Size- and age-related variation in the seasonal timing of nesting activity, nest characteristics, and female choice of parental male pumpkinseed sunfish (*Lepomis gibbosus*)

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Abstract: Parental males from a population of pumpkinseed sunfish (*Lepomis gibbosus*) were captured throughout the spawning season to examine age- and size-related seasonal trends in nesting activity. Females of spawning pairs were also captured to determine if male body size or nest characteristics influenced their selection of a mate. Large/old (≥80 mm; age 4–6 years) parental males commenced nesting earlier in the spring–summer spawning season than small/young (<80 mm; age 2 and 3 years) parental males. As the spawning season progressed, the proportion of large/old males in the nesting population decreased until more than 70% of the males nesting late in the season were small/young individuals. Small individuals nesting late in the season were inferior in body condition to those that nested earlier in the season. These findings support the hypothesis that size-related differences in energy reserves and metabolism in centrarchids result in size-dependent variation in the timing of nesting activity. The length of females captured spawning at a nest site was not significantly correlated with the length of the parental male, water depth, or distance from shore; however, females captured spawning in firm (sand and gravel) substrates were significantly larger than those spawning in soft (silt or woody debris) substrates. Although all observed nests in the various substrates contained eggs, the positive relationship between body size and fecundity in female pumpkinseeds suggests that a selective advantage for males nesting in firm substrate may accrue through the attraction of larger females.

Résumé : Des parents mâles ont été capturés durant toute la saison de la fraye au sein d'une population de Crapets-soleils (*Lepomis gibbosus*) dans le but d'étudier les tendances saisonnières des activités de nidation en fonction de l'âge et de la taille. Des femelles accouplées ont également été capturées pour déterminer si la taille du mâle ou les caractéristiques du nid jouent un rôle dans leur choix d'un partenaire. Les parents mâles plus gros/plus âgés (≥80 mm; âge 4–6 ans) commencent à nicher plus tôt au cours de la fraye du printemps que les mâles plus petits/plus jeunes (<80 mm; âge 2 et 3 ans). Au cours de la fraye, la proportion de mâles reproducteurs plus âgés/plus gros diminue jusqu'à ce que, à la fin de la saison, les mâles plus petits/plus jeunes représentent plus de 70% des mâles reproducteurs. Les petits individus qui nichent tard dans la saison sont en moins bonne condition physique que ceux qui nichent plus tôt. Ces résultats corroborent l'hypothèse selon laquelle les différences de réserves énergétiques et de métabolisme reliées à la taille chez les centrarchidés entraînent des variations du moment de la nidation en fonction de la taille. Chez des femelles capturées pendant la fraye à un site de nidation, la longueur n'était pas reliée à la longueur du parent mâle, à la profondeur de l'eau ou à la distance du rivage; cependant, les femelles capturées en train de frayer sur des substrats fermes (sable et gravier) étaient significativement plus grosses que les femelles capturées en train de frayer sur des substrats mous (boue, débris de bois). Bien que tous les nids observés sur les différents substrats aient contenu des oeufs, la relation positive entre la taille et la fécondité chez les femelles de ce crapet semble indiquer que les mâles qui font leur nid sur un substrat ferme ont un avantage évolutif parce qu'ils attirent des femelles de plus grande taille.
[Traduit par la Rédaction]

Introduction

Fish in north-temperate water bodies rely heavily on energy reserves for over-winter survival because feeding activity is severely restricted during long periods of low temperature (Keast 1968; Shuter and Post 1990). Since allometric relationships between body size and metabolic rate (negative) and between body size and energy stores (positive) exist in fish, small individuals are thought to have higher rates of over-winter energy depletion than larger individuals (Shuter and Post 1990).

Size-dependent differences in energy reserves between large and small individuals may result in asynchrony in the timing of reproduction. Noltie and Keenleyside (1987) found that larger, older male rock bass (*Ambloplites rupestris*) nested and spawned earlier in the season than smaller, younger males. In addition, Ridgway et al. (1991) found that small male smallmouth bass (*Micropterus dolomieu*) initiated reproductive activity later in the season than larger males. They

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suggested that small fish may initiate reproductive activity later in the season because they require more time to replenish over-winter energy deficits before allocating energy to reproduction.

