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Factors Influencing Reproductive Success Of Nesting Male Longear Sunfish (lepomis Megalotis Peltastes)

Helene Marie Dupuis

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FACTORS INFLUENCING REPRODUCTIVE SUCCESS OF NESTING MALE LONGEAR SUNFISH (*LEPOMIS MEGALOTIS PELTASTES*)

by

Hélène Marie Claire Dupuis

Department of Zoology

submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario
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Abstract

Most nesting male longear sunfish (Lepomis megalotis peltastes) excavate their nest in dense aggregations, while a small percentage nest solitarily. The importance of sexual selection in the evolution of this breeding system was evaluated by examining the influence of certain nest and male characteristics on spawning success and by comparing the reproductive success of social and solitary nesters. The hypothesis that males unlikely to attract mates benefit from group nesting because they increase their success by stealing fertilizations was tested.

Among social nesters, females spawned preferentially with males nesting early in the period and in central positions. Nest diameter and male size were also correlated with the predictors of spawning success, but apparently were not assessed directly by females. Positive relationships between predictors of success and the number of nest intrusions received and performed by each male were uncovered, indicating that unsuccessful males performed few intrusions into neighbours' nests. The success of fertilization stealing attempts is unknown.

Spawning period, which presumably reflected environmental conditions, was an important determinant of reproductive success. Solitary males tended to foster more larvae and probably enjoyed

greater certainty of paternity than did social nesters. They were also significantly larger than social males.

The existence of nesting aggregations can be interpreted from a sexual selection perspective, as suggested in a previous study. Males unable to attract females nest around attractive males and thereby create groups. The few intrusions they perform may represent their only possibility of successful reproduction. Attractive males risk reducing their success by nesting socially and probably attempt nesting solitarily. High spawning synchrony, however, may prevent them from renesting elsewhere once other males aggregate around them. Females comply with this system by preferentially spawning with attractive social males and tolerating the intrusions they receive, but spawning opportunistically with large males who remained solitary.

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Amanda Vincent, Marc Bégin and Frank Beletz provided valuable field assistance and (usually) genial company. I blame Dr. Roger Green, Keith Somers and Bob Bailey for moulding my current attitude toward statistics.

A fond farewell to all my fellow Collipers, who made my lengthy stay so enjoyable. My labmates in particular, Dr. Greg Goff, Doug Noltie, Mark Ridgway and Pete Steele, are responsible for several pranks, excessive verbal abuse, productive bull sessions, useful advice, and heated debates on diverse and unscientific topics. Marc Hormone Begin made me laugh, consumed great quantities of food at my expense, and generally challenged my sanity and good nature. I owe him a great deal. I have lost many beers to my squash partners and friends Barb Beez Neez Beasley, Hormone, Mark Zoltan Forbes, Jonathan Falk, Turkey Joe Weaver, Bob Squeak Bailey and Bob Mr. Fitness Roy. Thanks to my other Glad Club companions as well. My husband, Bob Roy, patiently put up with me while flaunting his own quirks, and provided limitless encouragement, moral support, thought-provoking discussions and homemade bread, among other things...

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Chapter 1. Introduction

Because of anisogamy (Maynard Smith, 1978), sexual selection operates predominantly on males, by means of female choice and male competition for access to females (Darwin, 1871; Fisher, 1930; Huxley, 1938; Borgia, 1979). The relative importance of these two mechanisms is often hard to ascertain, and many studies have failed to provide convincing evidence of female choice based entirely on male phenotype (Wiley, 1973; Lill, 1974; Sullivan, 1982, 1983; Arak, 1983; Boake, 1984; Perrill, 1984; but see Maynard Smith, 1956; Hogan-Warburg, 1966; Kruijt and Hogan, 1967; Whitney and Krebs, 1975; Ryan, 1980; Brown, 1981; Grant and Colgan, 1983). To demonstrate female choice, the phenotypic trait preferred by females must be identified, heritable (Fisher, 1930, Dominey, 1983b), and shown to confer higher fitness to the males possessing it (Searcy, 1979). Its genetic variance in the population must be sufficient (Cade, 1984) to allow perceptual discrimination by females (Arak, 1983; Cohen, 1984), and it should represent an "honest" advertisement of male quality (Searcy, 1979; Kodric-Brown and Brown, 1984). Females are most likely to evaluate genetic quality of males when the latter provide no material benefits to their offspring (Borgia, 1979). Under such circumstances, males often aggregate at communal display sites, which the females visit solely to mate (Emlen and Oring, 1977). Group displays intensify courtship signals and minimize the time that females spend searching and evaluating potential mates (Lill, 1974; Wilson, 1975; Emlen and Oring, 1977; see below).

