







MANAGEMENT BRIEF

Mark–recapture surveys affect nest site fidelity but not reproductive timing of male Smallmouth Bass

Erica Stegens¹  | Daniel D. Wiegmann¹ | Lisa M. Angeloni²  | Jeffrey R. Baylis³ | Robert A. S. Laroche⁴  | Steven P. Newman⁵ | Scott P. Egan⁴  | Greg G. Sass⁵  | Kelly L. Weinersmith⁴ 

¹Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio, USA

²Department of Biology, Colorado State University, Fort Collins, Colorado, USA

³Department of Integrative Biology, University of Wisconsin–Madison, Madison, Wisconsin, USA

⁴Department of BioSciences, Rice University, Houston, Texas, USA

⁵Wisconsin Department of Natural Resources, Office of Applied Science, Escanaba Lake Research Station, Boulder Junction, Wisconsin, USA

Correspondence

Erica Stegens

Email: esteg2018@gmail.com

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Abstract

Objective: Fish population surveys in north-temperate lakes are often conducted in the fall or spring when individuals are easy to capture with traditional fisheries techniques. Because some fishes are preparing to spawn or are spawning during these seasons, there is a critical need to better understand the potential influences of these surveys on decisions that are related to fish reproduction.

Methods: We tested whether spring mark–recapture surveys using fyke nets followed by electrofishing affect the reproductive behaviors of male Smallmouth Bass *Micropterus dolomieu* in a northern Wisconsin lake. Fyke netting, electrofishing, and whole-lake nest snorkeling surveys were conducted during 2001–2008, and Floy-tagged males were tracked across years to test whether capture in the fyke nets only or capture in the electrofishing survey influenced interyear nest site fidelity and reproductive timing.

Result: The mark–recapture surveys were conducted preceding the spawning of Smallmouth Bass, and returning males that were caught in the electrofishing survey nested ~50 m farther from their prior year's nest than both males that were captured only in fyke nets and males that were captured by neither method. Average interyear nest distances were ~200 m, and median interyear nest distances were ~90 m for males that were not captured in the electrofishing survey. Electrofishing and fyke netting did not influence the timing of reproduction.

Conclusion: Spring electrofishing surveys for Smallmouth Bass have the potential to displace breeding males from preferred nesting habitats. If displacement negatively influences fitness (i.e., age-0 survivorship to maturation), spring electrofishing surveys would not be recommended for assessing Smallmouth Bass populations. However, spring population surveys often occur soon after ice off, and surveys that are conducted at these colder temperatures are typically less stressful and less likely to result in mortality. Future research should test for fitness implications of reduced nest site fidelity following electrofishing in Smallmouth Bass while considering potential fitness trade-offs if surveys are moved later in the year.

KEYWORDS

behavior, ecology, fisheries management, lake and reservoir ecology, management, reproduction, survey methods

INTRODUCTION

In north-temperate lakes, fish population surveys are often conducted in spring and fall. Spring and fall represent periods of high capture vulnerability for north-temperate fishes due to prespawning movements and spawning in the littoral zones of lakes (Pope and Willis 1996). An additional benefit to conducting these surveys in the spring and fall is related to the positive relationship often observed between fish mortality and stress and water temperature (Gale et al. 2011). However, little is known about the potential influences of these surveys on the breeding behaviors of north-temperate fishes. Thus, there is a critical need to test for the influences of sampling methods on the spawning behavior and reproduction of fish.

Fyke nets are a passive fish collection technique that is commonly used in standing waters in North America (Miranda and Boxrucker 2009; Pope et al. 2009; Hubert et al. 2012). Fyke nets are often a preferred passive gear for surveying fish due to the expectation that they cause fish little harm (Miranda and Boxrucker 2009; Hubert et al. 2012), though they are not without health concerns. For example, Northern Pike *Esox lucius* that were held in fyke nets experienced starvation, chronic stress, and mortality, which increased with temperature and the number of days spent in the net (Colotelo et al. 2013b). Longer retention periods and higher temperatures were also associated with a greater risk of physical injury (e.g., scale loss and frayed fins; Colotelo et al. 2013a), which could result in infection and mortality following release. Passive entrapment techniques such as fyke nets often catch nontarget fish species as well (e.g., Larocque et al. 2012). Short-term retention alongside aggressive conspecifics or heterospecifics (including predators) can result in stress and infection-prone wounds and can be taxing or lethal (reviewed in Portz et al. 2006). Whether fyke-net-related stress influences reproductive behaviors when capture happens immediately preceding the breeding season is unclear.

Electrofishing is a common active fish collection technique for shallow water habitats (Miranda 2005; Miranda and Kratochvíl 2008; Miranda and Boxrucker 2009; Pope et al. 2009). The physical effects of electrofishing can include spinal injuries, hemorrhages, and mortality (Snyder 2003; Dolan and Miranda 2004). Electrofishing can also influence the behavior of fish following their release. In Bluegill *Lepomis macrochirus*, electrofishing resulted in reduced feeding for 3 h for juveniles and up to 12 h for adults. Juvenile Bluegill were more at risk of predation by Largemouth Bass *Micropterus nigricans* in the 10 min following an electrofishing event (Wahl et al. 2007). Largemouth Bass also responded with

Impact statement

Fish populations are often surveyed in the spring because many species move to the shoreline to spawn at this time. Being near the shoreline makes fish easier to catch, but we do not understand well how electrofishing surveys impact reproduction. This study helps address this gap to allow better management of Smallmouth Bass populations.

reductions in feeding for up to 2.5 h after electrofishing (Siepker et al. 2011). Electrofishing has also been shown to have physiological and behavioral influences on reproduction in several fish species. For example, females that experienced electrofishing when they were ripe for spawning released gametes prematurely and the gametes were less viable overall (Snyder 2003; Stewart and Lutnesky 2014; Huysman et al. 2018). Males may be influenced as well. For example, male Largemouth Bass that were electrofished while they were guarding a nest were more likely to abandon their nest relative to controls (Siepker et al. 2006). Electrofishing may therefore induce acute changes in the reproductive behavior of fish, especially when it occurs immediately preceding or during the breeding season.