Body size may also influence mating success in nesting male centrarchids. Large males may be better able to defend nests and provide care for their offspring than smaller males (Noltie and Keenleyside 1986; Jennings and Philipp 1992). Noltie and Keenleyside (1986) found that large male rock bass were chosen preferentially by females, renested more often, and had higher reproductive success than smaller males. Competition between males may prevent small individuals from gaining access to females; alternatively, females may select mates on the basis of phenotypic characteristics such as body size or reproductive traits such as nest size (Green 1992; Petrie 1992). In any case, if large body size in males leads to an increase in their reproductive fitness, females should choose to spawn with larger males.

If the quality of a male's nest influences brood survival, then it would be expected that certain nest characteristics would be sought by males and be more desirable to females. For example, Keenleyside (1979) suggested that eggs laid on firm substrates are likely less subject to smothering, since fanning by parental males would be more effective in keeping the nest free of fine debris. Although parental male pumpkinseeds (*Lepomis gibbosus*) have been reported to construct nests on a wide range of substrates such as marl, sand and gravel, rubble, and woody debris (Breder 1936; Ingram and Odum 1941; Miller 1963; Clark and Keenleyside 1967; Colgan and Ealey 1973), several studies have demonstrated that when given a choice, they prefer to nest on firm, small aggregates (Ingram and Odum 1941; Colgan and Ealey 1973). Assuming that there is an advantage to nesting in particular substrates, females should select mates on the basis of nest substrate or any other nest characteristics that may improve brood survival.

The objectives of this study were (*i*) to examine the relationship between body size and the timing of reproduction in nesting male pumpkinseeds; and (*ii*) to determine if parental male body size and (or) nest characteristics influence female choice. We predicted that if the seasonal timing of reproduction within a water body is related to body size and energy reserves, small individuals should nest later in the season than larger individuals. We also predicted that if parental male body size is a trait that influences female choice, large parental males should be preferentially selected over smaller males by spawning females. Finally, assuming that male preference for a firm nesting substrate is related to a survival advantage for the young, we predicted that a higher proportion of males nesting on sand and gravel substrate would obtain eggs than those nesting on softer, finer substrates.

Materials and methods

Study site and population characteristics

The study was conducted from early May to late August 1991 in Little Round Lake, Ontario (44°48'N, 76°42'W). Little Round Lake is a small, deep meromictic lake with a steep basin and narrow littoral zone (McNeely 1975). The life-history characteristics of the pumpkinseed population and the seasonal reproductive patterns of females in the lake have previously been reported in Danylchuk and Fox (1994*a*, 1994*b*) and Fox (1994).

Pumpkinseeds in Little Round Lake grow more slowly and mature earlier in life than other populations in eastern and central Ontario (Fox 1994). The size–age distribution of pumpkinseeds in Little Round Lake has also been shown to be skewed towards small/young fish, with individuals less than 4 years of age representing more than 90% of the population (Danylchuk and Fox 1994*b*). Furthermore, the density of pumpkinseeds in Little Round Lake is higher than in other small lakes in eastern and central Ontario (A. Danylchuk and M. Fox, unpublished data).

The pumpkinseed is the only species of sunfish inhabiting Little Round Lake, eliminating the possibility of interspecific competition for nesting habitat and interspecies hybridization (Clark and Keenleyside 1967). Little Round Lake is devoid of piscine predators of adult pumpkinseeds, such as northern pike (*Esox lucius*) or largemouth bass (*Micropterus salmoides*). Other fish species in Little Round Lake include yellow perch (*Perca flavescens*), banded killifish (*Fundulus diaphanus*), and stocked brook (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*).

