Journal of Fish Biology (2008) **73,** 2361–2370
doi:10.1111/j.1095-8649.2008.02084.x, available online at http://www.blackwell-synergy.com

No evidence of kin bias in dispersion of young-of-the-year Atlantic salmon *Salmo salar* L. in a natural stream

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(Received 17 April 2008, Accepted 18 August 2008)

Ninety-one young-of-the-year Atlantic salmon *Salmo salar* were captured using a non-invasive snorkelling technique in a 38 m section of Catamaran Brook, New Brunswick, Canada, to test whether related fish settle closer to one another than unrelated fish. A maximum likelihood estimate of parentage relationships assessed by genotyping eight microsatellite loci revealed five half-sibling families in the sample of fish. Related juvenile *S. salar* were not found closer to one another than unrelated fish in three analyses at two spatial scales: a comparison of the relatedness of focal fish to their nearest neighbour and to their four nearest neighbours, and a correlation of the pair-wise relatedness and distance matrices for all fish in the sample. The lack of a kin-biased dispersion pattern may be related to the lower density of fish or the scarcity of full-siblings at the study site compared to laboratory conditions.

Key words: dispersion; juvenile Atlantic salmon; kinship; microsatellites; relatedness.

INTRODUCTION

Kin-biased behaviour can have important population-level effects in territorial animals (Matthiopoulos *et al.*, 2002; Mougeot *et al.*, 2003). The adaptive value of recognizing kin is presumably related to an increase in the inclusive fitness of individuals who bias their behaviour either towards or away from kin compared to unrelated individuals (Hamilton, 1964). In a laboratory setting, juvenile salmonids, which have a remarkable ability to distinguish kin from non-kin using olfactory cues, typically prefer water scented by siblings to water scented by unrelated conspecifics (Brown & Brown, 1996; Olsén, 1999). Compared to

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unrelated groups, groups of related salmonids engage in less frequent aggression (Griffiths & Armstrong, 2000), defend smaller or more overlapping territories (Griffiths & Armstrong, 2002), exhibit higher rates of foraging by subordinate individuals (Griffiths & Armstrong, 2002), gain more mass and exhibit less variability in growth rate (Brown & Brown, 1996; Olsén, 1999).

In the wild, full-sibling and half-sibling families begin life in close proximity as they emerge from gravel nests (Hansen *et al.*, 1997). In contrast to laboratory observations, however, evidence that related individuals settle close to one another as they establish territories, a probable prerequisite for kin-biased behaviour in the wild is equivocal. Aggregated distributions of genetically similar individuals have been reported by Mjølnerød *et al.* (1999) and in one of two streams by Carlsson *et al.* (2004), but others have found either no effect of kinship on dispersion patterns (Fontaine & Dodson, 1999) or that kin may even avoid one another (Carlsson & Carlsson, 2002). The equivocal results from field studies may be related to the use of electrofishing as a method for detecting the spatial locations of individuals, although Fontaine & Dodson (1999) did attempt to sample fish in a localized manner. In the habitats frequented by young-of-the-year (YOY) salmonids, characterized by slow water velocities and small substratum sizes (Armstrong *et al.*, 2003), electrofishing can induce a fright bias, in which fishes are displaced from their natural location during capture (Heggenes *et al.*, 1990). Such a bias could disrupt the fine-scale localization of fishes and potentially obscure aggregations of kin at a local scale. In addition, juvenile salmonids in some populations occupy overlapping home ranges with a fluid spatial arrangement of foraging sites (Armstrong *et al.*, 1999). Hence, the lack of detection of a kin-biased dispersion pattern does not necessarily negate the potential for kin selection (Griffiths & Armstrong, 2002).

The present study tested the hypothesis that related YOY Atlantic salmon *Salmo salar* L. in the wild settle closer to one another than unrelated individuals, while addressing two of the potential limitations of previous field studies. First, the locations of *S. salar* were mapped *via* snorkelling, a method that produces little or no fright bias (Heggenes *et al.*, 1990). Second, YOY *S. salar* in Catamaran Brook are known to move relatively little after establishing a home range (Steingrímsson & Grant, 2003; Breau *et al.*, 2007), making it an ideal site for studying dispersion patterns in relationship to kinship.