We leveraged a multiyear data set where nearly all reproductive male Smallmouth Bass *Micropterus dolomieu* in a north-temperate lake were tagged and tracked during 2001–2008. We tested whether mark–recapture surveys using fyke nets and electrofishing in early spring prior to the reproductive season influenced male decisions about where and when to construct their nests. Smallmouth Bass in north-temperate populations breed in spring when water temperatures reach about 15°C (Hubbs and Bailey 1938; Shuter et al. 1980), and larger males initiate breeding earlier than smaller males (Ridgway et al. 1991b; Lukas and Orth 1995; Laroche et al. 2023). Males are generally monogamous (Ridgway et al. 1989; Raffetto et al. 1990; Wiegmann et al. 1992), build nests in the littoral zone (Saunders et al. 2002), and guard nests until shortly after the larvae become free-swimming (Ridgway 1988; Ridgway and Friesen 1992). Evidence suggests that male Smallmouth Bass exhibit nest site fidelity, with prior studies finding that about 50% of returning males nest within 20 m of their prior year's nest (Ridgway et al. 1991a; Barthel et al. 2008). Familiarity with a breeding site is generally expected to confer fitness benefits (reviewed in Piper 2011), but the benefit of nest site fidelity (e.g., its association with nesting success) for Smallmouth Bass has not been determined.

In Pallette Lake, Vilas County, Wisconsin, a roughly circular seepage lake with a shoreline of ~4 km, we observed that half of the male Smallmouth Bass that bred in consecutive years nested within 100 m of their prior year's nest, whereas some males nested much farther (e.g., moving over 1000 m from their prior year's nest). Other studies have also observed that a subset of reproductively experienced males nest far from their prior year's location (Ridgway et al. 1991a; Barthel et al. 2008), and we speculated that disturbance immediately preceding the nesting period may explain some of this variability in nest site fidelity. Specifically, we wondered if either stress or displacement that is associated with the spring mark-recapture survey might lower the nest site fidelity of reproductively experienced male Smallmouth Bass. In our population survey, Smallmouth Bass were collected in fyke nets, marked, and recaptured in an electrofishing survey. We suspected that stress associated with the fyke-netting survey was low, as nets were checked daily and water temperatures are low in early spring. Because the influences of electrofishing on physiology and behavior are typically more intense than those caused by fyke nets and because electrofishing was conducted in closer temporal proximity to spawning relative to the fyke-net survey, we hypothesized that electrofishing may have had a stronger influence on male nesting behavior than fyke netting in our study.

We tested for two potential behavioral effects of pre-nesting population surveys. First, we asked whether reproductively experienced males that were caught in the fyke-netting or electrofishing surveys exhibited less nest site fidelity than experienced males that were not captured. Second, we tested whether experienced males that were caught in the population survey acquired eggs in their nests later in the season than would be predicted given the male's length and condition (i.e., the residual deviation of observed weight from the weight predicted by length). Later egg acquisition may suggest that (1) it took longer for the male to return to its preferred breeding site after being displaced by the population survey or (2) that males required time to recoup energy or recover from stress associated with the procedures.

METHODS

Study site

Pallette Lake is a 73-ha, oligotrophic, seepage lake that is located in the Northern Highland Fishery Research Area in Vilas County, Wisconsin (46.067, -89.604; Figure 1). Pallette Lake has a maximum depth of 18 m and an average Secchi disk transparency of 5 m (Sass et al. 2022).

The lake is managed by the Wisconsin Department of Natural Resources (WDNR), Office of Applied Science, which imposes a mandatory angler creel census, minimum length limits, and daily bag limits (Sass et al. 2022). For the first 5 years of our study (i.e., 2001–2006), the Smallmouth Bass minimum length limit was 40.6 cm total length with a daily bag limit of two fish; males that were captured while guarding a nest met or exceeded this minimum length limit only 8% of the time during these years (i.e., in 95 instances out of 1161, we caught a male on a nest that met the minimum length limit). The minimum length limit increased to 55.9 cm total length with a daily bag limit of one fish for the remainder of our study (i.e., 2007–2008), and none of the males that were captured while they were guarding nests exceeded this minimum length limit during this period. Angler harvest of Smallmouth Bass on Pallette Lake was low and averaged 0.44 fish/ha per year during 2001–2008. Angler effort averaged 29 h/ha during this time (Greg G. Sass, unpublished data).

Each year, prior to the start of the reproductive season, a mark-recapture study was conducted to estimate the abundance of adult Smallmouth Bass. Fish were first marked during fyke-net surveys, and a recapture survey was conducted covering the entire shoreline using AC electrofishing. Following the mark-recapture procedures, we conducted daily snorkeling surveys of nesting males.

Mark-recapture survey

Five fyke nets (1.2 × 1.8 m frame, 1.3 m long, 0.95-cm bar mesh size) were set about equidistant from each other around the lake littoral zone at similar locations each year. The nets were checked daily and primarily captured Smallmouth Bass, Muskellunge *Esox masquinongy*, Northern Pike, and White Sucker *Catostomus commersonii*. The fyke-netting surveys were initiated in late April or early May annually (Table 1) depending on the ice-off date and water temperature. In 2006, the fyke-netting surveys began prior to the date indicated in Table 1. Although the data sheets from the beginning of the 2006 fyke-netting survey were misplaced, the observed presence of ventral caudal fin clips on males in the nest survey (see below) allowed us to determine which males had been caught during the fyke-netting survey on the days for which data sheets were lost. All fyke-net-captured Smallmouth Bass were measured for standard and total length (cm). The fish were sexed based on either the observation of gametes released from the fish during handling or using the broom straw procedure (Benz and Jacobs 1986). We were unable to