Nesting activity

Nests guarded by parental males were located while snorkeling or by walking along the shoreline. Parental males were captured off nests with a large dip net or by chasing them into a funnel trap. Captured individuals were measured (total length (TL), in millimetres), weighed (to the nearest 0.5 g), and individually marked by clipping a combination of hard- and soft-rayed fins, and scales were removed for age determination. Males were then held in the water in a dip net while their nest was numbered and the nest diameter, distance of the center of the nest from shore, and water depth were measured. In addition, the substrate in the centre of the nest was classified into one of four categories (sand–gravel, silt, rock, and matted vegetation), and the presence or absence of eggs was noted. Total time for processing the males and assessing their nest was usually less than 3 min per individual. Once processed, parental males were released and observed to ensure that they returned to their nests.

Nests were monitored for parental occupation and spawning activity on a daily basis during the peak period of reproductive activity (May 27 to June 21), and at 2- to 5-day intervals from June 21 to August 13. When a spawning bout was observed, the spawning pair was captured and unmarked parental males and spawning females were processed as described above. When a clipped fish was recaptured, its length and mass were remeasured. The length of time a male guarded his nest was estimated from the dates he was first and last seen on the nest. In estimating this parameter, we used only males that were captured at least twice and for which the period of uncertainty due to visitation interval was 2 days or less. When a male initiated or left a nest on a day when visitation did not occur, the date of initiation or termination was assumed to be the midpoint between the visitation periods. Male pumpkinseeds frequently rear more than one brood concurrently in the same nest, so the period a male remains at a nest can be longer than the elapsed time from nest building to guarding the fry from an initial mating.

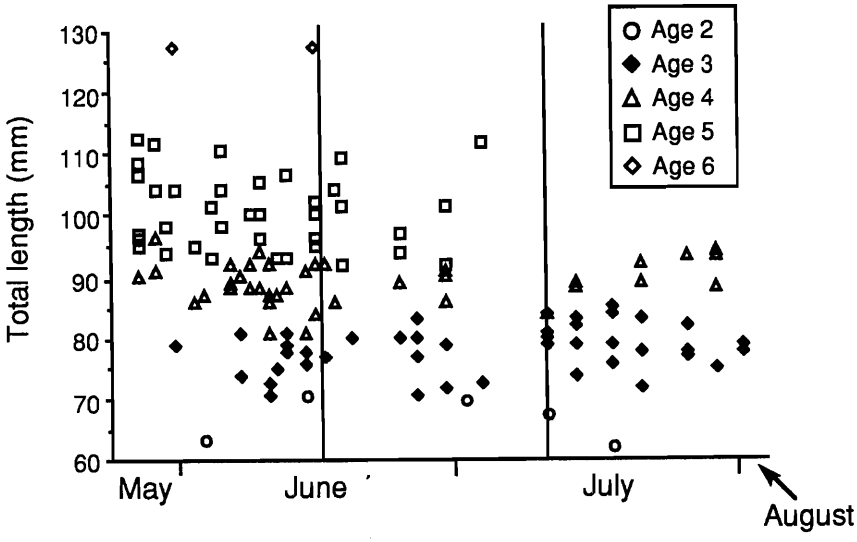
Age determination

Age was determined by reading acetate impressions of scales, with annuli identified using the criteria outlined by Regier (1962). The scale-aging technique used was cross-checked by comparing scale and otolith ages in a subsample of fish captured in late May (Danylchuk and Fox 1994*b*).

Data analysis

To test for seasonal trends in parental male body size, the spawning season was divided into three equal trimesters: May 27 – June 21; June 22 – July 17; and July 18 – August 13. We then compared

Fig. 1. Lengths and ages of nesting parental male pumpkinseeds collected during the 1991 spawning season. Vertical lines delineate trimesters.



TL, mass, and age of males initiating nests during each trimester of the spawning season, using one-way analysis of variance and Tukey's HSD test for paired contrasts.

Further examination of seasonal trends in nest initiation, duration of nesting, and body condition of nesting males was based on the division of nesting males into two length/age-class groups. A total length of 80 mm was used to delineate small and large males. This size was chosen because it generally separated 2- and 3-year-old males from the older age-classes during the period of study. However, there were some 3-year-old males that exceeded 80 mm TL. Therefore, data were analyzed according to age as well as size, with 2- and 3-year-old males classified as young and those aged 4 years and above as old. When statistical tests gave results synonymous with length and age groups, we report the actual test statistics for length comparisons only.

