Nest-site fidelity in parental male bluegill *Lepomis macrochirus*: spatial patterns and the influence of prior mating success

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A 4 year mark–recapture study examined the pattern of nesting site fidelity of parental-type male bluegill *Lepomis macrochirus*. The study results indicated that iteroparous male *L. macrochirus* choose new nest sites near their own previously used sites. The scale of site fidelity varied, but generally males choose to renest within shoreline areas rather than specific or exact nest locations (94% within-year, 86% among-years). Iteroparous males also displayed no preference to nest in proximity to neighbouring males from previous colonies to suggest social fidelity. Contrary to expectation, manipulating males' reproductive success had no significant effect on the pattern or scale of male reproductive site fidelity.

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Key words: dispersal; mating success; philopatry.

INTRODUCTION

Fidelity to breeding sites is commonly observed among nesting and territorial species. For example, Greenwood (1980) reviewed dispersal and philopatry among >100 bird and mammal species and observed that territory defence and repeated use of nesting sites by one or both sexes to be a common life-history trait across taxa. Life-history theory predicts philopatry or breeding site fidelity to evolve where reproductive success not only depends on the habitat and nest quality at such sites (Hoover, 2003; Ward & Weatherhead, 2005) but also where the bioenergetic investments in nest building and defence are exceeded by fitness benefits such as increased access to mates, protection for adults and their brood, improved foraging opportunities or other resources (Trivers, 1972; Gross, 1982; Mauck *et al.*, 1999). Moreover, iteroparous species in particular must balance current *v.* future reproductive success because they face a parental investment trade-off between allocating physiological resources

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towards current v. future broods (Trivers, 1972). Because of this trade-off, parents from iteroparous taxa may engage in a 'win–stay, lose–switch' decision (Shields *et al*., 1988; Schmidt, 2004), whereby reproductively successful adults are more likely to return to their previously used breeding sites while unsuccessful adults are more likely disperse to new sites (Ridgway *et al*., 1991; Knapp, 1993; Hoover, 2003; Naves *et al*., 2006; Pasinelli *et al*., 2007).

Ultimately, the decision to disperse or return to a nesting location based on reproductive success requires that parents have a capacity to assess their reproductive output and progeny survival to some critical ontogenetic milestone such as fledging. Repeat breeders can improve their chances of successful fledging of offspring by incorporating information (such as brood size, duration of care and fledgling success) from previous reproductive experiences to make critical life-history decisions regarding resource allocation for current reproductive bouts (Coleman *et al*., 1985; Knapp, 1993; Hoover, 2003; Ward, 2005). While not as extensive as the examples for other vertebrates, such assessment has been documented in fishes. For example, male bluegill *Lepomis macrochirus* Rafinesque are more likely to aggressively defend their current broods if past broods were large and they invested long periods in parental care (Coleman *et al*., 1985). Other fishes choose breeding locations based on prior reproductive success. Female bicoloured damselfish *Stegastes partitus* (Poey) for example, assess egg survival and predator presence and return more often to nesting territories of successful mates to lay their eggs (Knapp, 1993). Male smallmouth bass *Micropterus dolomieu* Lacépède display an affinity for returning to successful nest sites in subsequent breeding seasons (Ridgway *et al*., 1991), whereas a male experiencing a substantial brood loss is more likely to abandon his nest, especially when brood predators are abundant (Suski *et al*., 2003). Shultz (2007) further demonstrated increased male abandonment rates and dispersal for future nesting locations by increasing predation on the brood of nesting largemouth bass *Micropterus salmoides* (Lacépède) associated with temporary removal of the guarding male.

A primary emphasis for investigations of philopatry in fishes has focused on defining the breadth of home ranges and the specifics of homing to natal spawning grounds. Paukert *et al*. (2004) tracked the summer movement of *L. macrochirus* and observed that the average summer home range to be a within a few hectares. Stream sunfishes also have small home range estimates ranging from 21 to 61 m for longear sunfish *Lepomis megalotis* (Rafinesque) and *c*. 38 m for *L. macrochirus* (Gerking, 1953; Gunning & Shoop, 1963). McCairns & Fox (2004) documented high fidelity rates (73–93%) for dimorphic pumpkinseeds *Lepomis gibbosus* (L.) to specific ecotype habitats during foraging. Individuals transplanted to the opposite habitat type readily returned to their original sites, suggesting recognition of habitat differences. Some larger but more mobile fish species may also display high rates of reproductive site fidelity, especially to natal spawning sites (Quinn, 1993; Miller *et al*., 2001). For example, both sexes of semelparous and iteroparous anadromous Pacific salmon *Onchorhynchus* spp. typically return to breed in the rivers and in some cases specific stream reaches where they were hatched (Quinn, 1993). In a study of fine-scale genetic structure, Miller *et al*. (2001) observed in pike *Esox lucius* L. a pattern of microsatellite DNA variation that indicated fidelity to natal and previously used breeding sites.

This study examined the patterns of site fidelity and dispersal for nesting male *L. macrochirus*, a widely occurring species in North America (Scott & Crossman, 1973).

The breadth of information about this species' reproductive ecology and behaviour makes it a model for examining breeding site fidelity. In *L. macrochirus*, nest-building (or parental-type) males sweep out and defend densely packed nests within colonies ranging up to hundreds of nests. Breeding may occur in discrete bouts where colonies spawn lake-wide simultaneously, repeating every 1 to 2 weeks. Throughout the breeding season, *L. macrochirus* core home ranges typically average a few hectares (Paukert *et al.*, 2004) despite their capability to travel greater distances. During spawning, parental-type males court one or more females and externally fertilize eggs (Gross, 1982). 'Sneaker' males may also be present and attempt to steal fertilizations and cuckold parental care (Neff, 2008). The females depart after depositing their eggs leaving males to provide parental care and brood defence until the young disperse upon reaching a free-swimming stage and the onset of exogenous feeding (Avila, 1976; Gross, 1982). Some males are iteroparous and breed in multiple bouts or episodes within or among seasons (Cargnelli & Neff, 2006). Colony locations may be used repeatedly despite an abundance of seemingly suitable, unused habitat (Avila, 1976; Claussen, 1991).