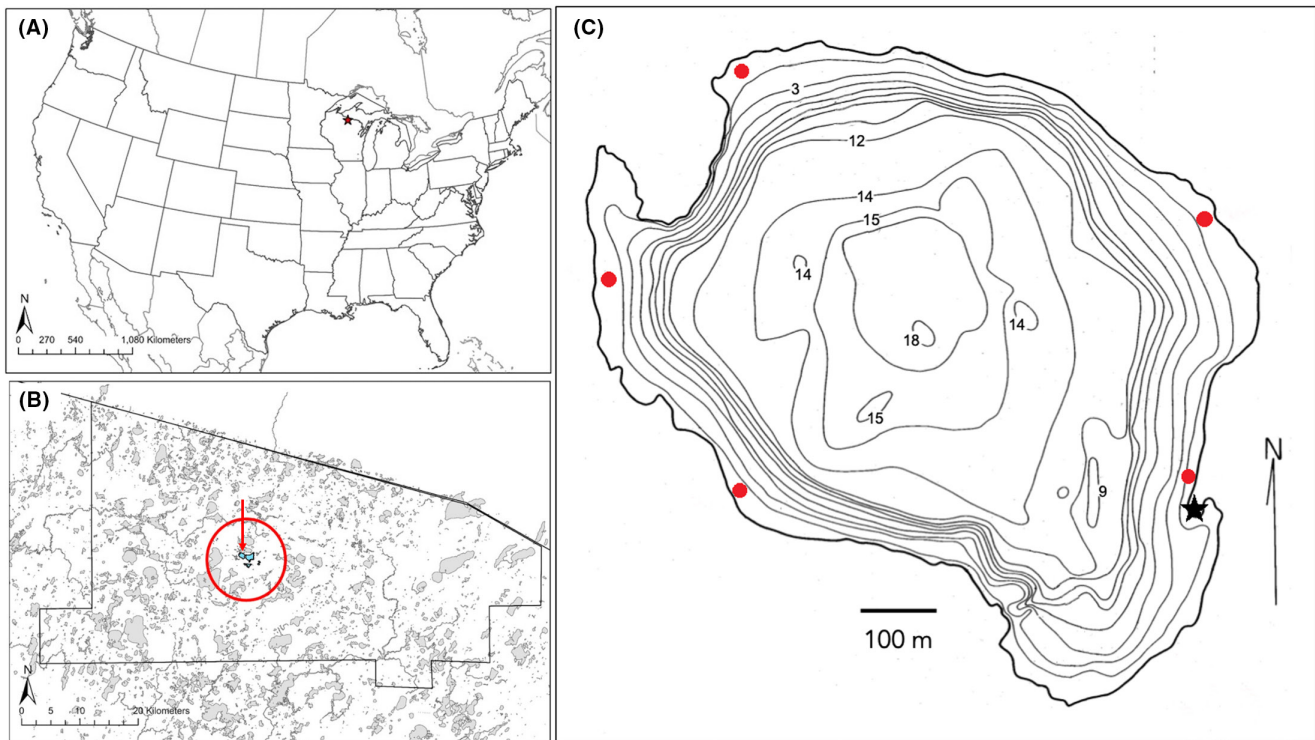


FIGURE 1 Palette Lake, Wisconsin. (A) Palette Lake is situated in Wisconsin, USA, and the location of the lake is marked with a red star. (B) Palette Lake is in Vilas County, Wisconsin (county border is indicated on the map). The lake is part of the Northern Highland Fishery Research Area (blue lakes in the red circle), and Palette Lake is marked with a red arrow. (C) Bathymetric map of Palette Lake. The numbers in the bathymetry lines are depth in meters. The approximate locations of the fyke nets are indicated by red circles, and the black star on the eastern shoreline indicates where the stationary Magellan GPS ProMARK X receiver was placed each year when nest location data were collected. Maps A and B are adapted from Sass et al. 2022, and map C is adapted from a Wisconsin Department of Natural Resources public image: <https://dnr.wi.gov/lakes/maps/DNR/1872100a.pdf>.

TABLE 1 Descriptive data for the spring population surveys of Smallmouth on Palette Lake, Wisconsin. For each year, we include the dates on which the fyke nets were checked (“Fyke dates”), the date on which the electrofishing survey occurred (“Efish date”), the voltage (“V”) and amps (“Amp”) output by the electrofishing boat that year, the date on which eggs were first observed (“First eggs”), and the last day in the season in which eggs were observed in Smallmouth Bass nests (“Last eggs”). Finally, the number of nests in which females spawned each year is indicated (“Nests”), as is the angler effort (h/ha, “Effort”).

Year	Fyke dates	Efish date	V	Amp	First eggs	Last eggs	Nests	Effort
2002	5/21–5/29	5/29	400	1.1	6/1	6/23	241	24.9
2003	5/15–5/19	5/21	285	1.5	5/27	6/30	268	30.3
2004	5/12–5/20	5/20	360	1.2	5/29	6/27	329	31.5
2005	5/4–5/23	5/23	260	0.9	5/26	6/10	242	36
2006	5/12 ^a – 5/25	5/25	450	0.9	5/26	6/9	214	32.5
2007	4/28–5/16	5/22	460	1.5	5/21	6/13	170	28.1
2008	5/14–5/28	5/28	400	0.8	5/30	6/22	211	26.1

^aIn 2006, a subset of the fyke data sheets was misplaced and surveying began before the date indicated. We were able to determine which males in our data set were on these missing data sheets by using fin clips. More information is available in the text.

sex small fish, and the smallest male we were able to sex was 15.4 cm total length. Scales were collected from beneath the pectoral fin using a forceps, and (depending on the year) either a top or bottom temporary caudal

fin clip was used to facilitate the mark–recapture population estimates (i.e., Chapman-modified Petersen estimator; Ricker 1975; Newman and Hoff 2000). When an untagged male was captured, he received a uniquely

numbered Floy FD-67C anchor tag (hereafter “Floy Tag”; Floy Tag and Manufacturing, Seattle, Washington). The fish were then released either near the fyke net from which they were collected or at the boat launch on the south shore of the lake. Each day, we also visually surveyed the shoreline from the boat to confirm that males had not begun to build nests, court females, or guard eggs. We monitored water temperature, and when the temperature approached 15°C the fyke nets were removed from the lake and the electrofishing survey was scheduled.

