Effects of social structure on reproductive activity in male fathead minnows (*Pimephales promelas*)

Andy J. Danylchuk and William M. Tonn
Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

The selection of alternative reproductive phenotypes is often thought to be the result of physiological state, with small individuals forced energetically to postpone the allocation of resources to reproduction. However, for male fathead minnows (*Pimephales promelas*), we show that seasonal reproductive activity is modulated by social status. In enclosure and pond experiments, small males advanced their reproductive condition, held nesting territories, and spawned earlier in the reproductive season only when large males were absent or removed from the population. Since differences in the timing of reproduction among small males were not size- or condition-dependent, the common explanation for the selection of alternative reproductive phenotypes, based on state-dependence, is insufficient. In the absence of large, socially dominant individuals, small males produced comparable numbers of offspring as the treatment with large males, although the offspring of these uninhibited small males were smaller at the end of the growing season than the young of large males. Thus, interactions among conspecifics may account for much of the phenotypic diversity observed within and among natural fathead minnow populations, through their direct and indirect effects on growth, recruitment and survival. *Key words:* alternative phenotypes, conditional strategy, fathead minnow, *Pimephales promelas*, reproduction, social environment, status-dependent. *[Behav Ecol 12:482–489 (2001)]*

To increase fitness, organisms must adopt a strategy that effectively trades off energetic resources between reproduction versus somatic maintenance and growth (Kozlowski, 1992; Stearns, 1977). Traditionally, selection of a particular strategy within a population was thought to be frequency-dependent and based on an average fitness of alternative reproductive phenotypes for each sex (e.g., Gross, 1991). However, the often extreme plasticity of reproductive phenotypes within sexes (Gross, 1984; Starks and Reeve, 1999) suggests that individuals make their life history trade off because of subtle differences in their immediate surroundings, and that those decisions may not have equal average fitness except at the switchpoint between alternative phenotypes (reviewed by Gross, 1996). Consequently, ecologists have begun to consider the notion that alternative phenotypes result from individuals switching among tactics within a conditional, rather than an alternative, or mixed, strategy (Gross, 1996).

Within a conditional strategy, switching between alternative reproductive tactics is commonly thought to be state-dependent (Gross, 1996; McNamara and Houston, 1996). Under this model, state is based on bioenergetics and an individual's physiological condition, with factors such as food supply (Kvarnemo, 1997), nutrition (Tartar and Carey, 1995), and habitat availability (Williams et al., 1995) influencing when and how energy will be allocated to reproduction.

The timing of reproductive activity, in particular, is often size-dependent (Diana, 1995; Gauthreaux, 1978), and nowhere is this more frequently documented than in fish (e.g., Carscadden et al., 1997; Danylchuk and Fox, 1994, 1996; Foote, 1988; Ridgway et al., 1991). Because of indeterminate growth, fish continue to increase in size after maturing and reproductively active individuals can therefore range consid-

erably in body size. Consistent with models of state-dependent selection, size-dependent differences in the timing of reproduction in fishes are commonly explained by variation in physiological condition (e.g., Danylchuk and Fox, 1994, 1996; Ridgway et al., 1991). Small fish should require more time to replenish over-winter energetic deficits than large fish because of their higher rates of energy use and lower available fat stores. As a result, small fish are forced to delay reproduction, resulting in asynchronous breeding activity between large and small individuals (Cargnelli and Gross, 1997; Ridgway et al., 1991).

In contrast to state-dependence, more recent selection models based on a conditional strategy suggest that an individual's social status drives the decision between alternative tactics (see Gross, 1996). In status-dependent selection, individuals use social interactions to evaluate their competitive ability in a population and the decision among alternative tactics is driven by the outcome of those interactions (Gross, 1996).

There is ample evidence that social interactions can be a potent force in regulating reproduction for a wide variety of organisms (reviewed in Huntingford and Turner, 1987). Individuals with higher social status can alter specific reproductive processes, such as ovulation in subordinate conspecifics by disrupting discrete neural and endocrine pathways (Bronson, 1985). Dominant individuals can also influence more general reproductive functions of subordinates, such as their ability to hold a reproductive territory (Bronson, 1985; Huntingford and Turner, 1987; Stamps, 1994).

Thus, an alternate explanation for variation in the timing of reproduction is that large individuals have a higher status in the population and socially interfere with the breeding opportunities of smaller individuals (Schultz and Warner, 1989). Large individuals will often dominate when competing for reproductive sites or for access to mates (Munro, 1990). Small individuals may thus evaluate their status from social encounters with larger, more dominant individuals and choose between alternative reproductive tactics accordingly. Consistent with this, the presence of large males has delayed testes de-

velopment and timing of reproductive activity of small males in laboratory experiments (Borowsky, 1973; Bushmann and Burns, 1994).

Evidence for social control of reproductive activity also exists for natural populations. The removal of large females from isolated coral heads advanced the ovarian development and reproductive activity of smaller females in the temperate wrasse, *Pseudolabrus celidotus* (Jones and Thompson, 1980). As well, the number of adult males and the size of juveniles affected the proportion of maturing individuals in a population of variable platyfish (Borowsky, 1978). More recently, Rodd et al. (1997) found that interactions with conspecifics influenced development and size at maturity of male guppies, *Poecilia reticulata,* which, in turn, may have influenced reproductive status.