The specific aim of this study was to examine the patterns and scale of parental-type male fidelity to nesting sites and social groups (*i.e.*, the repeated nesting with a common set of neighbours or social group). An exhaustive mark–recapture effort across five breeding seasons provided the opportunity to observe lake-wide, seasonal and interannual patterns of dispersal and fidelity. Given that previous observations suggest *L. macrochirus* colonies are not randomly distributed relative to available habitat and specific colony sites are repeatedly used within populations (Avila, 1976; Claussen, 1991), iteroparous males were hypothesized to choose colony and nest sites used previously (*i.e.* philopatry). Alternatively, males might choose colony site based on social factors, preferring to nest with colony mates from previous bouts. A key prediction under these hypotheses follows that males who mate successfully and thus gain large quantities of eggs from one or more females are more likely to be philopatric to colony locations or social groups, whereas unsuccessful males will disperse to new sites or groups. This prediction was tested by artificially reducing brood size (devaluation treatment *v.* unmanipulated control; Suski *et al.*, 2003) and measuring the effects of reduced mating success on site fidelity.

MATERIALS AND METHODS

STUDY AREA

Long Lake (44° 31′ 42·15″ N; 76° 24′ 7·77″ W; elevation = 139 m) is a 12 ha oligotrophic lake situated on Queens University Biological Station property in Frontenac County, Ontario, Canada. The lake's littoral zones along the eastern and western sides occur on a narrow shelf (2–5 m wide on average) dropping off steeply beyond the shelf to a maximum depth of 25 m (Fig. 1). The lake's steep riparian zone is densely populated with large conifers, where dead and fallen trees provide abundant protective habitat for fishes common to the littoral zone including *L. macrochirus*, *M. salmoides*, rock bass *Ambloplites rupestris* (Rafinesque), yellow perch *Perca flavescens* (Mitchill) and bluntnose minnows *Pimephales notatus* (Rafinesque).

Before undertaking the study in 2004, the lake was arbitrarily partitioned into four quadrants (Fig. 1), based on natural breaks in colony habitat and physical characteristics. Ultimately, each quadrant held roughly equal numbers of colonies each breeding season. The north bay (quadrant 1) is shallow and consists of rock and silt substratum and abundant small
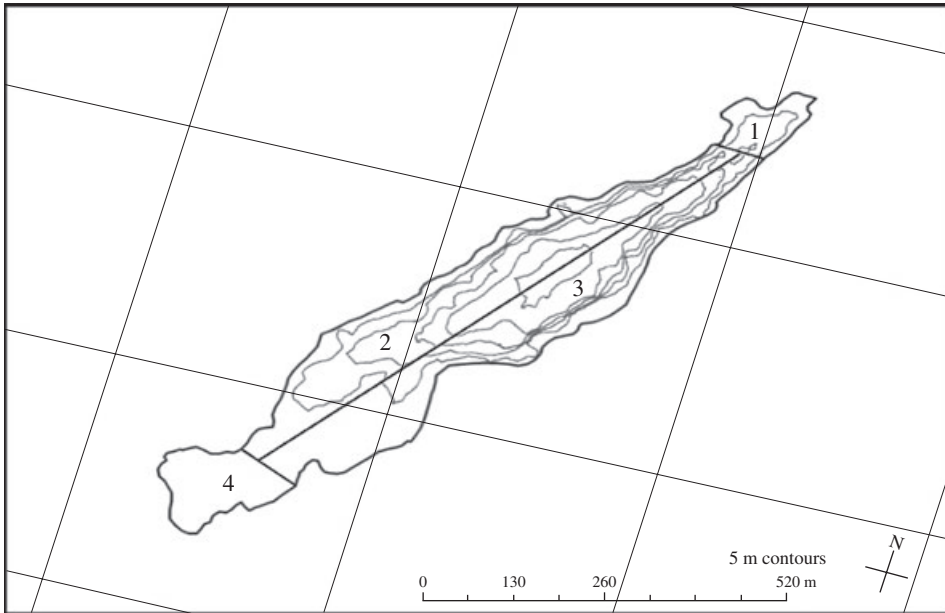
FIG. 1. Bathymetry map of Long Lake, showing a narrow band of littoral zone around the north, east and west sides of the lake. The lake's littoral zone drops sharply towards the 25 m deep centre of the lake. Quadrant delineations arbitrarily divided the lake into four zones.

woody debris. The east (quadrant 2) and west (quadrant 3) sides have small areas of narrow shallows interspersed by large stretches of steep drop offs. These habitats typically have cooler water temperatures and more submerged trees overlaying rocky substrata. Finally, the south bay (quadrant 4) is large and shallow with a dark silty bottom that heats up rapidly as the days warm throughout the breeding season, though there are a few areas of coldwater upwellings that may influence microhabitat temperatures. The first breeding colonies typically form when the surface water temperature warms to $17-18°$ C in late May or early June. Water temperatures may exceed $25°$ C by early July around the end of each breeding season.