An AC boom electrofishing boat (1978 Brown custom 5.5 m long aluminum boat, ETS Electrofishing Systems control box) was used to conduct the recapture surveys in late May, typically on the last day of the fyke-netting surveys (Table 1). The electrofishing surveys began at dusk and covered the entire shoreline. Voltage and amperage were set to maximize the capture of Smallmouth Bass and to allow for rapid recovery. The fish were collected with dip nets and held in a well-oxygenated live well until the entire shoreline was surveyed. All the Smallmouth Bass were measured for total length to the nearest cm, Floy Tags were read (if present), and a fin clip was collected. Smallmouth Bass that were easily identified as untagged males also received Floy Tags during the electrofishing surveys. The shoreline length of Pallette Lake is ~4 km, and the maximum distance that a male that was displaced by the electrofishing survey would need to travel to return to the location at which they were captured was ~2 km. The electrofishing survey and fish processing took about 2 h.

Males that bred in two consecutive years were divided into one of three categories based on their status in the second year: males that were captured in the fyke-netting survey only, males that were captured in the electrofishing survey, and “control males” that were not captured in the fyke-netting or electrofishing survey. During 2002–2008, the numbers of males in our data set that were caught in the electrofishing survey were 9, 9, 9, 14, 20, 15, and 6. Out of these, 6, 1, 3, 4, 13, 6, and 1 male had also been caught in the fyke-netting survey that same year. Males that were captured using both gears were placed in the electrofishing survey category due to the expectation that the electrofishing survey would be a more salient stressor because this survey happened closer in time to the onset of the reproductive season. Additionally, the sample sizes were too low to estimate potential interactions between capture history and year if we incorporated a fourth capture category. Males that were captured in the electrofishing survey tended to be shorter than those that were caught in the fyke-netting survey. Therefore, we restricted our data in all categories to males ≥ 25.6 cm TL and ≤ 43.5 cm TL, which was the

range of total lengths that was observed in the electrofishing survey.

Nest survey

The nest surveys began from the time nests were observed until fry had swum up from the nests (Table 1). Nest surveys were conducted daily by 2–4 snorkelers, who swam transects starting at the shoreline and continued until reaching a depth of around 4 m. The average nest depth in Pallette Lake is about 1.7 m, and 4 m is deeper than the maximum nest depths that have been observed in other Wisconsin Lakes (Saunders et al. 2002). An observer in a boat looked for nests as well and recorded the data that were collected by the snorkelers. The data included a description of the substrate, the stage of embryos in the nest (if present), nest depth, and any distinguishing features. All the nests received a unique identifier, which was recorded on a strip of Rite-N-Rain paper attached by fishing line to a sinker. This identifier was placed on the perimeter of the nest. At the end of the spawning season, all new nests in which eggs were found received a permanent marker (i.e., a yellow wooden stake with the nest identifier and year).

During 2002–2008, an average of 239 nests with eggs were found each year (Table 1). Males that were observed on an active nest were captured by a diver who placed a long-handled net over the nest and slowly lowered the net over the male as he returned to guard his eggs or larvae. The male was quickly brought to a nearby boat and measured for length and weight. Males that were captured for the first time received a Floy Tag, and scale and anal fin clip samples were collected from males that were caught for the first time that season (i.e., males that had not been caught in the fyke-netting or electrofishing survey). The male was then released to return to his nest. We were able to capture males from an average of 94% of all the nests that were observed with progeny during 2002–2008 (range: 89–98%).

We recorded a GPS location for each nest at the end of the breeding season. Two Magellan GPS ProMARK X receivers were used, one of which was placed on the shoreline at the same location each year (Figure 1C) and another that was held above each nest. We held a receiver above a nest until 120 data points were collected, and these points were subsequently averaged to achieve a differential GPS location. The precision of the GPS data (mean \pm SE = 3.54 \pm 0.07 m) was determined by calculating the straight-line distances between nests that were located within 1 m of the same permanent marker in two consecutive years ($N=911$).

Nest site fidelity

For the purpose of our study, nest site fidelity was defined as the interyear nest distance of an individual that nested in two consecutive years. The straight-line distance between a pair of nests was calculated using the GPS data. A subset of males bred twice in the same season. For these males, the interyear nest distances were calculated using the last nest that was used in the first season and the first nest that was used the next year.

Timing of reproduction

Laroche et al. (2023) developed a model for predicting the number of degree days—a measure of thermal energy experienced by individuals—that male Smallmouth Bass from Palette Lake experienced between when the average water temperature exceeded 10°C and the date that a male spawned. This model necessarily excluded 34.6% of males whose nests were discovered after eggs had hatched. Among the predictors that we included in this reproductive timing model were condition, male total length, a quadratic term for male total length—which captured a differential effect of length on reproductive timing among males of different lengths—and year, with an interaction term between each length term and year. Condition was calculated by extracting the residuals from a linear regression of weight (\log_e transformed) on length (\log_e transformed) for each year of the study. The Laroche et al. (2023) model explained a substantial portion of the variation in degree days before reproduction ($R^2=0.67$). We extracted the residuals from the Laroche et al. (2023) model to test whether capture in the spring population survey accounted for some of the unexplained variation in accumulated degree days before eggs were observed in the nests. That is, we assessed whether males that were captured in the fyke-netting or electrofishing surveys bred later than predicted (i.e., had large positive residuals) after accounting for male condition, total length, and year.

Statistical analysis

The statistical analyses were conducted in R Studio version 1.4.1103 (RStudio Team 2020) running R version 4.0.3 (R Core Team 2020). For nest site fidelity, linear mixed-effects models were run using the lmer function from the lme4 package (Bates et al. 2015) and compared using corrected Akaike information criterion (AIC_c) values (Burnham and Anderson 2002) using the model.sel function in the MuMIn package (Bartoń 2020). For the nest-site-fidelity analysis, interyear nest distances were

overdispersed. Thus, we added 1 to all distances and ran the analyses on the natural log of the interyear nest distance. Our analysis included 861 observations from 381 experienced males. The number of males observed in 2, 3, 4, 5, 6, or 7 consecutive years were 132, 113, 74, 38, 15, and 9, respectively. To account for males that appeared in the data set in multiple years, we included a random effect for Floy Tag (i.e., individual) in our models. We tested 14 competing models: a null model (containing only a random effect for Floy Tag) and 13 models with all possible combinations of survey year, male total length, capture history, and two-way interactions between these predictors. We examined any model with $\Delta AIC_c \leq 2$ in more detail, as such models have substantial evidence for being the most plausible model(s) out of the group of candidate models (Burnham and Anderson 2002). For reproductive timing, we ran a linear model to test whether the residuals from the Laroche et al. (2023) model were associated with capture history. This analysis was run on 593 observations from 323 males. In this data set, the number of males contributing 1, 2, 3, 4, 5, or 6 datapoints were 150, 104, 47, 17, 4, and 1, respectively. The model in Laroche et al. (2023) included a random effect for Floy Tag to account for the subset of individuals who bred in more than two consecutive years.