Although this evidence indicates that social status can influence the timing of reproduction in individual fish, few studies have examined the effects of social control of reproduction at the population level. Anecdotal evidence suggests that social status plays a role in the timing or occurrence of reproduction of male fathead minnows (*Pimephales promelas*; Hodson PV, personal communication; Tonn WM, personal observations). As part of our investigations into the factors influencing the population structure and life history characteristics of fathead minnows inhabiting boreal lakes, we conducted two field experiments in small ponds to determine if social environment modulates the timing of reproductive activity in male fatheads and, if so, how this might influence population growth or regulation. We predicted that if the decision to reproduce is state-dependent, differences in the social environment should have little impact on the seasonal timing of reproduction in male fathead minnows. If, however, the social environment influences the decision to reproduce, individuals of lower status should accelerate reproduction when dominant conspecifics are absent.

METHODS

We conducted an enclosure experiment in a small pond at the Meanook Biological Research Station (MBRS), Alberta, Canada, to determine whether social environment affects the seasonal timing of reproductive activity in small male fatheads. Given the results, we conducted a second experiment in larger dugout ponds to assess the effects of social structure on reproduction at the population level.

Enclosure experiment
Small males (50–58 mm) were stocked in enclosures under three different social regimes: (1) 15 small males and 5 large (63–70 mm) males, SM + LM; (2) 15 small males and 5 large males, with large males removed after approximately 3 weeks, SM + LM(R); and (3) 20 small males without large males, SM. Five mature females, + F, were also added to each enclosure to facilitate reproduction. We predicted that if large male fatheads socially interfere with the reproductive activity of smaller males, then some small males in the SM + F social group should become reproductively active earlier in the season than small males in the SM + LM + F or SM + LM(R) + F social groups. Moreover, if large males are socially dominant, then reproductive activity of small males in the SM + LM(R) + F social group should increase once the large males are removed relative to males in the SM + LM + F social group.

Five blocks of three enclosures each were built using impermeable polyethylene curtains, supported by wooden frames driven into the substrate of the pond. Sand and rocks secured the bottom of enclosures to the substrate. Enclosures were 3 × 2 m and we maintained pond water levels within

the enclosures at approximately 1 m. As a result, fish densities within the enclosures (4 fish/m³) approximated densities of natural populations within the region (Danylchuk AJ, Tonn WM, unpublished data). Each social group was randomly allocated to one enclosure within each block.

During the breeding season, reproductively active males establish territories around the underside of structures, such as snags, lily pads (Andrews and Flickinger, 1969; Wynne-Edwards, 1932), and introduced nesting substrates (Benoit and Carlson, 1977). From these territories, males actively court females and, if courtship is successful, females will deposit a batch of eggs on the underside of the defended structure via an ovipositor. As such, we added floating fence boards anchored to bricks to serve as spawning substrate. Seven nest boards were deployed in each enclosure (one large [100 × 4.5 cm], three medium [35 × 4.5 cm], and three small [25 × 4.5 cm]) and the placement of nest boards was identical for all treatments.

In early June, just prior to the onset of reproduction, we collected fatheads from a lake 70 km north of MBRS. Fish were transported to MBRS and allowed to acclimate for 4 days in large outdoor tanks. During this period we fed the fish freeze-dried Daphnia and flaked food.

Following the acclimation period, fish were measured (total length, mm), weighed (wet, 0.01 g) and sorted according to gender based on the presence of secondary sexual characteristics. We selected fish so as to minimize the range in total length within each gender or size group. The mean size of individuals in each group did not differ among social treatments (ANOVAs, $p > .1$).

We assigned each fish a score based on the degree to which secondary sexual characteristics were developed. During the breeding season, fatheads are sexually dimorphic. Reproductively active males develop rows of nuptial tubercles on the front of the head and lower jaw, a thick, spongy dorsal pad anterior of the dorsal fin for cleaning eggs, and dark body coloration broken by two golden vertical bands (Flickinger, 1969; Markus, 1934). Females develop an extrusion of the gonadal papilla (ovipositor) and a distended abdomen when gravid (Flickinger, 1969). Juveniles lack all of these characteristics, although we can use subtle differences in head, anal fin, and gonadal pore morphology to help identify gender prior to the onset of maturity; immature males have a broader, rounder head and a larger anal fin than females. As well, although quite small, the ovipositor appears well before females begin to mature and can be used as a final trait to differentiate gender in immature fatheads (Danylchuk AJ, personal observations).

The development of the secondary sexual characteristics is positively correlated with gonadal development; Smith (1978) found that peak tubercle and dorsal pad development in males coincided with the final stages of spermatogonia development and peaks in the gonadosomatic index. Therefore, secondary sexual characteristics not only provide a means of differentiating gender, but the degree to which they are developed is a good indicator of reproductive condition.

We scored males according to the development of tubercles and dorsal pad (maximum possible score = 6) and females according to the development of the ovipositor and the degree to which the abdomen was distended (maximum = 5; Table 1). Large males used in the experiment had secondary sexual characteristic scores of 5–6; all experimental females had scores of 4–5. Small males were all reproductively undeveloped and had a score of zero; we used the morphology of the head, gonadopore, and anal fin to sex fish in this size category (see below for validation procedure).

