu* Materials and methods), we estimate that YOY brook charr

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(Grant et al. 1989) and YOY rainbow trout (Keeley 2000) traveled on average 501 and 722 body lengths in 40 minutes, respectively. Furthermore, YOY brook charr in two lakes, most of which were cruising foragers, traveled a mean distance of 890 and 1187 body lengths in 40 minutes, while searching for prey (estimated from Biro et al. 1997). Hence, MCP drift-feeding fish are more mobile than single central-place foragers and may even travel similar distances to cruising fish in lakes. Unfortunately, most studies on stream-salmonids focus on the energetic basis of drift-feeding from a single focal point (e.g., Enders et al. 2003; Hughes et al. 2003), and the costs and benefits associated with switching among several stations have received limited attention.

Ecological determinants of territory use

Because the use of multiple foraging stations among salmonids has received limited attention (but see e.g. Nakano 1995), this study yields several novel findings on how their space-use patterns relate to ecological conditions. First, in harmony with most single central-place studies (Keeley 2000; McNicol and Noakes 1984; but see Dill et al.1981), MCP territories decreased in size as current velocity and prey drift rate increased. In MCP territories, this decrease in size is associated with a decrease in the distance traveled between consecutive foraging stations and a shorter foraging radius in faster, more productive waters (Keeley 2000). Interestingly, although fish that visit more foraging stations have larger territories, there is no evidence that they visit fewer stations in faster water where drifting prey is abundant. In contrast, Nakano (1995) found that among masu salmon (*Oncorhynchus masou*) in pools, dominant fish used one or few stations where prey were abundant, while younger subordinate fish switched among several low-quality stations. This discrepancy may be due to Nakano´s (1995) fish forming space-related dominance

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hierarchies across year-classes in a habitat where the best feeding sites (and food resources) are relatively predictable and clumped in space. YOY Atlantic salmon, however, are typically found in a territorial mosaic (Kalleberg 1956), where the input and distribution of drifting prey may play a less obvious role in shaping social status and space use.

Unexpectedly, and irrespective of how mobility was measured, YOY Atlantic salmon were not most mobile in slow-running waters where drifting prey is scarce. Instead, the most mobile fish were found at intermediate current velocities; this trend emerged when we examined (*i*) the total distance traveled, (*ii*) the rate at which YOY salmon switched between stations (rate of movement, *sensu* Ford 1983), but not significantly so for (*iii*) the distance traveled while switching. These findings, coupled with the fact that fish in slow waters did not forage more on the benthos, suggest that mobility in YOY salmon was not primarily associated with seeking out alternative prey where drifting invertebrates were rare (but see Armstrong et al. 1999). In this study, however, benthic foraging was greater (7.5%) than in an earlier study on Atlantic salmon in Catamaran Brook (< 1%), where fish used fewer stations (Keeley and Grant 1995). Hence, the link between benthic foraging and multiple central-place space use may warrant further study.

Why YOY Atlantic salmon travel more between stations at intermediate water current velocities remains unclear, but habitat selection and territorial behavior may play a role. First, although YOY salmon in Catamaran Brook use a wide range of habitats, they show consistent preferences for current velocities of 6-24 $cm \cdot s^{-1}$ (Girard et al. 2004; see also Morantz et al. 1987), which match the intermediate current velocities used by the most mobile fish in this study (Fig. 4ef). Second, among drift-feeding fish, preferred current velocities generally represent higher quality habitats, e.g. in terms of net energetic gain (Hill and Grossman 1993). Third, Johnsson et al. (2000) showed that brown trout in preferred habitats defend their territories more intensively

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than those in low quality habitat; a similar trend emerged in this study as aggression is slightly more frequent at intermediate current velocities. Consequently, because our fish rarely attack intruders across their large MCP areas (Steingrímsson and Grant 2008), rapid switches among stations at optimal water currents, may indicate more patrolling of territories. Although patrolling increases travel costs of territory holders, it may also reduce the traffic of intruders immediately upstream of many foraging stations, where a significant portion of the drifting prey may emerge from the benthos (Elliott 2002; McIntosh and Townsend 1998; see Steingrímsson and Grant 2008). Importantly, our data suggest that YOY Atlantic salmon occupying preferred current velocities do not grow faster than fish in other habitats (see also Girard et al. 2004). Obviously, the above ideas need to be verified in future studies.