Breeding aggregations, however, must also entail costs or risks to their members that could be minimized by dispersing uniformly throughout available habitat. Clumped territories undoubtedly increase the time, energy, or risk of injury associated with territorial defence (Bietz, 1981). Group members often face increased competition for resources (Alexander, 1974; Hoogland and Sherman, 1976; Krebs and Davies, 1981). Groups may also be more conspicuous to predators than solitary individuals (Alexander, 1974; Andersson and Wicklund, 1978). Breeding aggregations promote cuckoldry, nest parasitism and cannibalism (Hoogland and Sherman, 1976; Beecher and Beecher, 1979; Pugesek and Diem, 1983; Brown, 1984).

For group breeding to persist, benefits must compensate for costs or risks incurred (Alexander, 1974) unless, of course, groups form simply as a consequence of limited breeding habitat (Breder, 1936; Itzkowitz, 1978; Kodric-Brown, 1981). In some species, gains derived from 'information centres' or from cooperative hunting surpass individual foraging efficiency (Ward and Zahavi, 1973; Wilson, 1975; Bertram, 1978; McCracken and Bradbury, 1981; Andersson et al., 1981; Waltz, 1982b). In many cases, group members benefit from efficient predator detection (Bertram, 1978, 1980; Wittenberger, 1978) or defence, by mechanisms such as dilution, confusion, or predator mobbing

(Wilson, 1975; Hoogland and Sherman, 1976; Gross and MacMillan, 1981; Dominey, 1981a, 1983a; Wicklund, 1982).

The above benefits, however, are unlikely to pertain to all breeding aggregations, or alternately, may simply represent secondarily derived benefits rather than selection pressures leading to group formation. In particular, clustered territories, devoid of essential resources and used for male displays, probably arose in response to sexual selection (Emlen and Oring, 1977; Borgia, 1979; Cade, 1979; Foster, 1981; Arak, 1983). These male aggregations allow females the simultaneous evaluation of several potential mates, thereby minimizing searching or 'information gathering' time and risk (Wittenberger, 1983) and allowing the 'best' method of mate choice ('best-of-n-males', Janetos, 1980). Territory ownership is often resolved by male competition, further facilitating the female's decision process (Emlen and Oring, 1977; Wittenberger, 1983). Intensified courtship signals emitted by these aggregations may be more easily perceived by searching females (Lill, 1974; Wells, 1977; Cohen 1984), thereby conferring upon group members an advantage over solitary males.

Despite the benefits associated with breeding aggregations, some males in the population may adopt alternative behaviours and either establish a solitary territory (Wells, 1977; Andersson and Wicklund, 1978; Cade, 1979; Lott, 1984), or shun territoriality altogether and rely instead on fertilization stealing to achieve reproductive success (Emlen and Oring, 1977; Wells, 1977; Davies, 1978; Perrill et al., 1978, 1982; Dominey, 1981b; Gross, 1982; Arak, 1983; Fairchild, 1984; Howard, 1984). These alternatives should be used by males who would otherwise derive few benefits from aggregating (for example, males who can quite successfully attract females, or those who cannot compete successfully with the 'better' males vying for prime locations within the group). These males could thus evade the costs and risks associated with territorial defence (Alcock et al., 1977; Cade, 1978, 1980; Davies, 1978; Wirtz, 1981, Howard, 1984; Waltz and Wolf, 1984) and could increase their reproductive success above the level expected from group membership (Emlen and Oring, 1977; Wells, 1977; Dominey, 1981b; Waltz, 1982a; Austad, 1984; Howard, 1984; Waltz and Wolf, 1984).

Unfortunately there exists no conceptual synthesis to explain the mechanisms which lead to and maintain alternative reproductive behaviours in populations, although various classification schemes and mathematical models have recently been proposed (Gadgil, 1972; Alcock, 1979b; Cade, 1980; Rubenstein, 1980; Gross, 1982, 1984b; Waltz, 1982a; Austad, 1984; Dominey, 1984; Waltz and Wolf, 1984). Alternative breeding behaviours vary greatly among species, with respect to whether or not they occur in the same population, are temporally segregated, reflect competitive ability, are genetically fixed, facultative or stochastic, and whether or not they yield similar fitnesses. Recent models have yet to be empirically tested, and the genetic basis and fitness yields of specific behavioural alternatives remain largely unknown (but see Dominey, 1980; Cade, 1981; Schroder, 1981; Gross, 1982, 1984a,b; Fairchild, 1984; Howard, 1984).