We assessed model fit using the simulateResiduals function from the DHARMA package (Hartig and Lohse 2020) to extract and visualize the model residuals. The graphs of the predictions were generated using the function predictorEffect from the effects package (Fox and Weisberg 2018).

RESULTS

Most male Smallmouth Bass that were captured in the spring population survey and were known to have bred the prior year (i.e., experienced males) went on to breed in the upcoming or subsequent reproductive seasons. For experienced males that were caught in the fyke-netting survey, about 92% of the time the male was subsequently found guarding a nest that same year (i.e., in 254 out of 275 instances) and about 94% (260 out of 275) were found guarding a nest in any subsequent year. The numbers associated with the electrofishing survey were slightly lower. If an experienced male was caught in the electrofishing survey, about 86% of the time (i.e., in 74 out of 86 instances) the male was observed guarding a nest that year and about 90% of the time the male was observed guarding the nest in a subsequent year (77 out of 86 instances). This suggests that mortality due to the spring population survey was low or nonexistent and that capture in the survey rarely resulted in a male skipping a breeding season. These

survival percentages may be underestimated, as not all the tagged males that were observed guarding a nest were able to be caught during the nest survey. Additionally, one study on short-term retention of Floy Tags observed 100% retention over 3 months in an experimental pond but up to 48% loss over 4 months in a stream population (Walsh and Winkelman 2002). Although we rarely observed wounds that were indicative of Floy Tag loss from males that were caught while they were guarding their nests, we cannot rule out the possibility that the survival percentages were influenced by the loss of Floy Tags.

During 2001–2008, 381 males contributed to 861 instances in which breeding was observed in consecutive years. Of these instances, 525 males were not caught in the population survey in the second of two consecutive years, whereas 254 instances involved a male that was caught in the fyke-netting surveys and 82 instances involved a male that was caught in the electrofishing survey in the second year. The mean total length \pm SE for males that were not caught, caught in the fyke-netting survey only, or were caught in the electrofishing survey were 36.0 ± 0.2 , 36.5 ± 0.3 , and 34.9 ± 0.5 cm, respectively. To be included in the analysis of reproductive timing, it was necessary to discover the male's nest when it contained eggs. The sample size for this analysis was 352, 184, and 57, and the mean total length \pm SE for this subset of males was 36.4 ± 0.2 , 36.7 ± 0.3 , and 35.6 ± 0.5 cm for control, fyke-net-caught, or electrofishing-caught males, respectively.

Site fidelity

The mean \pm SE internest distance of males that spawned in two consecutive years was 203 ± 11 m for males that were not caught in either spring survey, 209 ± 17 m for males that were caught in the spring fyke-netting survey only, and 270 ± 33 m for males that were caught in the electrofishing survey. The median internest distances were 91, 85, and 145 m, respectively. Two models had $\Delta AIC_c \leq 2$, and the highest-ranked model included the term for capture history (Table S1 available in the Supplement in the online version of this article). After accounting for variation due to year and male total length, males that were caught in the electrofishing survey exhibited lower nest site fidelity than did males in the other two groups (Table S2; Figure 2). The model predicted, for instance, that a male of median length (i.e., 36.5 cm TL) in 2002 that was captured in the electrofishing survey would nest ~ 50 m farther away from the prior year's nest relative to males that were not caught in the mark–recapture survey. The top model revealed no difference in nest site fidelity between males that were captured in fyke nets and control males (estimate = -0.06 , 95% confidence intervals = -0.31 to 0.20 , $p = 0.66$).

The magnitude of nest site fidelity also differed between years (Table S2; Figure 3). In particular, nest site fidelity was found to be significantly higher in 2006 relative to the years 2002–2005 ($p < 0.01$ in all cases), and males in 2007 stayed closer to their prior year's nest than did males in 2004 ($p = 0.02$). No other differences between years were observed. Both models also indicated that longer males moved shorter distances between years (Table S2; Figure 4). The top models predicted that, for instance, the nest of a 40-cm TL male that was not caught in the spring population survey in 2002 was about 30 m closer relative to a 30-cm TL male in the same year.

Timing of reproduction

The spring population survey did not influence the reproductive timing of experienced males. Positive residuals from the Laroche et al. (2023) model indicate that a male waited longer in the season to breed than would be expected given their length, whereas negative residuals indicate that a male bred earlier in the season than expected. The mean \pm SE residuals from the model for control males (-0.019 ± 0.012) did not differ from those of males that were captured in fyke nets (0.009 ± 0.016 ; $t_{590} = 1.41$, $p = 0.16$). The residuals from the model also did not differ between the control and electrofished males (0.004 ± 0.030 ; $t_{590} = 0.74$, $p = 0.46$). Moreover, the residuals for males that were captured by the fyke-netting and electrofishing surveys did not differ ($t_{590} = -0.15$, $p = 0.88$).

DISCUSSION

Capture in a spring electrofishing survey reduced the nest site fidelity of male Smallmouth Bass but did not influence their reproductive timing. Although determining why the electrofishing survey reduced nest site fidelity was outside of the scope of our study, we propose a few mechanisms here. One mechanism by which electrofishing could have reduced nest site fidelity is through displacement. Although most fish in the fyke-netting surveys were released near their capture point, the fish that were caught in the electrofishing survey were not. Palette Lake is a small lake (73 ha), and given the shoreline distance (~ 4 km), the electrofishing survey could have resulted in a maximum displacement of 2 km. Smallmouth Bass are capable of moving more than 2 km in 1 day (e.g., Ridgway and Shuter 1996; Kaemingka et al. 2011), which suggests that males should have been able to return to a preferred nest site relatively quickly, and only the very earliest breeding males would likely be influenced by displacement from the electrofishing survey. Alternatively, displaced males may have been more