As an indicator of gross nutritional state, we calculated Fulton's condition factor ($K = 100 \times \text{mass (g)} \times (\text{TL (cm)})^{-3}$) for parental males collected during the spawning season (Weatherley 1972). The mean condition factors for length and age groups were compared among reproductive trimesters, using one-way analysis of variance to determine if body condition could account for size-related variation in the timing of reproduction.

Pearson's correlation was used to determine whether there was a size-dependent relationship between parental males and their mates. Correlations were also used to examine relationships between nest diameter, water depth, distance from shore, and parental male body size (TL and mass), and to determine if the body size of spawning females (TL and mass) was related to nest characteristics. One-way analysis of variance was used to determine if nest substrate type varied among male age and length groups.

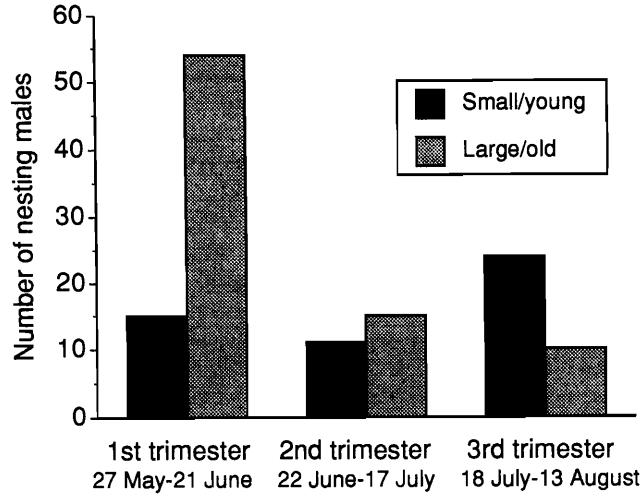
Results

Nesting activity

The first nest was observed on 27 May and the last nest was initiated on 2 August. In all, 139 nests were observed during the spawning season. A total of 129 parental males were captured, and 3 of these were recaptured on new nests later in the season.

Parental males ranged in size from 62 to 125 mm TL (4–36 g) and in age from 2 to 6 years (Fig. 1). During the first trimester, approximately 80% of the nesting males were large individuals (Fig. 2). However, as the season progressed, the proportion of large males in the nesting population decreased until more than 70% of the males nesting in the last trimester were small. The lengths and ages of parental males initiating nests were significantly different between the first and last trimesters (Tukey's test, $P < 0.05$). However, all of the nesting males observed were successful in obtaining eggs, regardless of body size or trimester of reproduction.

Fig. 2. Number of small/young and large/old parental males observed nesting in the first, second, and third trimesters of the 1991 spawning season.



The average period a male remained at his nest was 15.1 ± 2.6 (SE) days for the 24 individuals we could reliably assess. This duration was not related to body length, mass, or age of parental males (TL: $r = -0.04$, $P = 0.85$). The average period of time that males remained at their nest was longer in the second trimester (20.8 days) than in either the first (11.7 days) or third trimester (11.3 days), but the difference was not statistically significant ($F_{[2,21]} = 1.6$, $P = 0.23$).

Fig. 3. Condition factor of small/young and large/old nesting males during each trimester of the spawning season. Vertical bars represent ± 1 SE. Numbers above the bars are sample sizes.

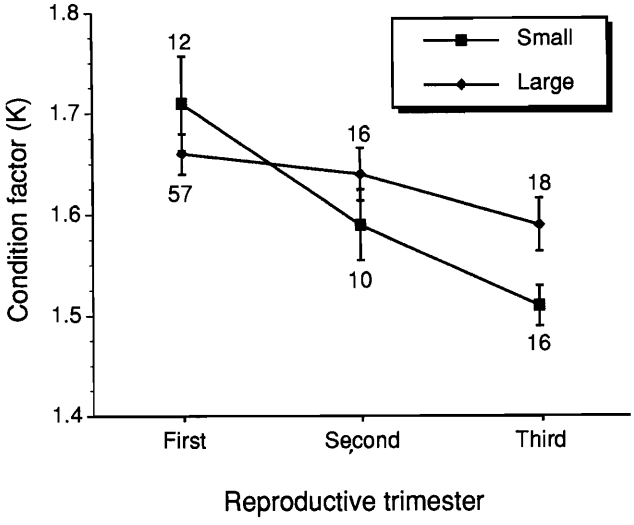


Table 1. Relationships between parental male body size, spawning female body size, and measured nest characteristics.