MATERIALS AND METHODS

FIELD SAMPLING

A wild *S. salar* population was studied in Catamaran Brook (46°52′45″ N; 66°06′00″ W), New Brunswick, a third order tributary of the Little Southwest Miramichi River. From 15 October to 22 November 2003, 97 anadromous adults (31 females and 66 males) were caught during the upstream spawning migration at a counting fence and fish trap located 216 m upstream from the mouth of the brook. To identify individual fish, a Floy tag was attached to the dorsal fin of each adult, and a small piece of caudal fin was clipped and preserved in 95% ethanol for genetic analyses, before the fish were released on the upstream side of the trap. Because of high water levels, the fence was temporarily removed from 27 October to 3 November 2003, which allowed untagged adults to move into the brook. Untagged and previously tagged adults were subsequently caught, sampled and

released, while migrating downstream out of the brook. Using the Petersen method (Seber, 1973), a total of 172 anadromous adults (95% CI = 126·6–271·8) were estimated to have entered Catamaran Brook during spawning time in 2003, of which an estimated 125 were anadromous males (95% CI = 81·3 − 236·9) and 46 were anadromous females (95% CI = 30·7–101·9).

The offspring resulting from the 2003 spawning season were sampled from 28 August to 1 September 2004, by snorkelling in an 8 × 38 m study site located at the mouth of the brook, *c.* 2 months after emergence from redds. The site was chosen because of the high density of YOY *S. salar*. Sampling was done between 1300 and 1800 hours, when *c.* 60% of YOY *S. salar* are active (Breau *et al.*, 2007). Fish were caught by a diver using dip nets moving slowly through the site in an upstream direction. A numbered orange marker was placed to mark the site of each capture. Onshore, fish were anaesthetized in clove oil, the mass (±0·01 g) and fork length (±1 mm) of each fish were measured, and an adipose fin-clip (*c.* 0·1–0·2 cm^2) was taken and preserved in 95% ethanol for genetic analysis. Each fish was left to recover in a numbered bucket filled with fresh stream water before being gently released by the diver back into the stream at its exact location of capture. The diver continued to sample the site until all individuals, which were distinguished by their clipped adipose fin, had been sampled. After five consecutive days, a total of 91 YOY *S. salar* were captured and their location (*i.e.* *x* and *y* co-ordinates to the nearest cm) was recorded. The wetted area of the site was measured for the calculation of the density of YOY *S. salar*. Because the fish were not tagged, it is possible that the same fish was sampled twice (see below). The YOY *S. salar*, however, are remarkably sedentary at this site during the summer (Steingrímsson & Grant, 2003; Breau *et al.*, 2007), which minimizes this possibility. Moreover, genetic analyses allow the identification of any potentially recaptured individuals.

GENETIC ANALYSIS

Genomic DNA was extracted from a 25 mg sample for the adults ($n = 97$) and from the adipose-fin sample for YOY ($n = 91$) using the QIAGEN DNeasy Tissue Kit (Qiagen, Valencia, CA, U.S.A.). Of the 91 YOY samples collected, 81 samples were successfully amplified by the polymerase chain reaction (PCR) at eight polymorphic tetranucleotide microsatellite loci: *SSsp1605*, *SSsp2215*, *SSsp2210*, *SSsp2213*, *SSspG7*, *SSsp2216* (Paterson *et al.*, 2004), *Ssa197* and *Ssa202* (O'Reilly *et al.*, 1996). Ten fish (numbers 16, 18, 22, 24, 26, 42, 46, 47, 48 and 64) were not genotyped (Fig. 1). The PCR reaction consisted of a reaction buffer (20 mM of Tris–Cl, pH 9·5, 25 mM of KCl, 0·05% of Tween 20, 100 μg ml^{-1} of bovine serum albumin and 1·5 mM of $MgCl_2$), 0·2 mM of dNTPs, 0·2 pmol μl^{-1} of forward and reverse primers and 0·05 U μl^{-1} of TAQ polymerase. The forward primer was labelled (Operon Technologies Inc., Alameda, CA, U.S.A.) at the 5′-end with one of three fluoresceins, 6-FAM, TET or HEX, to permit detection of the amplified DNA fragments on the ABI 310 Genetic Analyzer (Applied Biosystems, Foster City, CA, U.S.A.). The following PCR thermal cycling conditions were used: initial denaturation at 96° C for 3 min, 35 cycles of 96° C for 30 s (denaturation), 58° C for 30 s (annealing) and 72° C for 30 s (elongation) and a final extension at 72° C for 5 min. For loci *Ssa197* and *Ssa202*, the annealing temperature was set to 55° C. A negative control, with no DNA added, was included in each set of PCR experiments.