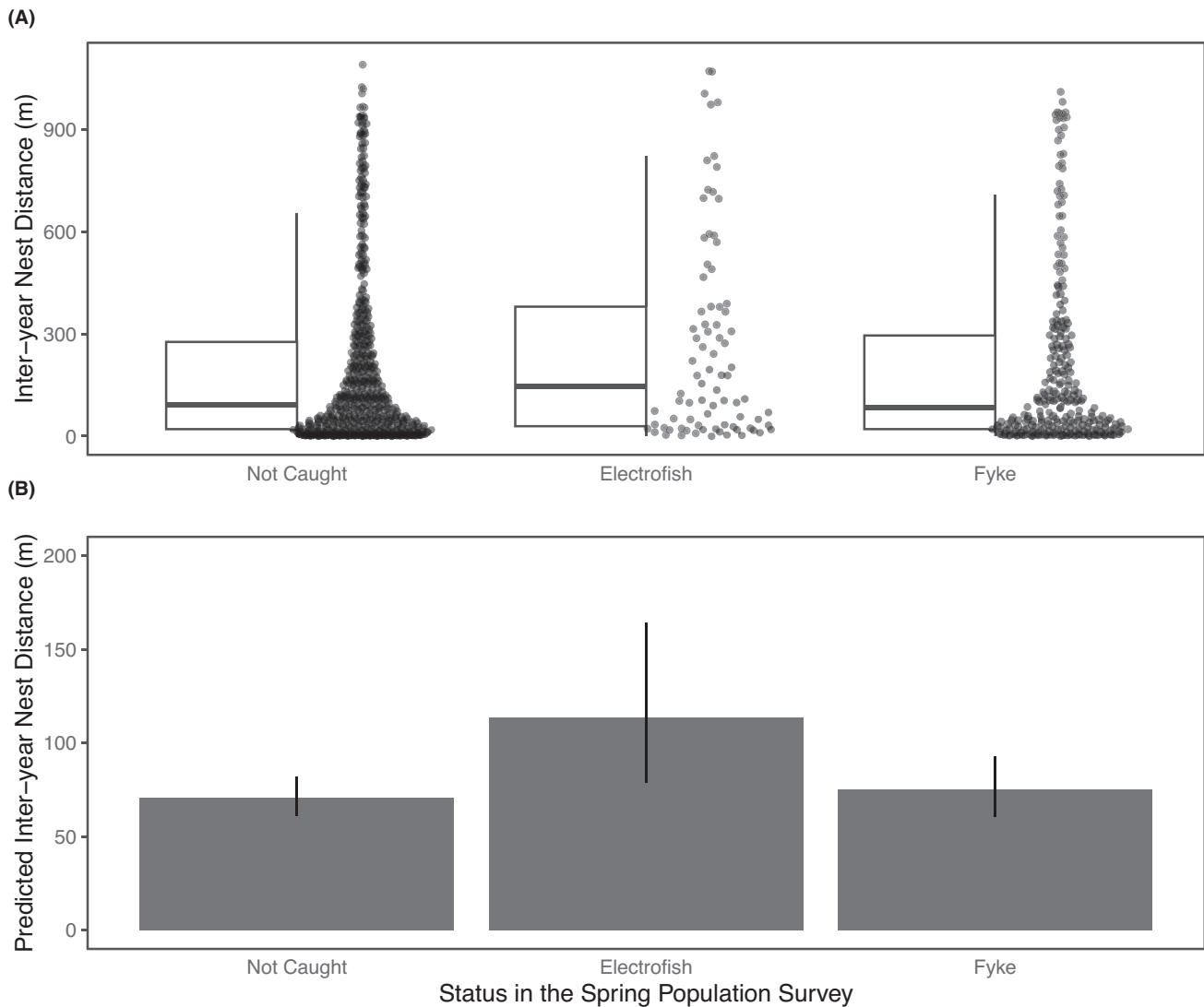


FIGURE 2 Reproductively experienced male Smallmouth Bass caught in an electrofishing survey in the spring exhibited reduced site fidelity. (A) Box-and-whisker plots alongside raw data, displaying the interyear nest distances (m, a measure of nest site fidelity) for males that were not caught in the spring mark–recapture population survey (“Not Caught”), males that were caught in the electrofishing survey (“Electrofishing”), and males that were caught in the fyke-net survey only (“Fyke”) in the second of two consecutive reproductive seasons. (B) Predicted mean ($\pm 95\%$ confidence intervals) interyear nest distances from the top-ranked model for males in each category for the spring mark–recapture population survey. Note that the y-axis is not the same in graphs (A) and (B).

vulnerable to competition and exhibited lower nest site fidelity because their preferred nesting site was occupied by the time they returned. A final potential explanation is that the nest-site preferences of experienced males changed following capture with this gear. If male Smallmouth Bass were in the vicinity of their prior nesting site at the time that they were collected in the electrofishing survey and the stress of this procedure created a negative association with the capture location, then captured males may have chosen to breed elsewhere. Any aversion to returning to a location where a male was captured via electrofishing could have implications for standardized spring surveys in large systems where surveying the entire shoreline is not feasible. For example, if the same stretch of shoreline is surveyed

year after year (e.g., Ross et al. 2016; Ohio Department of Natural Resources–Division of Wildlife 2023), catch per unit effort may be underestimated if individuals that are caught in the electrofishing survey subsequently avoid this area. If this is the case, randomly selecting sites to survey each year may be a more effective approach (as recommended by Miranda and Boxrucker 2009).