Long Lake is ideal for a mark–recapture study for several reasons. First, the *L. macrochirus* population is effectively closed to immigration and emigration because the inflow and outflow seeps are too small or subterranean to allow fish passage. Second, the lake is small enough and sufficiently clear for snorkellers to swim the entire shoreline in a single day ensuring that most, and probably all, nesting males are observed and collected. Finally, because the lake is confined to Queens University Biological Station property, it is not subjected to public use, shoreline development, angling, harvest or any supplementary stocking that might confound results.

MARK–RECAPTURE SURVEY

Throughout five breeding seasons (2004 to 2008), nesting parental males in Long Lake were located, marked and recaptured. Swimmers equipped with snorkelling gear swam the littoral zone of the lake every 2 to 3 days, visually identifying colonies of nesting males. A colony is defined as a group of parental males in densely packed adjacent nests (Gross & MacMillan, 1981). Any parental nesting >1 m from an occupied nest was considered a solitary nesting male (Jennings & Philipp, 1992). When the swimmer encountered a colony, the location was recorded on a shoreline map; the positions of the colonies were later recorded with either a hand-held GPS (www.garmin.com) (± 8 m) or a Trimble TSC1 GPS (www.trimble.com) (± 0.25 m) unit. These GPS co-ordinates were used to estimate the distance between colonies

locations to measure site fidelity. Numbered nest tags cut from 8 cm diameter PVC pipe were placed on the outside rim of each nest to identify individual males' nests. In 2007 and 2008, all nest tags remained in the lake throughout the breeding season to test if any males returned to the exact same nest. The swimmer sketched a nest map of the colony on a waterproof slate and recorded egg scores, using an established visual assessment of clutch size (Claussen, 1991).

A swimmer captured each parental male with a hand-net and brought it to an assistant in a nearby rowboat. So as not to disturb spawning, all collection of males was completed 1 to 2 days following spawning. Only successfully mated males remained on nests by the time of collection. In the boat, the assistant measured the male's total length (L_T) to the nearest mm, took scale samples and a fin clip, and tagged before releasing it back to its nest. Males were generally away from their nests for <2 min. Most males returned to their nests immediately or within minutes of their release. This study assumes that parental males behaviours including spawning, swimming, foraging and mortality rates are unaffected by marks and tags (Wagner *et al.*, 2007). During routine swims, all nesting males were examined for previous marks or tags (Wydoski & Emery, 1983) and new colony formation. Only males that successfully nested during subsequent spawning bouts were recaptured for analysis.

One of four fin clips was given to each male to indicate the quadrant of the lake where it originally nested. Specifically, males originally nesting in each quadrant received one of the following fin clips: upper caudal fin (quadrant 1); soft anal fin (quadrant 2); soft dorsal fin (quadrant 3); lower caudal fin (quadrant 4). In the first year, males from three of the quadrants (2, 3 and 4) received spine clips to identify a male to its spawning colony. Moreover, in each year, some males (quadrants 1 and 4) received an individual passive integrated transponder (PIT) tag (Table I). PIT tags are microchips with a unique machine-readable 10 digit code and are injected into the abdominal cavity. Finally, during two seasons, numbered disc tags were also used to identify individual males (Table I).

The specific combination of marking and tagging occurred in two phases. In the first phase (2004 to 2005), the basic strategy was to describe nesting-site dispersal or fidelity on a coarse (quadrant level) scale. In 2004, males in quadrants 2, 3 and 4 received a combination of fin and spine clips permitting identification to a specific spawning colony and location. When males were collected in 2005, the fin and spine clips of recaptured males were recorded. To provide a preliminary indication of movement patterns from individuals, all males captured in quadrant 1 during the 2004 and 2005 seasons were given uniquely identifying PIT tags.

In the second phase (2006 to 2008), based on the original PIT-tagged male data, the investigation focused on individual male nest-site dispersal or philopatry on a finer (colony

TABLE I. Marking and tagging combinations [including fin clips, spine clips, passive integrated transponder (PIT) and disc tags] used for identifying individual nesting *Lepomis macrochirus* males across years. Fin clips identified spawning quadrant, spine clips identified colonies and disc and PIT tags identified individual males

	Quadrant-specific fin clips	Individual-specific internal PIT tags	Colony-specific spine clip (anal and dorsal spine combinations)	Individual-specific external disc tags
2004	All males	Males in quadrant 1	Males in quadrants 2, 3 and 4	—
2005	All males	Males in quadrant 1	—	—
2006	All males	Males in quadrants 1 and 4	—	Males in quadrants 2 and 3
2007	All males	Males in quadrants 1 and 4	—	Males in quadrants 2 and 3
2008	All males	Males in quadrant 1*		

*Only males in quadrant 1 were collected in 2008.

level) scale. In 2006 to 2007, males were PIT tagged in quadrants 1 and 4 and disc tagged in quadrants 2 and 3 so that every nesting male in the lake was individually marked. In 2008, males were only captured and PIT tagged in quadrant 1.

To examine if age influences nest-site fidelity in *L. macrochirus*, scales were collected from each nesting male. Using scale samples, each male's age was estimated to the nearest year by two independent readers. Rare discrepancies among the readers' estimates were resolved through a consensus reading.

MATING SUCCESS MANIPULATION

During the 2006 spawning season, five colony pairs were selected based on similarities in size, location and spawn dates. All colonies were located in quadrants 1 or 3 and all males were PIT tagged. Only colonies that had reached the fry stage of development, *c*. 3 days after spawning, were used. One colony from each pair was randomly designated to receive the treatment devaluation and the other to be the control group. Brood scores were recorded from all 10 colonies before treatment. Within treatment colonies, the entire clutch was removed using a turkey baster. This treatment was designed to mimic natural clutch loss due to predation. Within control colonies, the turkey baster was introduced to each nest, although no fry were removed. Post-treatment brood scores for each nest were recorded, and movements between parental males' experimental and future spawning colony locations were measured. In 2008, 16 males from a colony in quadrant 1 were divided randomly into treatment and control fish. These fish were monitored until all fish left their nests. Spawning occurred on day 0. On day 2, prior to hatching, treatment fish had their clutches removed with a turkey-basting pump or by sweeping out the nests by hand. Subsequent observations on days 4, 6 and 9 indicated whether a male was present or absent.