To determine the repeatability of our assignments of secondary sexual characteristic scores, we placed 20 fish at vari-

Table 1
Scoring criteria for male and female secondary sexual characteristics

	Males		Females	
Score	Tubercles[a]	Dorsal pad	Ovipositor	Abdominal distention
0	No visible sign of tubercles	No visible sign of dorsal pad	No visible sign of ovipositor	Fish streamline, no noticeable lateral distention
1	Tubercles visible as white disks, not protruding above body surface	Epidermis between head and dorsal fin becoming 'spongy' along medial ridge	Ovipositor visible as small protrusion at gonadopore; soft and flaccid	Abdomen becoming somewhat distended laterally (when viewed dorsally)
2	Tubercles protruding above body surface but not sharp	Dorsal pad increasing in width; thickening but only a slight nape behind head	Ovipositor becoming rigid and increasing in length	Abdomen extremely distended; streamline form greatly compromised
3	Tubercles prominent and sharp	Dorsal pad wide and thick, forming a sharp nape posterior to head when viewed laterally	Ovipositor large and very rigid	

[a] Modified from Smith (1978).

ous stages of development in individual 1–L beakers and scored them according to external reproductive traits. We wrote the score on a label, adhered it to the bottom of the beaker, and after 1 h randomly rearranged the beakers and re-evaluated the secondary sexual characteristics of the fish. We repeated this process three times. We then coded the scores of individual fish as change or no change between trials and examined the consistency of scoring using Cochran's Q test for repeated measures of dichotomous variables (Zar, 1996). In addition, we compared the mean scores among these trials with a Kruskal-Wallis test to determine if changes in scores resulted in significantly different mean scores between trials.

To keep track of fish throughout the enclosure experiment, we batch-marked small males, large males, and females with distinct colors of non-toxic acrylic paint, which was subcutaneously injected on either side of the body just posterior to the base of the dorsal fin using a 1 cc tuberculin syringe with 23 ¾ G needle (Unger, 1983). We monitored marked fish for 24 h prior to stocking to determine if there were any adverse effects of marking. If a fish was considered distressed (six of 375 marked fish), it was replaced with an individual of similar size, gender, and secondary sexual characteristic score.

We stocked fish into enclosures on 14 June 1996. To examine the reproductive condition of individuals in each social group, we collected a subsample of fish with minnow traps approximately every 10 days. We measured, weighed, and scored individuals in each gender group for secondary sexual characteristics, then returned them to their respective enclosure. Concurrently, we checked nest boards for eggs.

We added Nutrafin® flaked food to each enclosure at 5% body mass per day throughout the experiment to ensure survival and reduce or eliminate effects of intraspecific competition for food resources. Feeding also helped control effects of density on food intake once adult males were removed from the SM + LM(R) + F social group.

Pond experiment
We divided three dugout ponds (30 m × 12 m) in half with an impermeable polyethylene curtain secured firmly into the substrate. We collected fatheads from a small lake 35 km southeast of MBRS, and measured, weighed, and sorted individuals by gender and size. For each gender group, we

scored individuals according to their secondary sexual characteristics and batch-marked fish with acrylic paint for future identification.

On 3 June 1997, we stocked SM + LM + F and SM + F social groups in either half of each pond using the same density (4 fish/m³) and ratios among small and large males and females as in the enclosure experiment. Because pond halves differed somewhat in size, total numbers stocked varied between 291 and 385 fish. To provide spawning substrate, we placed 17 nest boards in each pond half. We maintained the water level in each pond at 1 m throughout the experiment and placed a temperature data logger in ≈30 cm of water in each pond half, recording water temperature hourly throughout the experiment. The thermal regime of each pond half was characterized by calculating mean monthly cumulative degree-days (>15°C) for each treatment.

To assess the reproductive condition of individuals during the experiment, we made weekly collections of ≈100 fish from each pond half using unbaited minnow traps. Pond halves were processed in random order and the scorer of reproductive condition was unaware of the treatment group of the fish. We sorted fish by their acrylic mark for gender and size-class, measured, weighed, and scored individuals according to their secondary sexual characteristics, and then returned them to their respective pond half. To validate our sexing criteria, we determined the proportion of fish initially classified and marked as reproductively inactive males that later developed into clearly distinguishable males (based on secondary sexual characteristics).

To examine reproductive patterns, we checked nest boards weekly for the presence of eggs. When conditions permitted (e.g., low turbidity, bright sunshine), we conducted timed snorkeling surveys to classify the individuals holding nesting territories as either a large or small male. We defined a male as holding a nesting territory if he was observed aggressively defending the underside of a nest board, regardless of whether eggs were present.

To determine whether, in the absence of large males, small males were able to produce similar numbers and sizes of young as large males, and contribute equally to recruitment of young fish into the population, we collected young-of-the-year (YOY) towards the end of the growing season. We made five 5-m tows with a net (30 cm diameter, 2 mm mesh) and

three 5-m passes with a portable electroshocker. We euthanized young-of-the-year with tricaine methanesulfonate (MS 222), preserved them in 80% ethanol, and later enumerated and measured them (standard length, SL) to the nearest 0.1 mm.