Males in Palette Lake exhibited less nest site fidelity than in two prior studies of other populations of Smallmouth Bass. In those studies, ~50% of males nested within 20m of their prior year's nest (Ridgway et al. 1991a; Barthel et al. 2008). In Palette Lake, the median nest distance between years for all males was ~100m. Only about 24% of males that nested in consecutive years

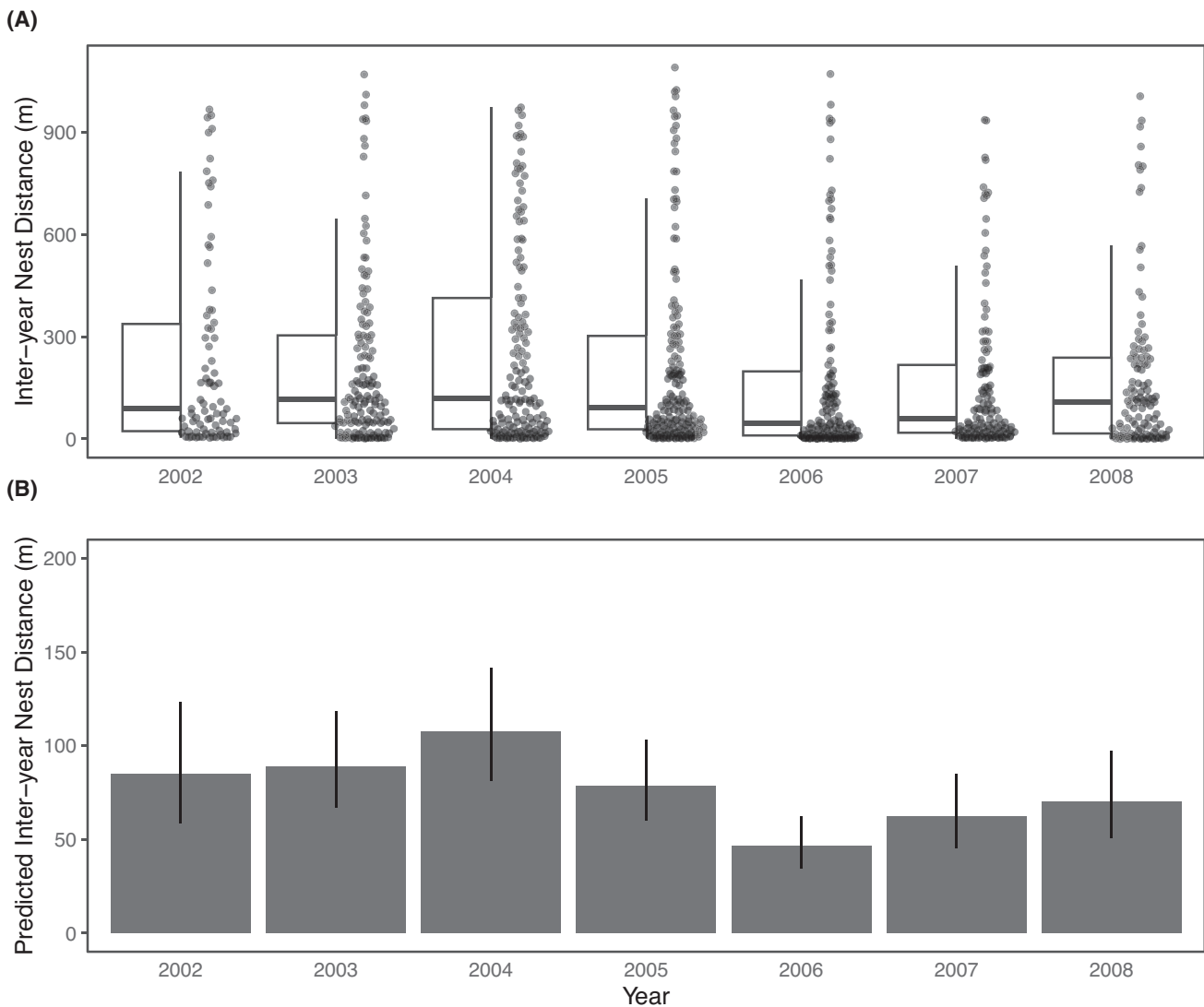


FIGURE 3 Variability in interyear nest distance (m, a measure of nest site fidelity) across years in reproductively experienced male Smallmouth Bass from Palette Lake, Wisconsin. Males bred significantly closer to their prior year's nest in 2006 relative to 2002–2005, and males in 2007 exhibited higher nest site fidelity relative to males in 2004. (A) Box-and-whisker plots alongside raw data, displaying the interyear nest distances where the year noted on the *x*-axis is the second of the two consecutive years in which a male bred. (B) Predicted mean ($\pm 95\%$ confidence intervals) interyear nest distances from the top-ranked model for each year. Note that the *y*-axis is not the same in graphs (A) and (B).

were within 20 m of their prior year's nest, and that percentage declined to about 18% when considering only males that were caught in the electrofishing survey. One potential explanation for why males in our study tended to show less nest site fidelity is that spawning habitat in Palette Lake is quite homogenous. In Palette Lake, sandy substrate makes up ~80% of the littoral zone and boulders or coarse woody habitat are low in abundance (Saunders et al. 2002). Palette Lake also has a high abundance of Smallmouth Bass (e.g., in 2000, there were about 10.3 adults/ha; Saunders et al. 2002). In this study, we found that males with longer total lengths nested closer to their prior year's nest (i.e., showed more nest site fidelity; Figure 4). In Smallmouth Bass, larger males spawn

earlier in the season (Goodgame and Miranda 1993; Lukas and Orth 1995; Wiegmann et al. 1997; Gingerich and Suski 2011; Laroche et al. 2023), and establishing a nest earlier may allow larger males to spawn closer to a preferred, prior nesting location. Thus, a combination of an abundance of high-quality nesting habitat and competition for sites may result in low nest site fidelity overall in Palette Lake.

The fyke-netting survey, which ended before the date that eggs were first observed in the nests, did not influence nest site decisions or reproductive timing in our study. However, our study design did not allow us to rule out the possibility that being caught in fyke nets influenced reproduction, especially for males that were caught