DATA ANALYSIS

Minimum distances travelled by recaptured (*i.e.* renesting) males were estimated between nest sites of subsequent nesting events using GPS location data of the approximate centre of each colony. Colony centres, rather than individual nests, were used as focal measurement points because the GPS units' precision (± 0.25 to 8.00 m) was generally much larger than the diameter of individual nests. Colony centres were determined visually by approximating the colony as either a line for small linear colonies ($n \leq 3$ nests) or a circle for larger polygonal colonies ($n \geq 4$ nests). This method also permitted an evaluation of the frequency of movement between quadrants. Distances between sites were used to determine the spatial scale of fidelity and movement to quadrant, colony or specific nest-site location. Significant relationships were tested among site fidelity and age, colony locations and mating success (as estimated by egg scores) using ANCOVA; *t*-tests and χ^2-tests of independence were used to evaluate within-year and among-year movements between quadrants and to compare ages, L_T and egg scores among different groups of males. For comparisons between single-time and multiple-time nesting males, only PIT-tagged males from 2005 to 2006 are included to ensure single-time males only nested once. These seasons are the only years flanked before and after by full lake surveys. All statistical analyses were performed with procedures in SPSS 16.0 (www.spss.com).

For the devaluation experiment, the colony was the experimental replicate and each nest within a colony is considered a sub-sample. All treatments were applied at the colony level and values of renest rates and distance travelled between nest sites were averaged from all sub-samples within a colony. Comparisons were initially made between paired control and treatment colonies. Similarities in distributions among paired colonies allowed the pooling of all treatment and control data for final comparison. Five males (three control and two treatment) were excluded from analysis because they were subjected to the devaluation treatment in prior nesting events. Significant relationships were tested between site fidelity and age, number of nests and mating success using ANCOVA and non-parametric methods. Non-parametric χ^2 analysis and Fisher's exact test were used because sample sizes were small and some distributions violated normality assumptions. Paired *t*-tests, *t*-tests and ANOVA

procedures were used to compare mating success and nest abandonment among treatment groups. All statistical analyses were performed with procedures in SPSS 16.0.

To determine colony fidelity, linear distances were calculated between the prior and subsequent nesting colonies using GPS locations. Because colonies often overlap or come within 8 m (the approximate error margin of the hand-held GPS unit) of one another, intervals of three colony distances (24 m) were used when evaluating philopatry. All fish that renested within 24 m of their previous nest site were considered philopatric to a colony location. Socially philopatric males nested with at least one male from a previous colony. Males were pooled across all nesting events (both within and among seasons) and the percentage of males who nested with a previous colony mate was calculated.

RESULTS

PATTERNS OF SITE FIDELITY

Across 5 years of the study (2004 to 2008), 1922 individual nesting males were collected from 2656 nests in a total of 338 colonies (Table II). The colonies ranged in size from 2 to 36 males with a mean ± S.E. of $7 \cdot 9 \pm 0 \cdot 3$ and were distributed relatively evenly across all four lake quadrants each year (Fig. 2). Males often nested at colony sites used in previous seasons or bouts within the same season (Fig. 2). In 2007, 78 of the 695 nests (11%) were reused within the breeding season, including nine nests that were reused by the same males. Again in 2008, 10 of 109 nests (9%) were reused within the same season, including two nests reused by the same males. New nests were typically built adjacent to or a few metres away from old ones.

TABLE II. Summary of number of recaptured nesting *Lepomis macrochirus* males caught from 2004 to 2008. Percentage of total fish per year for within-year recaptures or total fish of initial breeding season for among-year recaptures are given in parentheses

	2004	2005	2006	2007	2008*
Number of nesting males	318	477	549	497	81
Number of colonies	55	75	107	93	8
Number of captures (including renesting males)	409	671	772	695	109
Number of recaptured males within-year (% of nesting males)	74 (23%)	181 (38%)	169 (31%)	161 (32%)	29 (36%)
Number of recaptured males among-year (% of nesting males)	2 years	56 (18%)	75 (16%)	56 (10%)	28 (—)
	3 years		6 (2004–2006)	7 (2005–2007)	5 (2006–2008)
	4 years				1 (2005–2008)

*The data for 2008 do not represent whole-lake sampling.