Data analysis

In all cases, we determined mean values from replicates of each social group. Differences among social groups were considered marginally significant if $.1 > p > .05$ and significant if $p < .05$. We used a mix of parametric (Student's *t* test, one-way ANOVA) and nonparametric statistics (Kruskal-Wallis, Mann-Whitney *U* test, Kolmogorov-Smirnov two-sample test) to test our predictions, depending on whether the data were continuous or categorical, respectively. All statistical analyses were performed using Systat version 5.2 for the Macintosh.

RESULTS

The score repeatability test confirmed that our criteria for scoring secondary sexual characters were stable and repeatable. Among the three trials, repeated scoring did not differ (Cochran's *Q* test, $Q = 0.67$, $p > .05$) and the changes that did occur (20% of the fish) did not alter mean secondary sexual characteristics scores among trials (Kruskal-Wallis, $H = 0.360$, $p = .835$).

Similarly, our criteria used to identify gender of reproductively inactive fatheads was quite reliable. Of the fish collected for the seven sampling periods in June and July of the pond experiment, less than 12% of those marked as small males developed into females (number of fish marked as small males examined per assessment period, 52–139; mean proportion of misclassified small males for each pond half, 8.0–11.2%; standard deviations, 3.1–6.8%).

Enclosure experiment

Small males in the SM + F social group developed secondary sexual characteristics more rapidly and to a greater extent than small males in either the SM + LM + F or the SM + LM(R) + F social groups (Figure 1a). Within the first 2 weeks, mean secondary sexual characteristic score of small males was two units higher in the former social group than the latter two groups (Kruskal-Wallis, $H = 4.57$, $p = .10$). Although scores of individuals varied considerably within the SM + F group and the distributions of scores among treatments was only marginally significant (K–S test, $p < .1$), 58% of small males in the group had scores of 5–6, compared with a combined total of 28% for the other two social groups.

The proportion of small males expressing fully developed secondary sexual characteristics (scores of 5–6) in the SM + LM + F social group peaked in early July at 22%, declining to 10% 10 days later. Although initially similar to the SM + LM + F group, the proportion of small males expressing fully developed secondary sexual characteristic scores in the SM + LM(R) + F social group continued to increase, from 30% to 50%, after removal of the large males. By mid-July, mean scores of small males in the SM + LM(R) + F and SM + F social groups were equal, and both were greater than those in SM + LM + F social group (Figure 1a).

Nesting activity and spawning began within 2 days of each other in all treatments (Figure 2a). The number of active nests did not differ among social groups for all assessment periods (one-way ANOVA, $p > .1$), likely due to the high degree of variability among replicates. Nevertheless, small males held territories only in the SM + F social group or once large males were removed from the SM + LM(R) + F social group (Danylchuk AJ, personal observations). Peak nesting activity occurred at the same time in all social groups, however, nest-
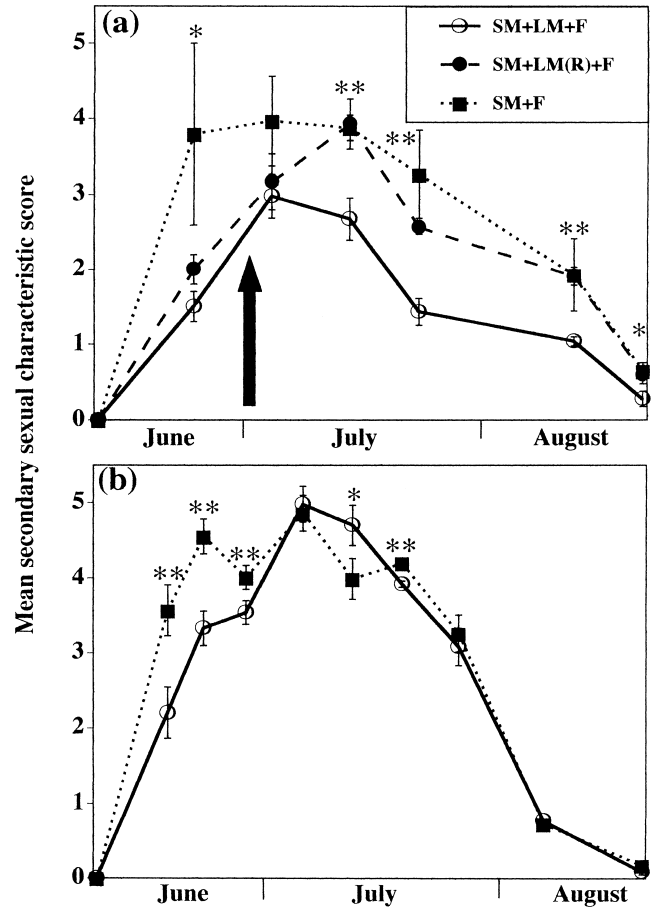

Figure 1
Mean secondary sexual characteristic score ($\pm$ SE) of small males for each social group sampled during the enclosure (a) and pond (b) experiments. The arrow in (a) indicates when large males were removed from the SM + LM(R) + F social group. $*p \leq 0.1$; $**p \leq .05$.

ing activity persisted longer in the SM + LM(R) + F and SM + F social groups than the SM + LM + F social group.

Despite these differences in development of secondary sexual characteristics and spawning activity among treatments, growth of small males was similar among the three social groups (Figure 3a; one-way ANOVAs on lengths, $p > .1$). Furthermore, fish condition measured as Fulton's condition factor (weight/length^{-3} × 100; Weatherley, 1972) did not differ among treatments during any assessment period (one-way ANOVA, $p > .1$), and temporal patterns of condition were similar for small males in all social groups.