DATA ANALYSIS

Hardy–Weinberg (HW) equilibrium, linkage disequilibrium, allelic frequencies, and expected and observed heterozygosity values were calculated for each locus using the web-based software, GENEPOP v.3.4 (http://genepop.curtin.edu.au/) (Raymond & Rousset, 1995). MICRO-CHECKER v.2.2.3 software (van Oosterhout *et al.*, 2004) was used to test for the presence of null alleles. All tests were corrected for multiple comparisons using the Bonferroni correction (Sokal & Rohlf, 1995).

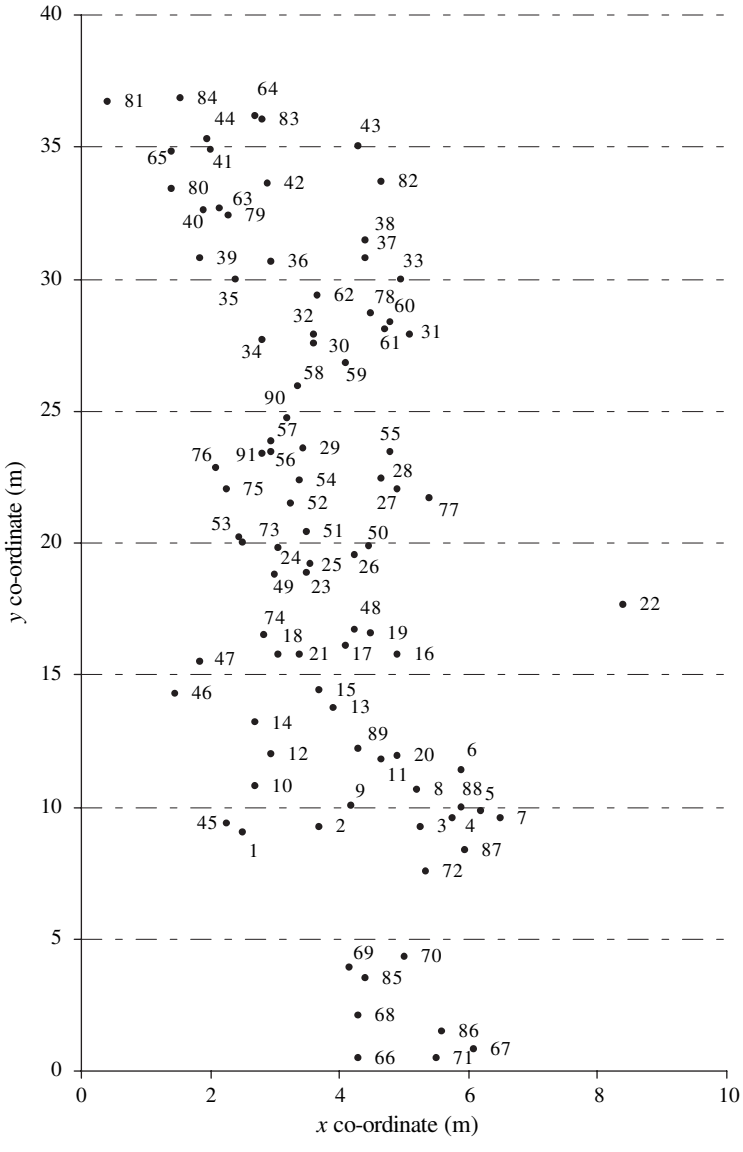

FIG. 1. Locations of 91 young-of-the-year *Salmo salar* caught in Catamaran Brook in the summer of 2004. Of these 91 fish, 81 were analysed genetically. Zero is the left bank of the 8 × 38 m site. Note the scale difference between *x*- and *y*-axes.