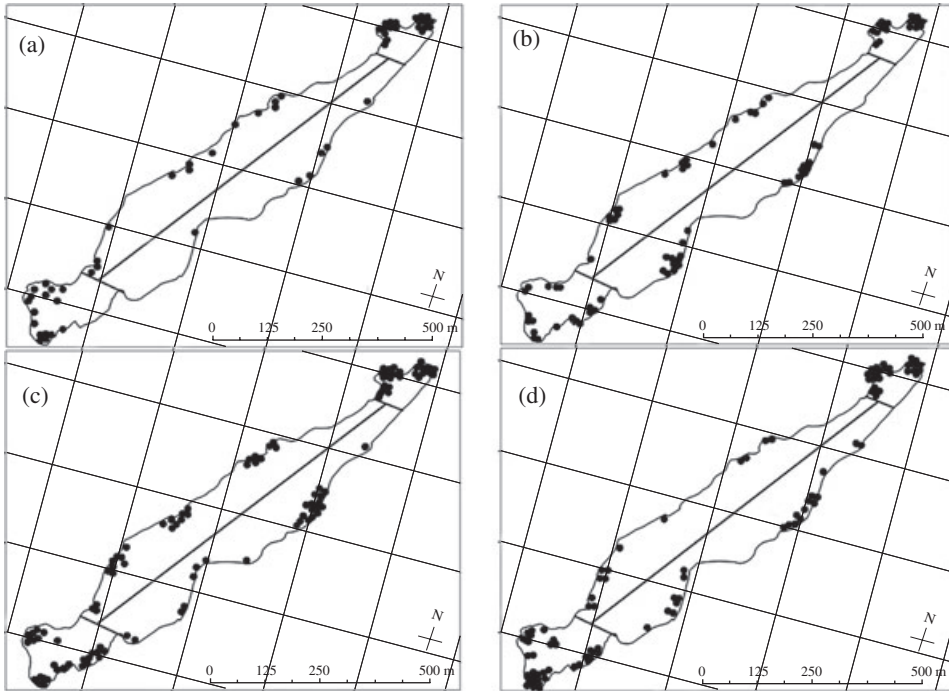FIG. 2. Colony locations for four breeding seasons: (a) 2004 (55 colonies), (b) (75 colonies), (c) 2006 (107 colonies) and (d) 2007 (93 colonies). Because colonies are often built on top of pre-existing nests, each point can represent one to four individual colonies.

The mean age of nesting males was 5·6 years and ranged from 3 to 9 years. Most parental males first spawned between the ages of 4 and 5 years and presumably continued spawning until death. Age was positively correlated with L_T (Pearson's correlation, $n = 1922$, $P < 0.01$) as expected for a species with indeterminate growth. Mean ± S.E. L_T, measured from mouth to the end of the tail, was $173.0 ± 0.2$ mm and ranged from 132 to 225 mm. Mean ± S.E. egg score, evaluated for all parentals from 2006 to 2008 on a scale from 1 to 5, was $3.10 ± 0.03$.

Most parental males ($n = 1247$, 65%) nested a single time during the study. In each of the 5 years, 23–38% of the males nested multiple times within a breeding season (Table II). Furthermore, 14% of males on average nested two consecutive years. For males that spawned more than once, mean number of spawning episodes across multiple years was 2·4, ranging from two to nine (Fig. 3). As expected, males that renested were older and larger than single-time nesting males, yet mating success did not differ (Table III). Only 18 males (<1% of all parental males) nested 3 years in a row, six which spawned 2004 to 2006 and seven which spawned 2005 to 2007 (Table II). A single male nested four contiguous years from 2005 to 2008.

At the quadrant level, parental males were highly faithful to breeding sites, particularly within a breeding season. Fidelity averages from 2004 to 2007 across the lake's four quadrants that ranged from 93% in quadrant 2 to 95% in quadrants 3 and 4 (Table IV). Dispersal from original nesting quadrants was typically to an
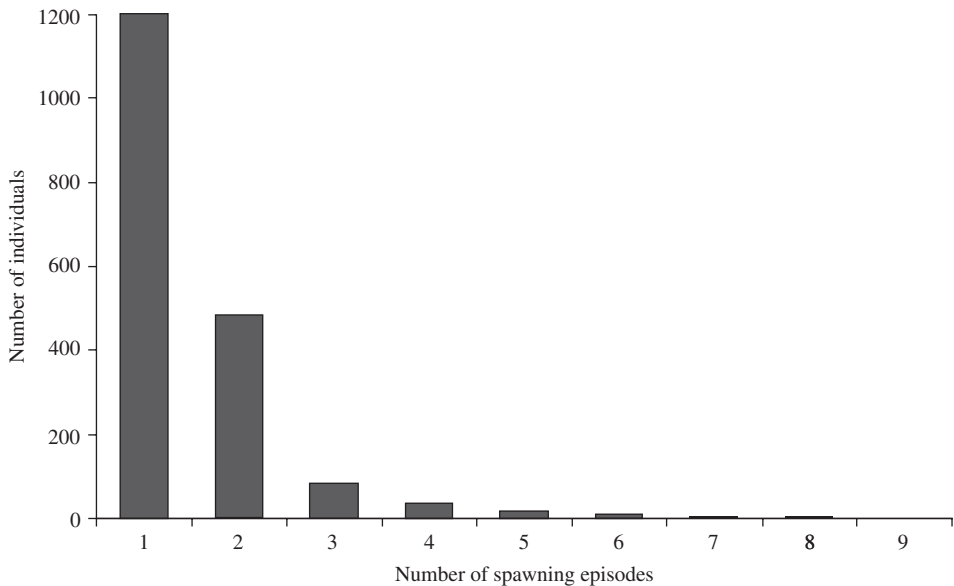
FIG. 3. Frequency histogram of the number of times each male spawned and was captured over four breeding seasons.

adjacent quadrant and rarely across the lake. In fact, only a single male moved >1 km between nest sites from quadrant 1 to 4. Even among adjacent quadrants, males swam a mean ± s.e. distance of 450 ± 120 m to new nests sites typically moving between the north and south ends of the lake. Most dispersers did not settle near quadrant boundaries. Egg scores were not associated with fidelity at any scale, age only related to among-year movement with younger fish more likely to disperse and smaller males were more likely to disperse both within a season and among-years (Tables IV and V). Dispersal rates among breeding seasons were higher than within a season. Among-year fidelity ranged from a low of 45% in quadrant 3 to a high of 91% in quadrant 1 and was positively associated with age and L_T (Table V).