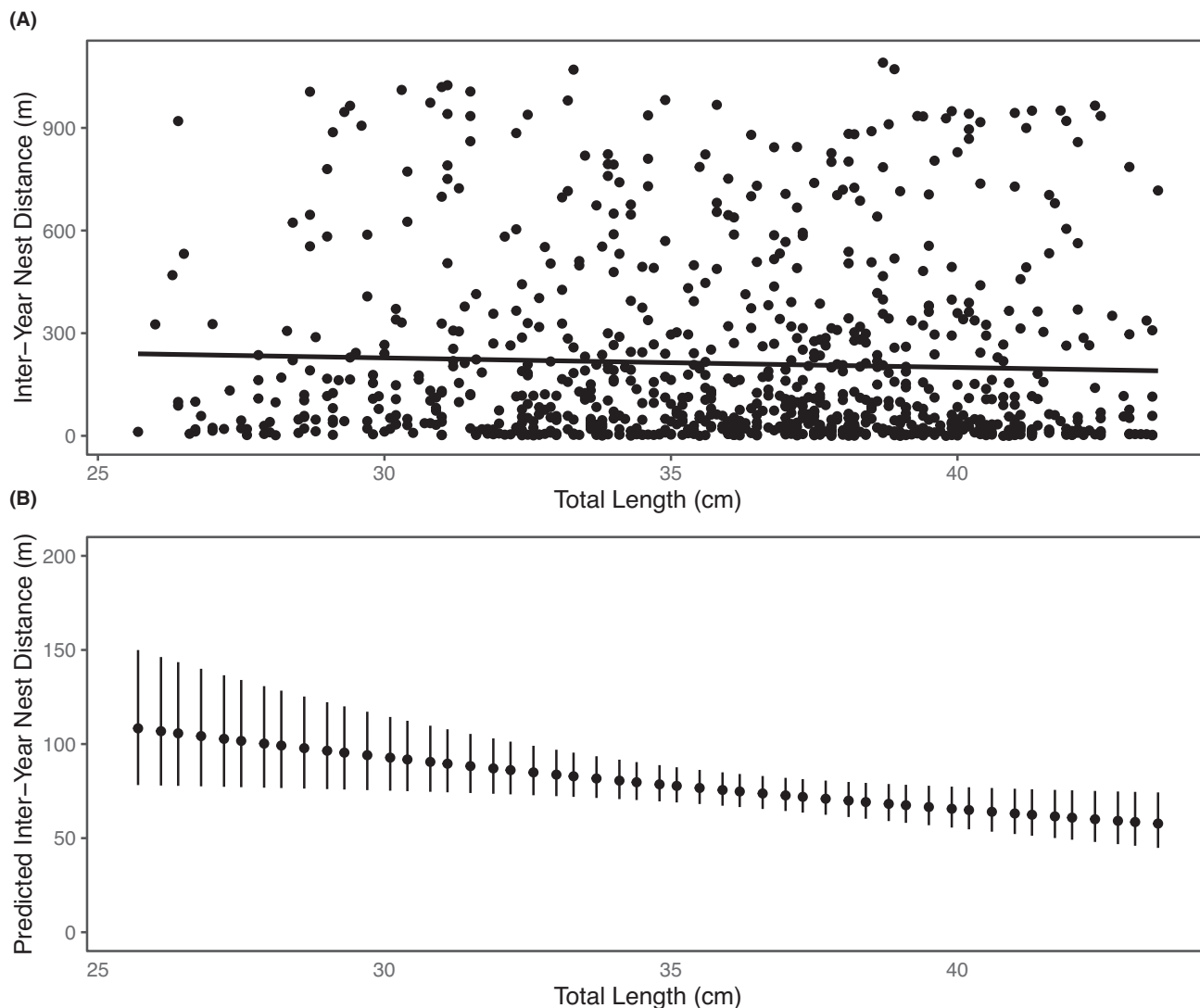


FIGURE 4 Longer male Smallmouth Bass exhibit higher nest site fidelity in Palette Lake, Wisconsin. (A) The relationship between interyear nest distances (m, a measure of nest site fidelity) and total length (cm) in the second of two consecutive reproductive seasons for male Smallmouth Bass. (B) Predicted mean ($\pm 95\%$ confidence intervals) interyear nest distances from the top-ranked model for males of varying total lengths. Note that the y-axis is not the same in graphs (A) and (B).

in both the fyke nets and the electrofishing survey. In our data set, the electrofishing survey always happened closer in time to the start of the reproductive season than did the fyke-netting survey (Table 1), leaving open the possibility that fyke netting could be equally or more influential than electrofishing relative to reproductive behavior if the order of these surveys were reversed. This seems unlikely, however, as fyke netting is a preferred passive capture method due in part to the expectation that this gear causes little harm (Miranda and Boxrucker 2009; Hubert et al. 2012), particularly when the nets are checked daily and water temperatures are low.

In summary, we found that a spring population survey influenced the nest site decisions but not the reproductive timing of experienced male Smallmouth Bass. In particular, males that were caught in the electrofishing survey

prior to the breeding season exhibited lower nest site fidelity. This is the second study to our knowledge that has documented the influence of an anthropogenic disturbance on nest site fidelity in black bass. Twardek et al. (2017) compared nest site fidelity across two sets of consecutive years and observed that Largemouth Bass exhibited much lower nest site fidelity (i.e., nested about 100 m farther) in the set of years when they were repeatedly angled while they were guarding a nest relative to the set of years when they were only angled once from their nest while they were guarding it. Given that anthropogenic disturbance appears to influence nest site fidelity in black bass, additional research is needed to better understand the fitness benefits that are associated with this behavior. If mark-recapture methods reduce nest site fidelity, the potential benefits of nest site fidelity should be weighed against

the benefits of spring sampling, which include not just high capture vulnerability (Pope and Willis 1996) but also lower stress and better survival outcomes for fish that are captured when water temperatures are low (Cooke and Hogle 2000; Portz et al. 2006; Gale et al. 2011; Colotelo et al. 2013a, 2013b; Hedger et al. 2018).

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CONFLICT OF INTEREST STATEMENT

The authors do not report any conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and R code are available upon request.

ETHICS STATEMENT

Procedures were approved by the University of Wisconsin–Madison RARC protocol A-48-9700-L00173-2-04-99.

ORCID

Erica Stegens  <https://orcid.org/0009-0009-3589-9523>

Lisa M. Angeloni  <https://orcid.org/0000-0002-2385-0599>

Robert A. S. Laroche  <https://orcid.org/0000-0002-6599-4101>

[org/0000-0002-6599-4101](https://orcid.org/0000-0002-6599-4101)

Scott P. Egan  <https://orcid.org/0000-0001-5208-1875>

Greg G. Sass  <https://orcid.org/0000-0002-9100-7421>

Kelly L. Weinersmith  <https://orcid.org/0000-0002-3886-3480>

[org/0000-0002-3886-3480](https://orcid.org/0000-0002-3886-3480)

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