Kinship determination

Parental assignment to offspring was performed using the Parental Allocation of Singles in an Open System (PASOS v.1.0.0.1) software (Duchesne *et al.*, 2005) to create groups of siblings with at least one parent in common. The correctness probabilities of assigning offspring to parents were obtained by simulations using PASOS. Simulated offspring genotypes were created from the genotypes of the sampled anadromous adults using 50 iterations, with an error model set at 0% and a maximum offset tolerance of 0. The degree of genetic relatedness of offspring dyads was estimated using pair-wise

relatedness values ($r_{x,y}$) calculated using the KINSHIP v.1.3.1 software (Queller & Goodnight, 1989) for 81 offspring. Threshold values were determined by simulation to classify each pair of YOY as either unrelated ($r_{x,y} < 0{\cdot}240$), half-sibling (having one parent in common; $r_{x,y} \geq 0{\cdot}240$) or full-sibling (having two parents in common; $r_{x,y} \geq 0{\cdot}489$) (Brodeur, 2006). Using the most conservative method (*i.e.* when no parents are known), the calculation of the probability that two individuals have identical genotypes at eight loci is based on the allelic frequencies of the population in the general equation: $N_{L_i} = S{\times}1 + (1 - S){\times}2$; where the probability of homozygosity at locus (L_i) is equal to the sum (S) of the squared frequencies for each allele and the probability of heterozygosity at locus (L_i) is ($1 - S$), and N is the number of possible genotypes per locus (L_i). The product (N_T) of all possibilities over all loci is: $N_T = N_{L_1}{\times}N_{L_2}{\times} \ldots {\times}N_{L_i}$; where i is the locus number. The inverse of N_T is the probability of two individuals having identical genotypes in a given population.

Relatedness as a function of linear distance

Two comparisons were used to test for a relationship between relatedness and distance. In the nearest-neighbour analysis, each YOY in the site was tested to see if its nearest neighbour (*i.e.* the YOY with the shortest linear distance) was more closely related (based on $r_{x,y}$ values from the software KINSHIP) than a random YOY in the site. In an expanded analysis of the four nearest-neighbours, each YOY in the site was tested to see if its four nearest-neighbours (*i.e.* four YOY with the shortest linear distances), were more related than the average relatedness of all other YOY in the site.

On a larger spatial scale, a Mantel test using the R-Package v. 4.0d6 software (Casgrain & Legendre, 2001) was performed to test for a correlation between the pair-wise relatedness matrix (output file obtained from KINSHIP) and the pair-wise distance matrix from the x, y co-ordinates for all 81 fish.

RESULTS

POPULATION GENETICS

All eight microsatellite loci were polymorphic with the number of alleles ranging from nine to 27 in the adults (mean = 15·6) and seven to 18 in the offspring (mean = 11·6). Six of the eight loci in the adults and seven of the eight loci in the offspring were in Hardy–Weinberg (HW) equilibrium (Table I). Heterozygote deficiency was detected for *SSsp2213* and *SSspG7* in the adults only. Linkage disequilibrium for the eight loci used in this study was detected in both adults and in offspring (*i.e.* five of 28 and seven of 28 pair-wise comparisons, respectively). Since loci chosen for this study have been genetically mapped and shown not to be on same linkage groups (Gilbey *et al.*, 2004), factors other than physical linkage *per se* (*e.g.* over-representation of some families, see below) are probably responsible for the observed linkage disequilibrium. The presence of a null allele at locus *SSsp2213* was detected in the adults only. Locus *SSsp2213* was not excluded from the analysis, however, to avoid reducing the estimated correctness probabilities of assigning offspring to female and male adults from 93·5 to 87·9% and 88·1 to 82·7%, respectively. Moreover, omitting *SSsp2213* from the analyses would also result in few changes in the parent-offspring assignments (Brodeur, 2006). A third DNA fragment (128 bp) was present in every individual genotyped at locus *SSsp2216*. This fragment was omitted from further analyses.

TABLE I. Allelic diversity, expected (H_e) and observed (H_o) heterozygosity and Hardy–Weinberg (HW) equilibrium test results for (a) 97 anadromous adults captured in the autumn of 2003 and (b) 81 offspring, sampled in the summer of 2004

Locus	Number of alleles	H_e	H_o	HW equilibrium test
(a) Adults				
SSsp1605	11	80·8	79	NS
SSsp2215	15	83·5	89	NS
SSsp2210	9	56·9	58	NS
SSsp2213	15	88·3	75	***
SSspG7	16	88·9	83	**
SSsp2216	27	90·8	89	NS
Ssa197	16	87·6	84	NS
Ssa202	16	89·8	89	NS
(b) Offspring				
SSsp1605	12	69·2	70	NS
SSsp2215	14	68·3	71	NS
SSsp2210	7	53·5	52	NS
SSsp2213	12	70·1	65	***
SSspG7	14	73·1	75	NS
SSsp2216	18	73·8	68	NS
Ssa197	16	72·4	76	NS
Ssa202	16	72·9	76	NS

NS, not significant; **Significant after Bonferroni correction, $\alpha < 0{\cdot}01$; ***Significant after Bonferroni correction, $\alpha < 0{\cdot}001$.