Of the 338 colonies, only five colonies (consisting of 31 fish) formed in unique locations that were used only once. Three of these five colonies nested in 2006

TABLE III. Comparison of mean ± s.e. ages, total lengths (L_T) and mating success of single-time and multiple-time nesting *Lepomis macrochirus* males from 2005 to 2006*

	Single-time nesting males	Multiple-time nesting males	t	d.f.	P
Age (years)	5.3 ± 0.1	5.8 ± 0.1	-6.50	230	<0.01
L_T (mm)	165 ± 1	174 ± 1	-4.68	230	<0.01
Egg score	3.4 ± 0.1	3.4 ± 0.1	-0.18	230	>0.05

*Only passive integrated transponder-tagged males from 2005 to 2006 are included to ensure single-time males only nested once. These seasons are the only years flanked before and after by full lake surveys. Only fish in quadrant 1 (see Fig. 1) were captured in 2008, so data from 2007 could not be used.

TABLE IV. Within-year return to nesting quadrants (see Fig. 1) and corresponding statistical tests table for *Lepomis macrochirus* males which nested twice, consecutively. Data are pooled from 2004 to 2007 and include all males whose spawning quadrants are known

	Quadrant				
	1	2	3	4	Total
Total number of nesting males	229	112	78	165	584
Number of males renesting in the quadrant of original spawning	216	104	74	157	551
Percentage of males philopatric to quadrant within a season	94	93	95	95	94

	Test	Test statistic	d.f.	P
Quadrant	χ^2-test of independence	0·71	3	>0·05
Age	χ^2-test of independence	8·48	5	>0·05
Egg score	χ^2-test of independence	7·32	4	>0·05
L_T	t-test	−2·27	582	<0·05

L_T, total length.

and one colony each in 2004 and 2005. All other colonies were within 8 m (the approximate error rate of the hand-held GPS unit) of prior or future colonies during the 4 year period, and many were in the exact same location as determined by landmarks (*i.e.* downed trees and rocks).

Most males were philopatric to smaller scale colony locations. Nest-site choices of 411 males nesting in 594 episodes were estimated from individually tagged fish captured in 2004 to 2008. For all fish, 62% renested in sites that were within 24 m of their former nest site and 78% renested within 48 m (Fig. 4). Fidelity distributions

TABLE V. Among-year returns of *Lepomis macrochirus* males to nesting quadrants (see Fig. 1). These data include fish which nested 2 and 3 years consecutively

	Quadrant				
	1	2	3	4	Total
Total number of nesting males	92	44	20	51	208
Number of males renesting in the quadrant of original spawning	84	39	9	39	171
Percentage of males philopatric to quadrant among seasons	91	89	45	76	82

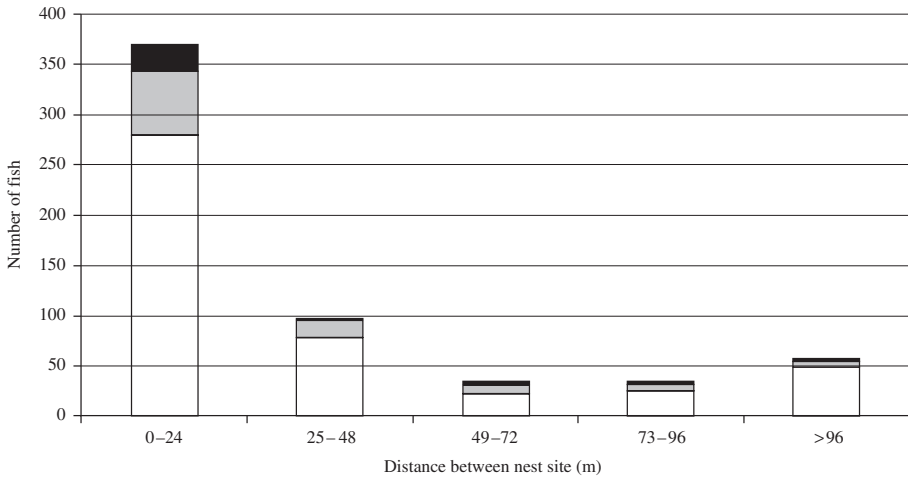|	Test	Test statistic	d.f.	P
Quadrant	χ^2-test of independence	42·07	3	<0·01
Age	χ^2-test of independence	18·12	5	<0·01
Egg score	χ^2-test of independence	6·48	4	>0·05
L_T	t-test	−4·88	206	<0·01

L_T, total length.

FIG. 4. Distances travelled between nest sites for all individually tagged fish with known colony locations including within-year (□) and among-year (▨) renesting males, and control and treatment (pooled under experimental; ■) renesting males. Fish that travelled 0–24 m to new nest sites are considered philopatric to nest sites.

were similar among within-year, among-year and experimental fish (χ^2 homogeneity test, d.f. = 8, $P > 0.05$). Distances between nests were not associated with individual characters (Table VI). The farthest dispersal of any fish was from quadrant 3 to quadrant 1, totalling 1040 m.

As mentioned previously, 11 fish in 2007 and 2008 renested in the exact same nest during the season. The relative locations of these males' nests to other nests within their respective colonies were consistent across the multiple nestings; all were either on the outer rim of the colonies or within one nest from the rim. When compared to other males that renested in 2007 and 2008, these 11 fish did not differ in age (*t*-test, d.f. = 517, $P > 0.05$) or L_T (*t*-test, d.f. = 811, $P > 0.05$).