	Body size (TL), mm			
	Parental male		Spawning female	
Nest characteristic	r	P	r	P
Diameter	0.41	0.0001	0.10	0.52
Water depth	0.17	0.09	−0.02	0.88
Distance from shore	0.08	0.43	−0.004	0.98

Body condition

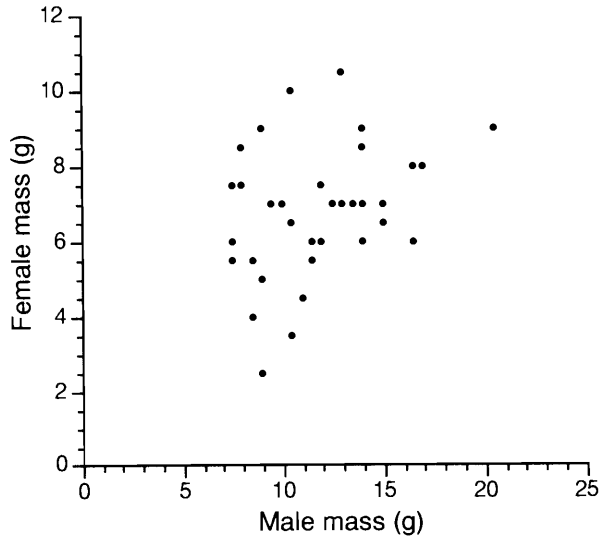
The condition factor of nesting males ranged from 1.3 to 2.0 over the course of the study. Condition factor generally declined over the breeding season in both small/young and large/old nesting males (Fig. 3); however, the difference in large/old males was not significant among trimesters (TL: $F_{[2,88]} = 1.6$, $P = 0.21$). In contrast, small/young males that nested during the last reproductive trimester were in significantly poorer body condition than those that nested during the first trimester (Tukey's test, $P < 0.01$).

The condition factor of small/young nesting males was higher, on average, than that of large/old nesting males in the first and second trimesters; however, the differences were not significant ($F_{[1,67]} = 1.0$, $P = 0.31$; $F_{[1,24]} = 1.6$, $P = 0.21$, respectively). During the last trimester the difference in body condition between small and large males was nearly significant ($F_{[1,32]} = 3.5$, $P = 0.07$), and there was a significant difference in this trimester when age groups were compared ($F_{[1,32]} = 4.6$, $P = 0.04$).

Nest characteristics and spawning pairs

Nest diameter was positively correlated with parental male body length; however, water depth and the distance of the nest from shore were not (Table 1). Within trimesters, correlations between male body length and both water depth and distance from shore were generally higher than those obtained with aggregate seasonal data ($0.06 < r < 0.36$), but none of these relationships were significant. The main substrate types used by parental males to build nests were sand–gravel (68.2%) and silt – wood debris (19.4%). To a lesser extent, bare rock and matted vegetation were also used (10.1 and 2.3%, respectively). The proportion of nests found in the various substrates did not differ throughout the reproductive season ($\chi^2 = 6.8$, $P = 0.34$), nor was the size/age of males nesting in the four substrate types significantly different (TL: $F_{[3,128]} = 0.58$, $P = 0.63$).

Fig. 4. Total length of females captured spawning in 1991, relative to the length of their mate.