Ecological variables other than current velocity and invertebrate drift had limited effects on the space use of YOY salmon. Not surprisingly, foraging radius was positively related to fork length (see e.g. Elliott 1990; Grant et al. 1989), in part because larger fish are better swimmers and may see farther (Dunbrack and Dill 1983). The study fish also used larger territories in deeper water, perhaps because they tend to attack prey at a greater distance, and travel longer distances between consecutive stations. To date, however, any explanations on the ultimate causes for this trend would remain speculative.

## Implications for salmonids and MCP foragers

Multiple central-place behavior of YOY Atlantic salmon adds a new dimension to the existing literature on how space use relates to environmental conditions, and how these factors combine to shape individual fitness and population dynamics of stream-dwelling salmonids. First, large

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MCP territories, although not defended as efficiently as smaller territories, suggest that territorial behavior plays an important role during competition for food and space, even at low population densities where habitats appear not to be highly saturated (see discussion in Steingrímsson and Grant 2008). Second, this study shows that salmonid species differ in the foraging mode they typically adopt, and the flexibility they exhibit in response to different ecological conditions. For example, brook charr (*Salvelinus fontinalis*) (Biro and Ridgway 1995; Grant and Noakes 1987; McLaughlin et al. 1999), Dolly Varden charr (*Salvelinus malma*) (Fausch et al. 1997) and coho salmon (*Oncorhynchus kisutch*) (Puckett and Dill 1985) can adopt both a sit-and-wait and an active foraging mode, where the latter is associated with utilizing benthic (Fausch et al. 1997) or pelagic prey (McLaughlin et al 1999) in slow waters where drifting prey is rare. Other species, such as white spotted charr (*Salvelinus leucomaenis*) (Fausch et al. 1997) and Atlantic salmon (Nislow et al. 1998; but see this study), may respond to reduced drift via increased benthic feeding, but without the corresponding switch to active search (but see Armstrong et al. 1999). Although this study indicates that YOY Atlantic salmon are mostly sit-and-wait foragers, it demonstrates that "less flexible" salmonids, may still exhibit great variability in their space-use patterns, e.g. in the number of foraging stations visited and mobility. Finally, this study suggests that YOY salmon may grow faster, or as fast (Girard et al. 2004) in slow waters where drift-feeding is presumably less beneficial, without switching to alternative prey such as benthos.

To date, multiple central-place foraging has been primarily viewed as a foraging tactic used among mammals and birds to increase encounter rate with a depletable food supply while minimizing travel costs (Chapman et al. 1989; McLaughlin and Montgomerie 1989). This study, however, differs in two important ways from earlier MCP studies, because YOY Atlantic salmon (*i*) defend territories and (*ii*) feed on drifting prey, often viewed as a rapidly-renewing resource

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(Sutherland 1996). Hence, this study extends MCP theory to situations where foraging from multiple sites does not obviously increase encounter rate or decrease travel costs, and may rather be related to how intensively home ranges are patrolled and defended (*sensu* Mitani and Rodman 1979; Paton and Carpenter 1984). The generality and the ultimate causes of multiple central-place foraging among stream-dwelling fish and other animals warrant further study.

**Acknowledgements** We thank Cindy Breau for her help in collecting the data, Rick Cunjak, Peter Hardie, Danielle Caisse and coworkers for the logistical support at Catamaran Brook, and Grant E. Brown, Edward J. Maly, and Donald L. Kramer for comments on an earlier version of the paper. This study was financed by a Concordia University Graduate Fellowship, a Concordia University International Tuition Fee Remission Award and a Garnet Strong Scholarship awarded to S.Ó.S., and a Discovery Grant issued to J.W.A.G. from the Natural Sciences and Engineering Research Council of Canada. When finishing the manuscript, S.Ó.S. was employed by Hólar University College. Our research plan was approved by the Concordia University Animal Research Ethics Committee and conforms to the policies of the Canadian Council on Animal Care. This paper is contribution no. 104 of the Catamaran Brook Habitat Research Project.