TABLE VI. ANCOVA results comparing distances between nesting male *Lepomis macrochirus* original nest sites and subsequent renest sites both within- and among-years. Total length was not included in the analysis because it is strongly correlated with age ($r^2 = 0.42$, $P < 0.01$)

	Mean square	d.f.	F	P
Overall	11 530	67	1·01	>0·05
Age	4480	5	0·23	>0·05
Number of times an individual male nested	4843	4	0·25	>0·05
Egg score	1775	4	0·09	>0·05
Age × nests	6521	10	0·34	>0·05
Age × egg score	8851	16	0·46	>0·05
Nests × egg score	2273	8	0·12	>0·05
Age × nests × egg score	2778	21	0·14	>0·05

Males that nested more than once were equally likely to nest with a previous colony mate (50%, $n = 463$) as not (50%, $n = 464$) for any given nest across all seasons. Males from the same colony did not always renest on the same date, although they still returned to nearby nest sites; thus, social fidelity was highly correlated to rates of nest-site fidelity (Pearson's correlation, d.f. $= 612$, $P < 0.01$), suggesting philopatry to a location rather than to males with which they previously bred.

SIMULATED BROOD REDUCTION

Renesting did not significantly differ between control ($n = 22/34$, 65%) and treatment colonies (*i.e.* nests that were devalued; $n = 17/34$, 50%; paired *t*-test, d.f. $= 4$, $P > 0.05$). Renesting for both of these groups was similar to the 2006 average of 49% for all males captured in quadrants 1 and 3 (χ^2 homogeneity test, d.f. $= 2$, $P > 0.05$).

Relative brood (fry) scores, as well as the reductions associated with the treatment, are summarized in Table VII. The presence and success of removing fry by the turkey baster caused parents to respond very aggressively towards it during treatment engaging in anti-predator behaviours ranging from flaring opercula, charging and nipping. Average brood scores for control colonies did not differ from all 2006 average colony brood scores (*t*-test, d.f. $= 100$, $P > 0.05$). Brood scores for renesting males following devaluation treatments did not differ from renesting males in the control group (paired *t*-test, d.f. $= 4$, $P > 0.05$). Average brood scores also did not differ among males in the control and treatment groups following renesting, 2006 renesters and all 2006 fish ($F_{3,755}$, $P > 0.05$; Fig. 5). Nest abandonment following egg stage devaluation did not differ between control and treatment colonies in 2008

TABLE VII. Comparison of *Lepomis macrochirus* nesting colonies chosen for control and treatment (brood reduction). Two colonies were combined into treatment 1 for analysis because of their close proximity and identical spawn dates with each other and control 1

Colony designation	Number of nests (n)	Number of males which renested/number of males used in analysis (N_R)	Mean ± s.e. fry or brood score
Control colonies			
Control 1	16	12/12	2·9 ± 0·2
Control 2	5	3/3	3·0 ± 0·0
Control 3	7	5*/3	2·8 ± 0·7
Control 4	4	3*/2	3·3 ± 0·3
Control 5	5	2/2	3·6 ± 0·5
Treatment colonies (devalued brood success)			
Treatment 1	14	9/9	0·9 ± 0·1
Treatment 2	4	2/2	0·0 ± 0·0
Treatment 3	5	1/1	0·5 ± 0·3
Treatment 4	6	4*/3	0·8 ± 0·3
Treatment 5	7	3*/2	0·2 ± 0·2

*An individual from control 4, treatment 4 and treatment 5 and two individuals from control 3 were discarded prior to analysis because they were previously subjected to devaluation in earlier treatments.
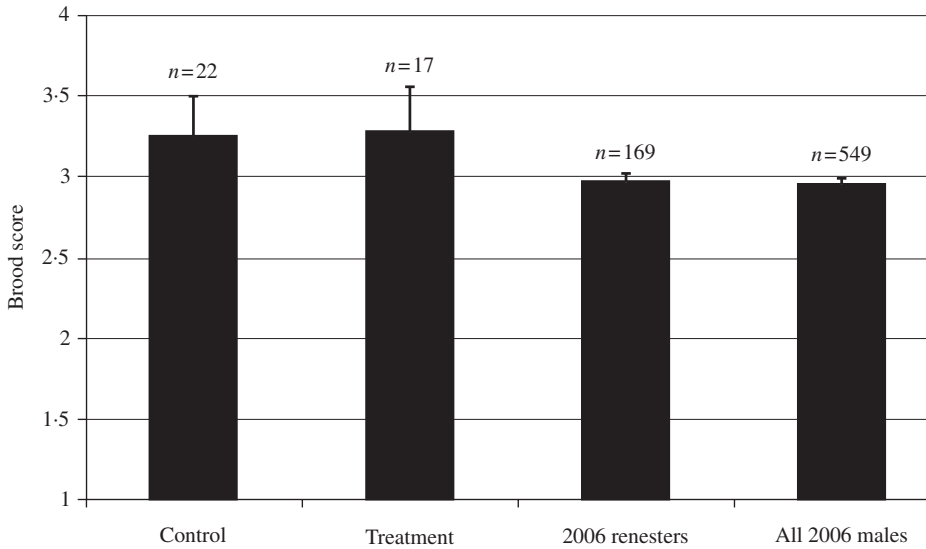
FIG. 5. Mean ± S.E. brood scores of males nesting in 2006.

(*t*-test, d.f. = 14, *P* > 0·05). All fish in the colony left by day 9 when fry swam out of the nests.

Fidelity to previous colony sites did not differ between treatment and control colony pairs (Fisher's exact test, *P* > 0·05). The majority of fish from both control (73%) and treatment (65%) colonies renested within 24 m of their previous nest sites. This is consistent with fish throughout Long Lake both within and among years (Fig. 4). Nonetheless, variation within both treatment and control colonies was large ranging from no movement to moving across the lake. Most dispersing males remained within a few colony sites of their original colony. Individual male characteristics are not important predictors of colony fidelity or dispersal for any fish nesting in 2006. Age, number of times nested and brood score were unrelated to distances travelled by males between nest sites ($F_{3,38}$, *P* > 0·05).