SIBLING GROUPS

Out of 97 anadromous adults, 30 offspring were assigned to four females (probability of correctness of 93·5%, as calculated by the software PASOS) and 18 offspring to 10 males (probability of correctness of 88·1%), respectively, for a total of 41 of the 81 YOY in the site. Of these 41 offspring, seven were assigned to two parents, two of which were identical at eight loci (fish two and 12). Of all 81 YOY sampled, a total of four pairs of offspring (one and seven, two and 12, three and 19, and 11 and 20) were genetically identical at all eight loci, an unlikely event by chance alone (all *P*-values $<<$ 0·01). Because these pairs of fish were also found close to one another (mean = 3·65 m *v.* mean = 8·56 m for randomly selected pairs; *t*-test, d.f. = 6, $P < 0{\cdot}05$), they were probably the same fish captured on two different days (Fig. 1). Therefore, full-siblings could not be identified using information gained from parental assignment, since only one parent was assigned to each family. Although some full-sibling pairs of fish were present in the site (Fig. 2), no full-sibling families could be resolved using KINSHIP. Two adult females accounted for 28 of the 30 female assigned offspring. Based on the results of PASOS, five half-sibling groups were identified (Table II).

RELATEDNESS OF NEIGHBOURS

Focal fish were not significantly more closely related to their nearest-neighbours (mean $r_{x,\,y} = -0{\cdot}004$) than to a randomly selected fish (Fig. 1; mean $r_{x,y} = 0{\cdot}005$;

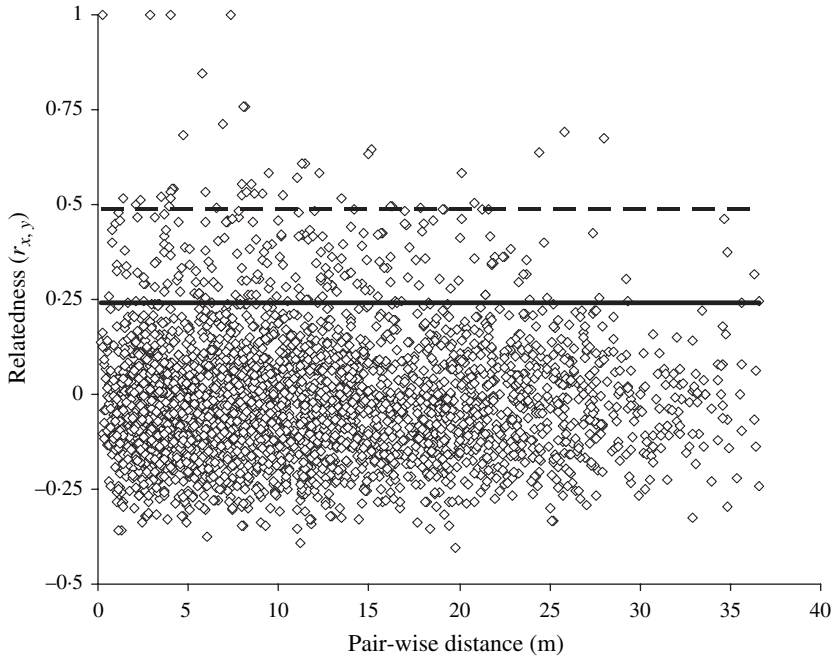

FIG. 2. Pair-wise relatedness as a function of pair-wise distance for 81 young-of-the-year *Salmo salar* (3240 dyads). The 95% CL for half (——) and full-siblings (----) are identified.

paired *t*-test, d.f. = 80, $P > 0{\cdot}05$). Similarly, focal fish were not significantly more closely related to their four nearest-neighbours (mean $r_{x,y} = -0{\cdot}01$) than to non-neighbours (mean $r_{x,y} = -0{\cdot}007$) (paired *t*-test, d.f. = 80, $P > 0{\cdot}05$). No significant correlation was found between the pair-wise relatedness and pair-wise distance matrices of the 81 YOY in the site (Mantel test, $n = 81$, $P > 0{\cdot}05$) (Fig. 2). This result included the four fish that were probably sampled twice. The Mantel test results were even more non-significant, when the four potentially 'duplicated' fish are removed from the analysis (Mantel test, $n = 77$, $P > 0{\cdot}05$).