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**Table 1** Variability in space use associated with foraging from a station, switching between foraging stations, and chasing intruding fish, by 50 young-of-the-year Atlantic salmon in Catamaran Brook

| Variable | Mean | Median | Range | CV |
|---|---|---|---|---|
| Distance traveled foraging (m·40min$^{-1}$) | 19.4 | 15.6 | 8.2-49.6 | 0.507 |
| - Foraging rate (no. attempts·10min$^{-1}$) | 44.9 | 42.3 | 19.0-93.0 | 0.349 |
| - Mean foraging radius (cm) | 5.3 | 4.9 | 3.6-12.2 | 0.285 |
| Distance traveled switching (m·40min$^{-1}$) | 23.5 | 16.3 | 2.4-79.2 | 0.852 |
| - Switching frequency (no.·10min$^{-1}$) | 14.4 | 9.7 | 1.0-46.5 | 0.805 |
| - Mean switching distance (cm) | 43.0 | 41.0 | 22.3-117.0 | 0.382 |
| Distance traveled during chases (m·40min$^{-1}$) | 1.3 | 1.0 | 0.0-6.1 | 1.089 |
| - Aggressive frequency (chases·40min$^{-1}$) | 3.4 | 3.0 | 0-11 | 0.886 |
| - Mean aggressive radius | 15.9 | 15.2 | 1.9-31.8 | 0.409 |

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**Table 2** Multiple regression model[a] describing the behavioral correlates of $\log_{10}$ territory size ($m^2$) in young-of-the-year Atlantic salmon using multiple foraging stations in Catamaran Brook

| Correlate | Slope | $r^2$ | *p*-value |
|---|---|---|---|
| $\log_{10}$ mean switching distance (cm) | 1.2407 | 0.622 | < 0.001 |
| Stations visited (no.·40 $\text{min}^{-1}$) | 0.0273 | +0.171 | < 0.001 |
| $\log_{10}$ mean foraging radius (cm) | 0.5225 | +0.013 | 0.019 |
| Total number of observations (n) | -0.0007 | +0.016 | 0.047 |
| Full model | -- | 0.822 | <0.001 |

[a] The model was selected using the Akaike´s information criteria; $\log_{10}$ foraging attempts (no.·10 $\text{min}^{-1}$) and $\log_{10}$ station switches (no.·10 $\text{min}^{-1}$) were removed from the model.

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## Figure legends

**Fig. 1** Variability in the space-use patterns of YOY Atlantic salmon in Catamaran Brook. The 100% minimum convex polygon (wide solid line) encircles the location of all aggressive acts and foraging attempts (solid circle), the foraging stations visited (crossed circle), and the travel pattern (thin solid line) of selected individuals. The left column depicts (a) the smallest and (b) the largest territory, and (c) the frequency distribution of territory sizes. The right column depicts the fish that traveled (d) least and (e) most, and (f) the frequency of the total distances traveled in 40 minutes within the 50 territories

**Fig. 2** Individual variability in the distance traveled within the territories of 50 YOY Atlantic salmon in Catamaran Brook. Each column shows one fish (1-50, in the order of observation), and indicates the percentage of the total distance traveled in 40 minutes, allocated toward switching between stations (grey), foraging attempts (empty), aggression toward intruding fish (hatched), and fleeing from intruders (dotted)

**Fig. 3** The effect of water current velocity on (a) the territory size, (b) the number of foraging stations, and (c) the total distance traveled within territories of 50 YOY Atlantic salmon in Catamaran Brook. The equations best describing these relationships are represented either by a solid (significant) or dashed line (not significant). For visual clarity, transformed values on both axes were replaced with the original, back-transformed values. All dependent variables were estimated over 40 minutes

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**Fig. 4** The influence of current velocity on foraging behavior (a, b, c) and switching between foraging stations (d, e, f) of 50 YOY Atlantic salmon in Catamaran Brook. The equations best describing these relationships are represented by a solid (significant) or dashed line (not significant).