DISCUSSION

The results from this study indicate that *L. macrochirus* males are largely philopatric to specific shoreline breeding areas from one spawning event to the next. While few males dispersed great distances including across the lake (*c*. 1 km) between spawning events, most recaptured males displayed reproductive philopatry at a relatively fine spatial scale and return to within 24 m of previous nests (approximately the same colony location) over 60% of the time. This general pattern was observed consistently across shorelines of the lake as well as within and among breeding seasons. These findings are consistent with Paukert *et al.* (2004) who concluded that despite their capability of swimming long distances, *L. macrochirus* home ranges were restricted during spring and summer months. Males and females averaged home ranges of only a few hectares and site fidelity (though not specifically nest-site fidelity) was *c*. 50–60%.

Social group fidelity, independent of colony or nest location, was also not evident. An association among previous colony neighbours would require that individuals could recognize and preferentially associate with previous neighbours. Dugatkin & Wilson (1992) demonstrated experimentally that *L. macrochirus* are capable of distinguishing successful foraging partners from non-successful partners. Ultimately, in this study not only were males no more likely to renest with previous colony neighbours than unfamiliar ones but also that males did not appear to preferentially choose to associate with a previously reproductively successful male. This result is important because in some avian lekking systems, it has been shown that males may join colonies with so-called 'hotshot' males which attract females, thus increasing their own likelihood of successful matings (Sæther, 2002). Thus, *L. macrochirus* males either do not recognize or preferentially associate with hotshot males.

More importantly, this pattern of fidelity (or conversely, dispersal to distant nests locations) was not affected significantly by low or reduced mating success. This latter result indicates that males do not make nesting site or group choices specifically based on an assessment of their own or their colony neighbours' mating success despite the hypothetical advantages of such choices to indirect fitness, reduced intraspecific competition, quality mate selection and improved defence against predators (Ward & Hart, 2003). This latter finding also differs from several studies on Centrarchidae that found removing offspring simulating nest predation leads to increased male abandonment or decreased paternal care of future broods (Coleman *et al.*, 1985; Philipp *et al.*, 1997; Suski *et al.*, 2003). An untested explanation for this difference may be related to differences among species regarding duration and overall bioenergetic investment of paternal care. *Micropterus salmoides* and *M. dolomieu* males, for example, provide extended periods of care and expend substantial bioenergetic resources rearing and defending broods. Therefore, while *L. macrochirus* may lose a brood and renest within a week or two, *Micropterus* spp. males may not have sufficient time remaining in the season to fledge a successful brood or the energy reserves to expend on protecting a new brood after an earlier one is lost.

An important caveat for this study is that mating success was chosen as a surrogate response variable for reproductive success. Here, mating success referred to the relative clutch size (volume of eggs deposited) in a nest approximated by a qualitative egg score (1 to 5, smallest to largest) shortly after spawning (Claussen, 1991). Conversely, nesting success is more a binary (that is, yes or no) response to raising a brood to independence (Suski, 2000). Ultimately, both mating and nesting success contribute to reproductive success and fitness (Suski, 2000). Ultimately, mating success can easily be assessed visually by a swimmer following spawning with minimal disturbance to the nesting male. As a practical matter, a male's ability to assess its longer term reproductive success is not supported and is probably limited to the period when it is guarding its young in the nest before they fledge.

A second caveat for this study is that it did not specifically quantify habitat quality at spawning sites, the variation and limitation of which are expected to influence site fidelity. Spotte (2007) identified several key habitat qualities commonly attributed to *L. macrochirus* colony and nest-site selection including light levels, water depth and substratum composition, among others. Regardless, there are two primary reasons why limited suitable habitat is unlikely to account for the high site fidelity. First, while colonies in Long Lake are distributed throughout available spawning habitats along the shoreline and the four quadrants, similar areas and habitats adjacent to

colonies remain unused year after year and appear similar (especially for the qualities identified by Spotte, 2007) to that observed within colonies. Second, males did not routinely return to the exact same colony sites, even when these were unoccupied and probably within visual range. These suggest, ultimately, that the appearance of habitat quality is not the sole or most important attribute for colony formation. Pheromonal or other olfactory cues, disease and predator avoidance, and other as-yet unknown microhabitat quality remain untested candidates.

A final caveat is that ultimately the choice of a colony location may not be entirely decided by the parental-type males. Field guides and the published literature generally describe that males form colonies, construct nest and then attract females. It remains uncertain, however, whether gravid females amassing near littoral areas may attract and instigate males to form colonies nearby through their behaviour or the release of pheromones associated with the maturation of eggs.

In conclusion, the variation in scale and pattern of reproductive fidelity suggests that decisions are made at the individual rather than a social group level. By examining philopatry at multiple spatial levels (quadrant, colony and nest), this study focused on movement at a much finer scale during breeding and highlights that *L. macrochirus* males are highly philopatric and they are not assessing their own mating success or that of their neighbours to make their decision. Animals that exhibit fidelity to nest sites are expected to receive some relative fitness benefits from returning to breed in a location with a group relative to dispersers (Greenwood, 1980; Ridgway *et al.*, 1991; Switzer, 1997). Although the predominance of nest-site fidelity in *L. macrochirus* coupled with the prevalence of links between philopatry and reproductive success across many species strongly suggests that parental males garner a fitness benefit from fidelity, the data from Long Lake suggest that this may be a more complex relationship that is not simply classified in the terms of win–stay, lose–switch. Further examination of the role of females in selecting colony locations and subsequently dictating the males' high site fidelity is warranted.

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