Pond experiment

Small males in the SM+F social group developed secondary sexual characteristics more rapidly than small males in SM + LM + F social group, attaining significantly higher scores during the first three assessment periods (Figure 1b; Mann-Whitney *U* test, $p < .05$). The distribution of small males at each secondary sexual characteristic score also differed between treatments during this period (K–S test; $p < .05$), with over 62% of small males in the SM + F group having scores of 5–6, compared to 33% for the SM + LM + F social group. Mean secondary sexual characteristics scores of small males in the SM + LM + F social group eventually equaled that of small males in the SM + F social group, but this peak occurred approximately 2 weeks later in the season.
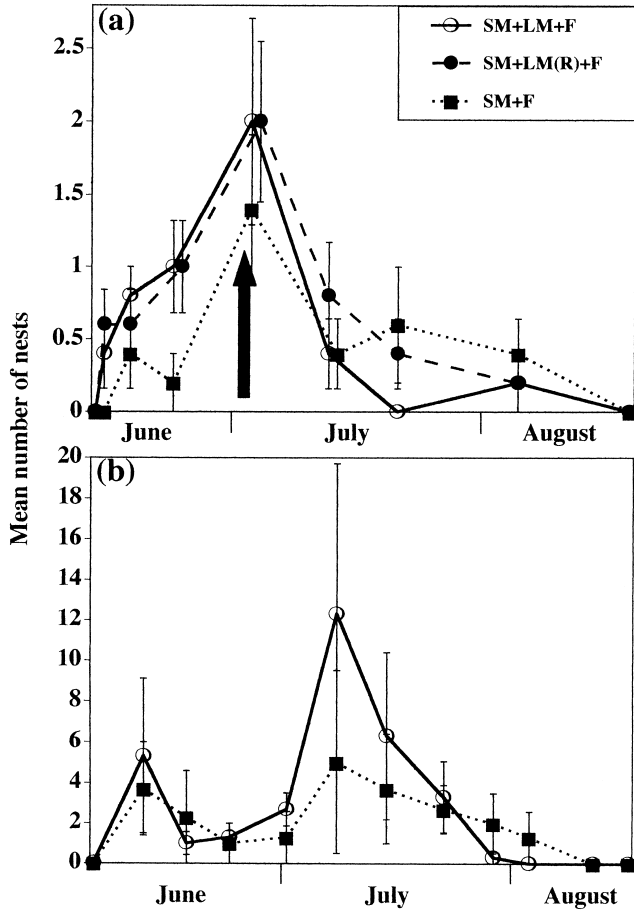
Figure 2
Mean number of nests observed (± SE) for each social group during the enclosure (a) and pond (b) experiments. The arrow in (a) indicates when large males were removed from the SM + LM + F social group.

Figure 3
Mean total length (± SE) of small males for each social during the enclosure (a) and pond (b) experiments. The arrow in (a) indicates when large males were removed from the SM + LM(R) + F social group. * $p \le .1$; **$p \le 05$.

In both social groups spawning began soon after fish were stocked and two distinct peaks in activity occurred, one in mid-June, the other in mid-July (Figure 2b). The mean number of nests observed during the first peak in spawning activity was similar for both social groups, but was higher for the SM + LM + F social group during the second peak than for the SM + F treatment. However, due in part to the high degree of variability among the three replicates, differences in mean number of nests between social groups were not significant for any assessment period (Student's t test, $p > .1$).

Thermal regimes at the end of each month during the experiment were similar for both social groups (Student's t test; June, $p = .29$; July, $p = .30$; August, $p = .31$), although mean monthly cumulative degree-days >15°C was 11–17% lower in the SM + F ponds than in the SM + LM + F ponds. Nevertheless, there were no apparent trends between thermal regime and the initiation and intensity of spawning activity for either social group.

Snorkeling surveys were conducted four times throughout the pond experiment. During each survey, the mean number of males holding territories was similar for the two social groups (Table 2; Mann-Whitney U test, $p > .05$). However, during the June survey, only large males held nesting territories and spawned in the SM + LM + F social group. These large males aggressively defended their nesting territories associated with nest boards, successfully deterring small males from establishing territories. This happened regardless of
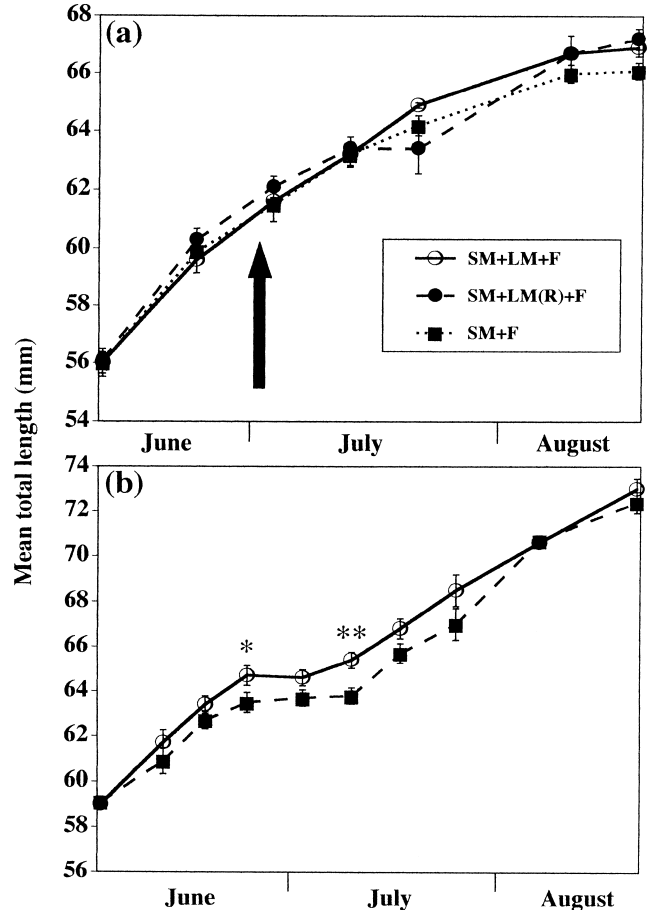
whether a large male was holding a territory on that particular board or on an adjacent board. By mid-July, some small males began to hold nesting territories in the presence of large males; however, the number of small males doing so was relatively low (Table 2).