DISCUSSION

There was no evidence of a kin-biased dispersion pattern in YOY *S. salar* in Catamaran Brook, despite attempts to address two potential limitations of previous field studies. This study contributes to the growing literature suggesting that kinship plays a less important role in determining the dispersion patterns of salmonids in the wild than in laboratory studies. Two important differences between laboratory and field studies may explain these contrasting results.

First, the genetic difference between related and unrelated individuals is higher in laboratory (full-siblings *v.* unrelated individuals) than in field studies (half-siblings *v.* unrelated individuals). Few full-siblings were identified in this study and are generally rare in other observational field studies (Fontaine & Dodson, 1999; Carlsson *et al.*, 2004). In laboratory studies, however, experiments

TABLE II. Assignment of offspring to female ($n = 2$ of 31) and male ($n = 3$ of 66) anadromous adults at the site (see Fig. 1)

Adult	Number of offspring	Offspring number
Female 827	15	2, 5, 6, 12, 14, 50, 56, 58, 59, 62, 67, 68, 75, 76, 84
Female 837	13	4, 11, 20, 21, 23, 30, 34, 39, 44, 55, 61, 73, 82
Male 897	3	2, 12, 82
Male 809	4	3, 19, 37, 55
Male 824	4	13, 17, 62, 65

typically compare full-siblings and unrelated individuals. The relative rarity of full *v.* half-siblings in field samples may reflect the mating system, in which females mate with several anadromous males, sneaker males fertilize up to 20% of eggs and offspring disperse long distances from nests (Fontaine & Dodson, 1999). Second, the density or perceived density of juvenile salmonids is higher in laboratory than in field studies. The density of YOY *S. salar* was only 0·27 m^{-2} in this study, unusually low for this site at Catamaran Brook (Imre *et al.*, 2005). Similarly, the density of salmonids reported in field studies are typically <1 m^{-2} (Fontaine & Dodson, 1999; Carlsson & Carlsson, 2002). In the clear exception to this generalization, kin-biased dispersion occurred in the field study with the highest population density 2·6 YOY m^{-2} (Carlsson *et al.*, 2004). In contrast, most laboratory studies of kin-biased behaviour report densities of fishes ranging from 1·85 to 50·00 m^{-2} (Brown & Brown, 1993*b*; Brown *et al.*, 1996; Olsén & Järvi, 1997; Griffiths & Armstrong, 2002). The high densities of fishes in laboratory experiments could amplify behavioural responses between kin and non-kin groups (Fontaine & Dodson, 1999). Moreover, if fishes are using chemical cues to recognize kin, then high concentrations of odour, caused either by high densities of fishes or the re-circulation of water in experimental tanks, may be required to stimulate kin-biased behaviour (Griffiths & Armstrong, 2000; Hiscock & Brown, 2000).

Taken together, the relatively low genetic relatedness and low population density of field populations may reduce the power of attempts to detect kin-biased dispersion in the field. Alternatively, the benefits of settling near half-siblings may not be sufficient for kin biasing to be a fitness advantage, particularly at the low population densities in most field studies. Such context dependant benefits of kin-biased dispersion have already been shown in laboratory studies; kin groups outperformed non-kin groups in high-quality environments but not in low-quality environments (Brown & Brown, 1993*a*).

We thank R. Cunjak for facilitating our research at Catamaran Brook, and the following people for helping us sample the anadromous adults for this study, I. Benwell, C. Breau, F. de Bie, C. Doyle, A. Fraser, S. Leblanc, T. Linnansaari, T. McMullan, D. Sigourney, D. Stewart and L. Weir. We also thank P. Duchesne for his advice on the use of the software PASOS. This research was financially supported by research grants from the Natural Sciences and Engineering Research Council of Canada to L.B., S.D. and J.W.A.G., a Canada Foundation for Innovations (CFI) infrastructure grant to S.D., and Teaching Assistantship from Concordia University to N.N.B. This paper is contribution No. 102 of the Catamaran Brook Habitat Research Project.

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