**Fig. 5** The association between current velocity and (a) the number of aggressive acts directed toward intruding fish and (b) the growth rate of YOY Atlantic salmon in Catamaran Brook. The solid lines represent the best fit to the data. Growth rate is measured between 12-13 July and 20-23 August, 2000, and is only reported for fish caught in both surveys

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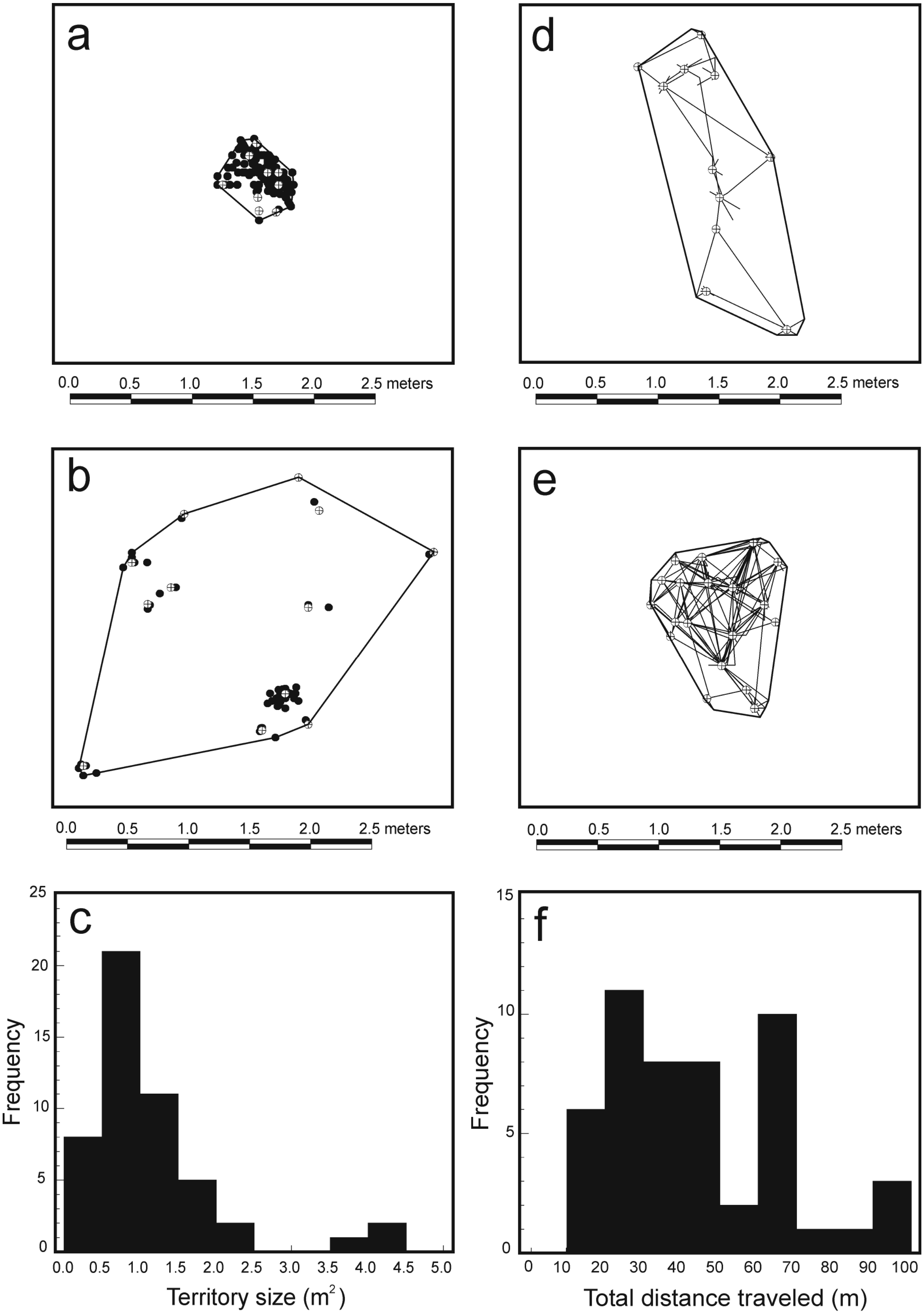
a
0.0 0.5 1.0 1.5 2.0 2.5 meters
d
0.0 0.5 1.0 1.5 2.0 2.5 meters
b
0.0 0.5 1.0 1.5 2.0 2.5 meters
e
0.0 0.5 1.0 1.5 2.0 2.5 meters
c
Frequency
0 5 10 15 20 25
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0 4.5 5.0
Territory size (m²)
f
Frequency
0 5 10 15
0 10 20 30 40 50 60 70 80 90 100
Total distance traveled (m)