The average length of small males increased by > 22%

Table 2
Mean number of large and small males observed holding nesting territories in each treatment (social group) during snorkeling surveys in the pond experiment

Survey date	Treatment	Mean no. territory holders		
		Large	Small	Unknown
11 June	SM + LM + F	15	0	0
	SM + F	—	12	0
14 July	SM + LM + F	14	1	3
	SM + F	—	17	0
23 July	SM + LM + F	7	2	1
	SM + F	—	9	0
4 August	SM + LM + F	0	0	0
	SM + F	—	0	0

Individuals that could not be identified as large or small males (using their paint mark) were classified as unknown territory holders.
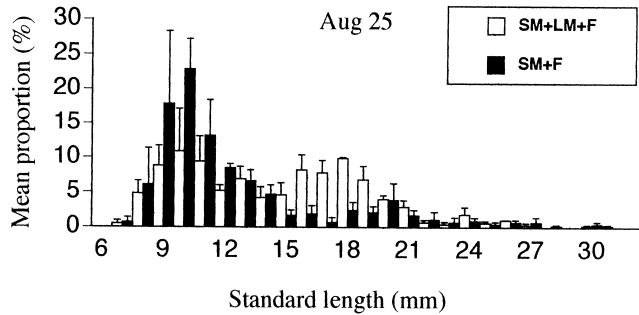
Figure 4
Length-frequency distributions (+ SE) of young-of-the-year fathead minnows collected on 25 August from the SM + LM + F and SM + F social groups during the pond experiment. The proportion of fish in each size category was determined for each replicate (sample sizes ranging from 93 to 277), from which means were derived for each social group ($n = 3$ for each group).

throughout the course of the experiment and did not differ between social groups when the experiment ended in late August (Figure 3b; Student's t test, $p > .1$). Between late June and mid-July, however, small males in the SM + LM + F social group were larger than small males in SM + F social group (Student's t test, period three, $p < .1$, period five $p < .05$). Despite these differences, condition of fish was similar between treatments during each assessment period (Student's t test, $p > .1$).

At the end of the summer (25 August), the number of YOY produced by each social group was similar (Student's t test, $p > .5$). Moreover, the size of YOY ranged between 7 and 31 mm standard length (SL) for both social groups (Figure 4) and mean size did not differ (Student's t test, $p > .1$). However, the size distributions of the YOY (measured by a randomly selected subsample of 75 YOY from each replicate pond for each treatment) differed between treatments (K–S test; $p < .05$). In the SM + LM + F social group, the distribution was bimodal (ca. 11 and 18 mm SL), with similar numbers in each mode, where the size distribution of YOY produced by the SM + F social group was unimodal (10 mm) with relatively few individuals >15 mm.

DISCUSSION

Our study indicates that social environment can modulate the seasonal timing of maturation and reproduction in male fathead minnows. In both the enclosure and pond experiments, the presence of large males inhibited or delayed the reproductive activity of small, initially immature males. Indeed, small males held nesting territories only after large males were removed from the population (enclosure experiment), or when nesting activity of large males began to drop off (pond experiment).

If small males postponed reproduction due to their physiological state, as is frequently postulated (e.g., Cargnelli and Gross, 1997), small males in better condition, regardless of their social group, should have initiated reproductive activity earlier. In contrast to this prediction, however, small males that initiated reproduction were neither larger nor in better condition than reproductively inhibited small males. In fact, inhibited males in the pond experiment displayed somewhat faster growth than small males that occurred without large males, particularly during peak weeks of nesting by large males and by the latter group of small males. Thus, it appears that social status influenced the bioenergetic trade-off decision of small males, consistent with the model of status-dependent selection (Gross, 1996).

In status-dependent selection, individuals select between alternative phenotypes based on their status relative to that of other individuals in the population (Gross, 1996; Pusey and Packer, 1997). For example, the choice between holding a reproductive territory or wandering among territories in male wood-carder bees, *Anthidium manicatum,* depended on relative, not absolute, body size (Starks and Reeves, 1999). Thus, when large territory holders were removed, they were replaced by small males that previously employed the wandering tactic (Starks and Reeves, 1999). Although we did not follow individuals in our experiments, the ability of small males to quickly become territory holders once we removed large males from the SM + LM(R) + F social group (enclosure experiment) shows that small males have the capacity to switch between alternative tactics in response to changes in their social status.