Spawning bouts were observed between 28 May and 13 August. A total of 35 spawning pairs were captured throughout this period. Spawning females that were captured ranged in size from 58 to 86 mm TL (2.5–10.5 g) and in age from 2 to 5 years (Fig. 4). Body size (length and mass) of these females was negatively correlated with elapsed days into the spawning season (length: $r = -0.35$, $P = 0.04$). Although nesting males also showed a decline in body size over time (Fig. 1), the correlation between male and female body length in spawning pairs was not significant ($r = 0.25$, $P = 0.15$). The strength of this correlation increased when mass was used instead of length ($r = 0.33$, $P = 0.057$). Male and female body sizes of spawning pairs were not significantly correlated within any of the reproductive trimesters ($r < 0.44$, $P > 0.20$ in all cases).

There was no relationship between the size of spawning females and parental male nest diameter, nest water depth, or distance of the nest from shore (Table 1). When these relationships were examined within trimesters, correlations between female body size and male nest characteristics were higher than those obtained with aggregate seasonal data ($0.21 < r < 0.48$), but none of these relationships were significant. Females observed spawning in sand–gravel were larger than those observed spawning in silt – wood debris nests (77.0 vs. 73.0 mm TL; $F_{[1,32]} = 4.12$, $P = 0.051$), and the difference in mass of females spawning in these respective substrates was significant (7.3 vs 6.0 g; $F_{[1,32]} = 5.3$, $P = 0.028$). However, since all nests observed

contained eggs, we were unable to determine whether any of the nest characteristics observed affected spawning success.

Discussion

Large males in Little Round Lake initiated nesting activities earlier in the season than small males. This finding is consistent with the results of two other studies conducted on populations of rock bass (Noltie and Keenleyside 1987) and smallmouth bass (Ridgway et al. 1991) and provides additional support for the size-dependent over-winter energy-deficit hypothesis proposed by Ridgway et al. (1991).

Small parental males in Little Round Lake may require more time than large males to compensate for an over-winter energy deficit before allocating resources to reproductive activity. Shuter et al. (1980) showed that for smallmouth bass, smaller individuals accumulate a higher over-winter energy deficit than larger individuals. Small females in five of six pumpkinseed populations studied (including Little Round Lake) have been shown to allocate energy to gonadal development later in the season than large females (Danylchuk and Fox 1994*a*). Thus, the annual schedule of gonadal recrudescence and reproductive activity of centrarchids may be directly affected by size-dependent differences in metabolism and energy stores (Ridgway et al. 1991).

Males unable to establish nests early in the season may postpone reproduction until the following season in order to grow to a more competitive size. Alternatively, if the probability of survival is low, waiting to spawn until the next season may eliminate the opportunity to reproduce altogether (Kozlowski 1992). Small males may have no choice but to spawn late in a given season in spite of the fact that this may result in reduced fitness of their offspring. Young of the year from late-season spawning events may not accumulate sufficient energy to successfully overwinter (Newsome and Leduc 1975; Oliver et al. 1979; Shuter et al. 1980; Post and Evans 1989; Shuter and Post 1990). Thus, poor survival of late-season young of the year may contribute little to the parent's annual reproductive fitness.

Small/young parental males spawning later in the season may also compromise their own over-winter survival. Our findings show that the condition of small parental males nesting late in the season was significantly lower than that of early-nesting small parental males. Thus, small parental males nesting late in the season may not accumulate sufficient energy reserves to survive over winter.

Although delayed seasonal reproduction in small male pumpkinseeds is consistent with the size-dependent over-winter energy-deficit hypothesis, it is also consistent with the hypothesis that the optimal proportion of the growing season devoted to growth decreases with increasing size and age of individuals (Kozlowski and Uchmanski 1987; Kozlowski 1991) if most of the growth occurs early in the season. The allocation of surplus energy first to growth and subsequently to reproduction and storage is considered an optimal strategy, assuming that conditions over the growing season are uniform for adult pumpkinseeds and their offspring, and that the energy allocated to reproduction is not carried past the end of the season (Kozlowski 1991). However, in the case of pumpkinseeds, much of the somatic growth occurs after reproduction (see Fox and Keast 1990), so the energy-switching scenario does not apply. The absence of this switching pattern may reflect the fact that conditions in the growing season are not uniform for young pumpkinseeds, as prey resources for young fish tend to peak early in late May – early June and decline through the summer until August (Keast 1980, 1988). Furthermore, there is a clear evolutionary advantage to producing offspring as early as possible in the growing season in the north-temperate zone because this gives the young a longer growing period, and as previously noted, body size going into the winter is critical to survival.