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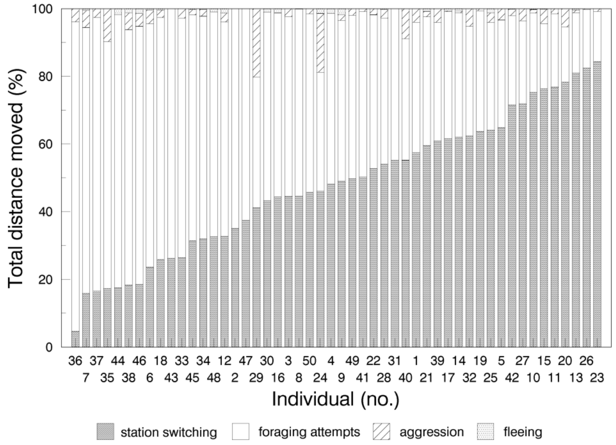
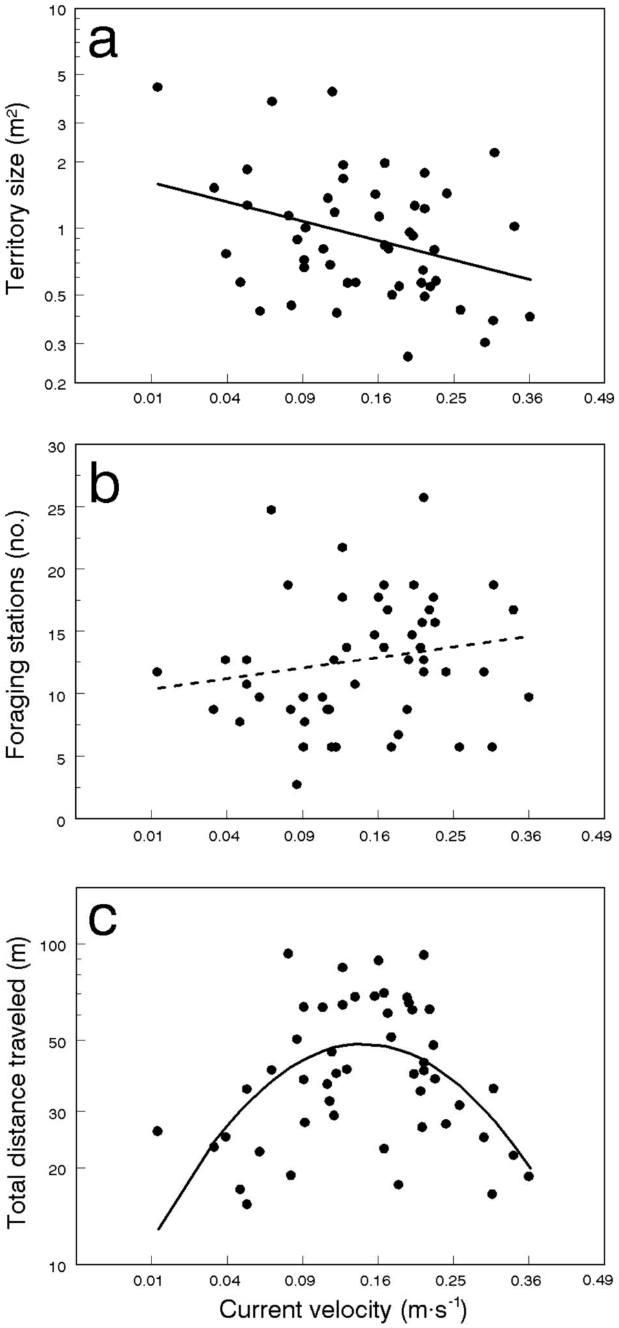
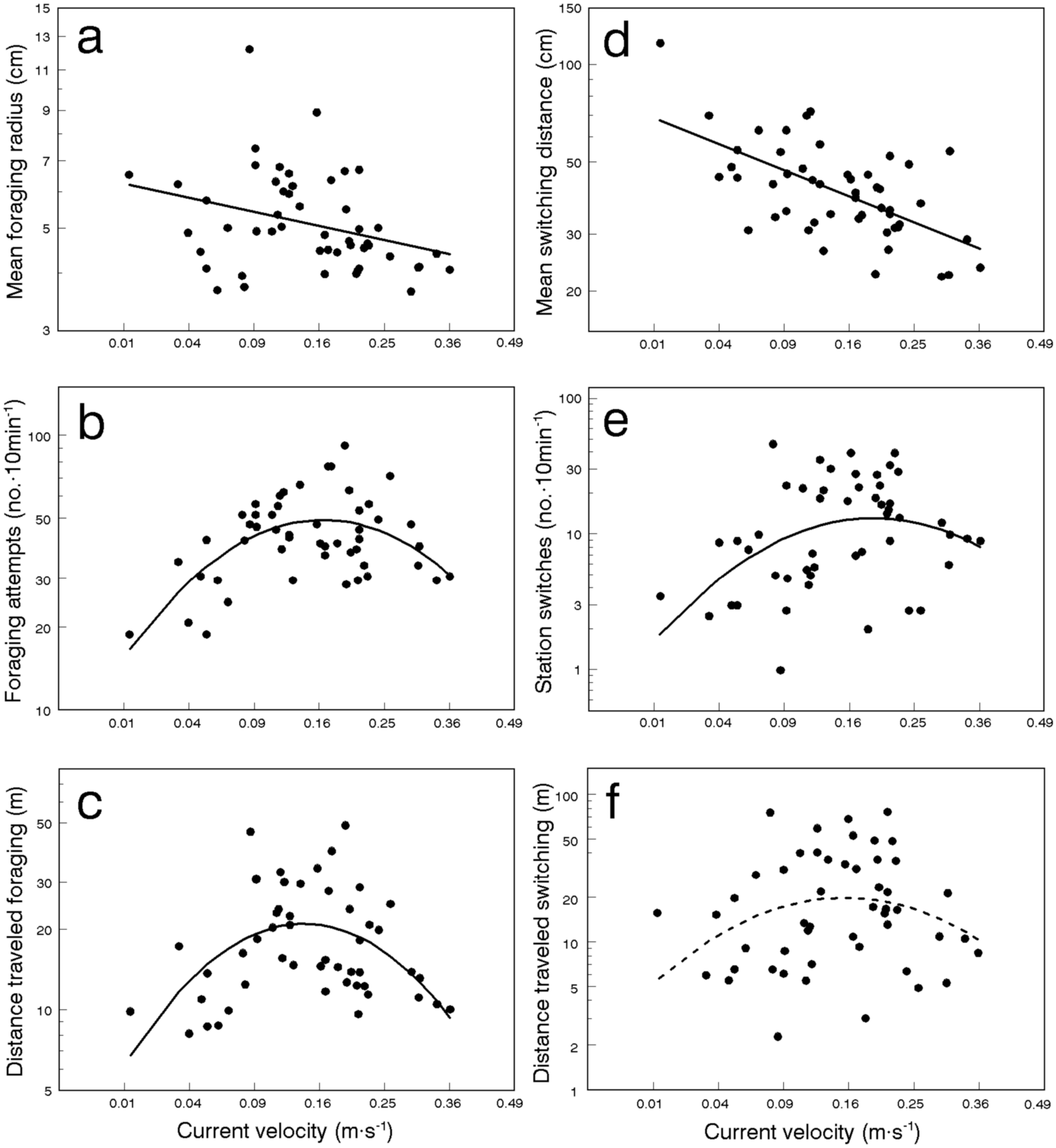
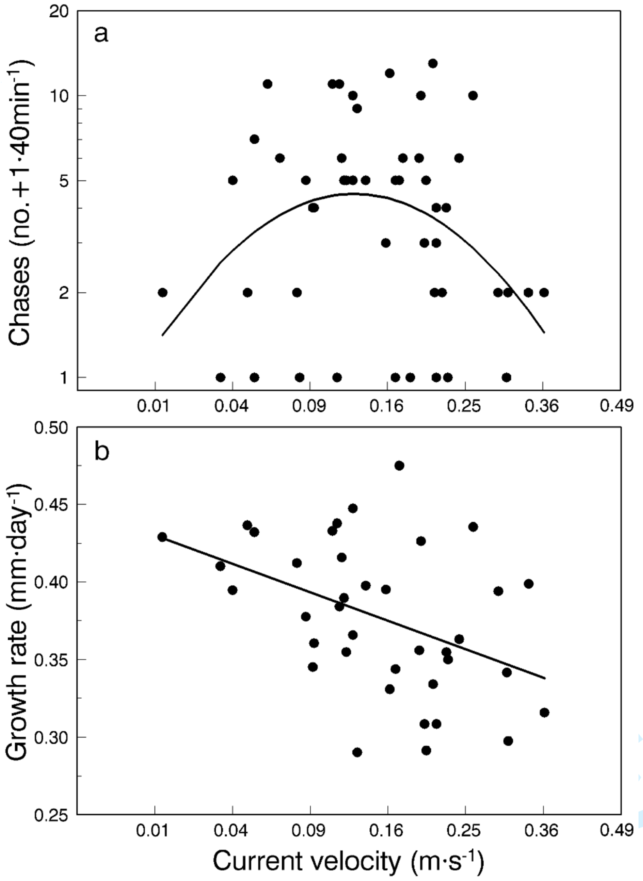



a
Territory size (m²)
10
5
3
2
1
0.5
0.3
0.2
b
Foraging stations (no.)
30
25
20
15
10
5
0
c
Total distance traveled (m)
100
50
30
20
10
0.01
0.04
0.09
0.16
0.25
0.36
0.49
Current velocity (m·s-1)


a
Mean foraging radius (cm)
15
13
11
9
7
5
3
d
Mean switching distance (cm)
150
100
50
30
20
b
Foraging attempts (no.·10min$^{-1}$)
100
50
30
20
10
e
Station switches (no.·10min$^{-1}$)
100
30
10
3
1
c
Distance traveled foraging (m)
50
30
20
10
5
f
Distance traveled switching (m)
100
50
20
10
5
2
1
0.01
0.04
0.09
0.16
0.25
0.36
0.49
Current velocity (m·s$^{-1}$)
Current velocity (m·s$^{-1}$)


a
Chases (no. + 1·40min-1)
20
10
5
2
1
0.01
0.04
0.09
0.16
0.25
0.36
0.49
b
Growth rate (mm·day-1)
0.50
0.45
0.40
0.35
0.30
0.25
0.01
0.04
0.09
0.16
0.25
0.36
0.49
Current velocity (m·s-1)