Since interactions among conspecifics affect individual status, the switchpoint between alternative phenotypes should be sensitive to ecological and demographic events that influence those interactions (Gross, 1996). For example, north-temperate fishes inhabiting small productive lakes and ponds are often subjected to low winter oxygen conditions causing overwinter mortality, or winterkill, that tends to affect larger individuals disproportionately (Barica and Mathias, 1979; Casselman and Harvey, 1975; Robinson and Tonn, 1989). Although the fathead minnow is tolerant of low winter oxygen conditions, the demographic characteristics (size structure and abundance) of fathead populations in northern lakes and ponds are influenced by the severity of oxygen depletion, which can vary dramatically from year to year (Danylchuk AJ and Tonn WM, unpublished data). As such, the relative size-dependent status of individuals likely varies from year to year in lakes that are prone to winter oxygen depletion, and is more stable in lakes that do not winterkill. Thus, it is reasonable to hypothesize that phenotypic diversity is greater in lakes that are prone to winterkill, because of selective pressures that result from social interactions and the drive to increase fitness when social environments change rapidly.

In north-temperate fishes, parents may try to maximize their fitness by producing young earlier in the breeding season. Spawning early in the season could increase the probability of the recruitment of young into the future population (reviewed in Daan and Tinbergen, 1997) because over-winter survival of small individuals is highly dependent on prior accumulation of sufficient energy reserves (Keast, 1968; Oliver et al., 1979; Post and Evans, 1989; Shuter and Post, 1990). In our pond experiment, the numbers of young produced in the two treatments (SM + F versus SM + LM + F) were similar, although the size distribution of young produced in the SM + F social group was skewed towards small body sizes at the end of the growing season. Because the intensity of competition for food in fathead minnows is related to their similarity in body size (Vandenbos, 1996), competition on YOY may have been stronger in the SM + F social group than in the SM + LM + F group, especially since the number of potential SM competitors in the former group was greater than in the latter at the end of the growing season (Danylchuk AJ and Tonn WM, unpublished data). Alternatively, the difference in size distributions between treatments may be the outcome of offspring expressing inherited paternal traits resulting from the indirect genetic effects of ''interacting phenotypes'' (sensu Moore et al., 1997) and the structure of the social environment. Regardless of the underlying mechanism, the potential reduced fitness of the uninhibited small males in the pond experiment is consistent with the model of status-dependent selection under a conditional strategy, which predicts unequal average fitnesses of alternative phenotypes (Gross, 1996).

Phenotypic diversity observed within and among fathead

minnow populations inhabiting boreal lakes is quite high (Danylchuk AJ, Tonn WM, unpublished data), and our results suggest that the structure of the social environment may account for much of this variability. At the population level we found that social environment affected the seasonal timing of reproduction in males and the size distribution of their young, which may, in turn, influence key processes such as recruitment and population growth. However, to refine these predictions, a better understanding of the mechanisms through which social interactions affect population-level processes is needed. Social structure within populations is both an environment and an evolving trait and, as a result, the potential population-level consequences of this structure are numerous.

REFERENCES

Andrews AK, Flickinger SA, 1974. Spawning requirements and characteristics of the fathead minnow. Proc Southeast Assoc Game Fish Comm 27:759–766.

Barica J, Mathias JA, 1979. Oxygen depletion and winterkill risk in small prairie lakes under extended ice cover. J Fish Res Board Can 36:980–986.

Benoit DA, Carlson RW, 1977. Spawning success of fathead minnows on selected artificial substrates. Prog Fish Culturalist 39:67–69.

Borowsky R, 1973. Social control of adult size in male *Xiphophorus variatus*. Nature 245:332–335.

Borowsky R, 1978. Social inhibition of maturation in natural populations of *Xiphophorus variatus* (Pisces: Poeciliidae). Science 201:933–935.

Bronson FH, 1985. Mammalian reproduction: an ecological perspective. Biol Reprod 32:1–26.

Bushmann PJ, Burns JR, 1994. Social control of male sexual maturation in the swordtail characin, *Corynopoma riisei*. J Fish Biol 44:263–272.

Cargnelli LM, Gross MR, 1997. Fish energetics: larger individuals emerge from winter in better condition. Trans Am Fish Soc 126:153–156.

Carscadden J, Nakashima BS, Frank KT, 1997. Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). Can J Fish Aquat Sci 54:781–787.

Casselman JM, Harvey HH, 1975. Selective fish mortality resulting from low winter oxygen. Verh Internat Verein Limnol 19:2418–2429.

Daan S, Tinbergen JM, 1997. Adaptation of life histories. In: Behavioural ecology: an evolutionary approach (Krebs JR, Davies NB, eds). London: Blackwell Science; 311–333.

Danylchuk AJ, Fox MG, 1994. Seasonal reproductive patterns of pumpkinseed (*Lepomis gibbosus*) populations with varying body size characteristics. Can J Fish Aquat Sci 51:490–500.

Danylchuk AJ, Fox MG, 1996. Size and age-related variation in the seasonal timing of nesting activity, nest characteristics and female choice of parental male pumpkinseed (*Lepomis gibbosus*). Can J Zool 74:1834–1840.