Another problem with explaining delayed reproduction of small male pumpkinseeds in Little Round Lake in terms of optimal allocation theory relates to their slow growth pattern. By back-calculating the size at annulus formation of a sample of immature males collected on 2 July 1990, we estimated that the average increase in length of small individuals from the start of that growing season to its midpoint was only 4.5 mm. The potential benefit of small individuals achieving a larger body size by means of a seasonal delay in reproduction appears to be minimal, whereas the potential cost in terms of increased mortality of young produced late in the season is likely to be substantial. We therefore conclude that the energy-deficit hypothesis is a more feasible explanation than optimal allocation theory for the body size – seasonal reproduction patterns observed in our study.

Because fecundity in fish is size-dependent, large females have more energy to invest in egg production than small females, and may therefore be more selective when choosing mates. If body size and aggression are positively correlated, large parental males should be better able to defend their broods, and thus be selected by large females. Several studies have examined or made reference to the aggressiveness of nesting male sunfish (Ingram and Odum 1941; Witt and Marzolf 1954; Keenleyside 1971; Colgan and Gross 1977), but none have directly tested the relationship between aggression and parental male body size. However, observations made in Little Round Lake suggest that some small parental males are more aggressive than their larger parental conspecifics (A. Danylchuk, personal observation). Therefore, large body size of parental male pumpkinseeds in Little Round Lake may not be associated with an increased willingness to defend a nest, and females may not be heavily influenced by this trait in the selection of mates. The weak correlation between male and female body size in spawning pairs suggests that this is the case.

In our study, all of the nesting males we identified received eggs from at least one female. Studies of other nesting centrarchids suggest that spawning success is usually high, although not as high as in Little Round Lake. Spawning success of nesting males ranged from 74 to 83% in a 5-year study of a bluegill population in Lake Opinicon, Ontario (Claussen 1991), and from 64 to 76% in a 2-year study of a longear sunfish (*Lepomis megalotis*) population in Jordan Creek, Illinois (Jennings and Philipp 1992). The high degree of nesting success of male pumpkinseeds in Little Round Lake is probably the result of a high ratio of mature females to nesting males. Assuming that the number of nests observed in 1991 was close to the total number constructed, the ratio of mature females to nests would have been approximately 22:1 (calculated from population data in Danylchuk and

Fox 1994*b*); the result of high population density, a very early mean age at first maturity (Fox 1994), and the narrow littoral zone in Little Round Lake (McNeely 1975). In other pumpkinseed populations with a higher nest to mature female ratio, nesting success of males may be closer to that reported for other sunfish species.

Keenleyside (1979) suggested that large centrarchid females may select mates whose nests are constructed of sand–gravel to increase their reproductive fitness. However, Noltie (1982) found that female choice in rock bass was not related to nest site selection, and later, Noltie and Keenleyside (1986) found that nest "quality" had no measurable effects on reproductive success in this species. Our study did not directly demonstrate female selection by substrate type, since all observed nests in Little Round Lake obtained eggs and we did not quantify the number of eggs in individual nests. However, we did show that the females that spawned in nests constructed in coarse, firm substrate were significantly larger than those that spawned in nests constructed in soft, silty substrate. Because fecundity is a function of body size, these data suggest that a selective advantage for males nesting in a particular substrate type may accrue because larger females are attracted.

In summary, our study shows that size-related variation in the timing of reproduction occurs in male pumpkinseeds, and provides further evidence supporting the hypothesis that this variation is the result of a size-dependent over-winter energy deficit. The difference in body size of females electing to spawn in various substrates has not been previously studied, and suggests a potential mechanism by which the choice of nesting site by males can provide a selective advantage. Further studies of centrarchids are required to assess the relationship between body size and number of eggs spawned in a bout, and the relationship between substrate type and egg survival.

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