Diana JS, 1995. Biology and ecology of fishes. Carmel, Indiana: Cooper Publishing Group.

Flickinger SA, 1969. Determination of sexes in the fathead minnow. Trans Am Fish Soc 98:526–527.

Foote CJ, 1988. Male mate choice dependent on the male size in salmon. Behaviour 106:63–80.

Gauthreaux SA Jr, 1978. The ecological significance of behavioral dominance. In: Perspectives in ecology, vol. 3. Social behavior (Bateson PPG, Klopfer PH, eds). Plenum Press; 17–54.

Gross MR, 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In: Fish reproduction: strategies and tactics (Potts GW, Wootton RJ, eds). Toronto: Academic Press; 55–75.

Gross MR, 1991. Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. Phil Trans R Soc Lond B 332:59–66.

Gross MR, 1996. Alternative reproductive strategies and tactics: diversity within the sexes. Trends Ecol Evol 11:92–98.

Huntingford F, Turner A, 1987. Animal conflict. London: Chapman and Hall.

Jones GP, Thompson SM, 1980. Social inhibition of maturation in females of the temperate wrasse *Pseudolabrus celidotus* and a comparison with the blennioid *Tripterygion varium*. Mar Biol 59:247–256.

Keast A, 1968. Feeding of some Great Lakes fishes at low temperatures. J Fish Res Board Can 25:1199–1218.

Kozlowski J, 1992. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. Trends Ecol Evol 7:15–19.

Kvarnemo C, 1997. Food affects the potential reproductive rates of sand goby females but not of males. Behav Ecol 8:605–611.

Markus HC, 1934. Life history of the blackhead minnow (*Pimephales promelas*). Copeia 1934:116–122.

McNamara JM, Houston AI, 1996. State-dependent life histories. Nature 380:215–220.

Moore AJ, Edmund DB III, Wolf JB, 1997. Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. Evolution 51:1352–1362.

Munro AD, 1990. Tropical freshwater fishes. In: Reproductive seasonality in teleosts: environmental influences (Munro AD, Scott AP, Lam TJ, eds). Boca Raton, Florida: CRC Press; 145–239.

Oliver JD, Holeton GF, Chua KE, 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Trans Am Fish Soc 108:130–136.

Post JR, Evans DO, 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ, and field experiments. Can J Fish Aquat Sci 46:1958–1968.

Pusey AE, Packer C, 1997. The ecology of relationships. In: Behavioural ecology: an evolutionary approach (Krebs JR, Davies NB, eds). London: Blackwell Science; 254–283.

Ridgway MS, Shuter BJ, Post EE, 1991. The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieui* (Pisces: Centrarchidae). J Anim Ecol 60:665–681.

Robinson CLK, Tonn WM, 1989. Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. Can J Fish Aquat Sci 46:81–89.

Rodd FH, Reznick DN, Sokolowski MB, 1997. Phenotypic plasticity in the life history traits of guppies: responses to social environment. Ecology 78:419–433.

Schultz ET, Warner RR, 1989. Phenotypic plasticity in life-history traits of female *Thalassoma bifasciatum* (Pisces: Labridae). 1. Manipulations of social structure in tests for adaptive shift in life-history allocations. Evolution 43:1497–1506.

Shuter BJ, Post JR, 1990. Climate, population variability, and the zoogeography of temperate fishes. Trans Am Fish Soc 119:314–336.

Smith RJF, 1978. Seasonal changes in the histology of the gonads and dorsal skin of the fathead minnow, *Pimephales promelas*. Can J Zool 56: 2103–2109.

Stamps J, 1994. Territorial behavior: testing the assumptions, In: Advances in the study of behavior (Slater PJB, Rosenblatt JS, Snowdon CT, Milinski M, eds). San Diego, California: Academic Press; 173–232.

Starks PT, Reeve HK, 1999. Condition-based alternative reproductive tactics in the wood-carder bee, *Anthidium manicatum*. Ethol Ecol Evol 11:71–75.

Stearns SC, 1977. The evolution of life history traits: a critique of the theory and a review of the data. Ann Rev Ecol Syst 8:145–171.

Tartar M, Carey JR, 1995. Nutrition mediates reproductive trade-offs with age-specific mortality in the beetle *Callosobruchus maculatus*. Ecology 76:2066–2073.

Unger LM, 1983. Nest defense by deceit in the fathead minnow, *Pimephales promelas*. Behav Ecol Sociobiol 13:125–130.

Vandenbos RE, 1996. Regulation of recruitment in fathead minnows (*Pimephales promelas*): multi-stage effects and consequences of size variation (MSc thesis). Edmonton: University of Alberta.

Weatherley AH, 1972. Growth and ecology of fish reproduction. London: Academic Press.

Williams DD, Williams NE, Hogg ID, 1995. Life history plasticity of *Nemoura trisponosa* (Plecoptera: Nemouridae) along a permanent-temporary water habitat gradient. Freshwater Biol 34:155–163.

Wynne-Edwards VC, 1932. The breeding habits of the black-headed minnow (*Pimephales promelas* Raf.). Trans Am Fish Soc 62:382–383.

Zar JH, 1996. Biostatistical analysis. Upper Saddle River, New Jersey: Prentice Hall.