The longear sunfish, <u>Lepomis megalotis peltastes</u> (Scott and Crossman, 1973 : 724 - 727) is a small centrarchid that utilizes alternative reproductive behaviours (Keenleyside, 1972). The "typical" males excavate their nest in aggregations of up to a hundred or more individuals. The nests are often rim to rim, and their approximately hexagonal boundaries (Grant, 1968) delimit each male's territory. However, a few nesting males do not join nesting groups but rather, nest solitarily (Boyer and Vogele, 1971; Bietz, 1981). A third behavioural alternative is adopted by small, non-territorial males ("satellites") who congregate above nesting groups during spawning activities, dart into nests while spawning is occurring and apparently release sperm and steal fertilizations from nesting males (Keenleyside, 1972). Whether or not individual males practice a single behaviour throughout their lifetime is unknown, and the fitness of the three types and the mechanism maintaining their coexistence have never been investigated. Because of the satellites' small size, Keenleyside (1972) assumed that fertilization stealing and nesting were size-linked, sequential tactics adopted by all male longears. This has yet to be confirmed. Bietz (1980, 1981) examined the adaptive significance of nesting aggregations in longear sunfish. He first demonstrated that nesting habitat was not limiting, and then explored the possibility that foraging efficiency, predation pressure or sexual selection could have led to the evolution of group nesting. He was, however, unable to gather adequate support for any of these hypotheses. His a posteriori hypothesis is summarized below.

Alternative reproductive behaviours have recently been examined in the bluegill sunfish, Lepomis macrochirus. Dominey (1980, ~~1981b~~), Gross and Charnov (1980) and Gross (1982) proposed that the behaviours seen in bluegills are not adopted sequentially by individual males but rather, are used by distinct factions of the population. They also argued that the success of cuckoldry and nesting should be equal, the proportion of males using each behaviour thus being frequency-dependent. As for the significance of 'colonial' nesting, Dominey (1981a) and Gross and MacMillan (1981) suggested that it lay in protection of the brood from predators. They found isolated nests to be the most vulnerable to brood predators, followed by those at the periphery of a group; central nests enjoyed the highest protection from predators.

Bietz (1980), however, found no evidence of such advantages for group-nesting longear sunfish. Furthermore, since nesting males never leave their territory to feed (Huck and Gunning, 1967; Bietz, 1980), the foraging efficiency hypothesis was inapplicable. Finally, contrary to predictions stemming from mate choice theory, Bietz found that a male's probability of mating declined with increasing group size and bore no relation to his position within the group. In fact, solitary males were more likely than social males to reproduce successfully.

Bietz (1980) therefore proposed that for a male with low probability of attracting mates, group nesting is advantageous because he can increase his reproductive success by stealing fertilizations from his nesting neighbours. For example, if female choice were based on male size, then large males should try to nest solitarily while smaller males should seek "attractive" males and nest around them to steal fertilizations.

I intended to evaluate the importance of sexual selection in the evolution of the longear breeding system, by comparing the reproductive success of social and solitary nesters, by examining the influence of male and nest characteristics on reproductive success, and by testing Bietz' fertilization stealing hypothesis. Although Bietz briefly examined potential advantages of social nesting, his measure of reproductive success was simply the presence of larvae in the nest, without regard to their quantity or to fertilization stealing. I decided to collect and count the larvae, and to record all spawning activities, particularly the nest intrusions performed by nesting neighbours and satellite males. I also wanted to determine the success rate of such intrusions by electrophoretically tracing the paternity of larvae spawned under controlled laboratory conditions. If nesting aggregations are favoured because of intensified courtship signals or minimal female searching-time, then group nesters should enjoy greater reproductive success than solitary nesters. If females prefer large, aggressive males, then these males should occupy solitary nests or central locations within aggregations (and obviously, achieve greater reproductive success). If Bietz' hypothesis is correct, then small males, unlikely to attract many females, should nest around the preferred males and steal fertilizations from them.

Chapter 2. Materials and Methods

The field work was executed in a 400m section of the Middle Thames River, 1.8km north of Highway 2, near Thamesford, Ontario. This section was slow-flowing, warm and shallow, with only a few pools reaching a depth of 1m or more. Water temperature was continuously monitored in a shaded area close to shore by a Dickson^{R} thermograph, and depth was measured at a fixed location every day (Figure 2.1). Occasional heavy rains temporarily increased water turbidity, level and flow, and decreased temperature. Heavy siltation ensued, as the flooding subsided.

Longears were found nesting on a substrate of gravel mixed with sand, mud, or less frequently, clay. Most nests were located near the shoreline in depths of 10 to 70cm, often near aquatic vegetation (_Elodea canadensis_, _Nuphar variegatum_) or under overhanging willow shrubs (_Salix interior_).

2.1 1981 Behavioural Observations

Nesting activity was monitored daily by wading through the inshore areas. On the first day of nest construction, I selected a nest cluster and erected a mapping grid around it by driving metal stakes into the substrate at 1m intervals. This usually disturbed some males, but they soon returned. All nests in the group were then drawn to

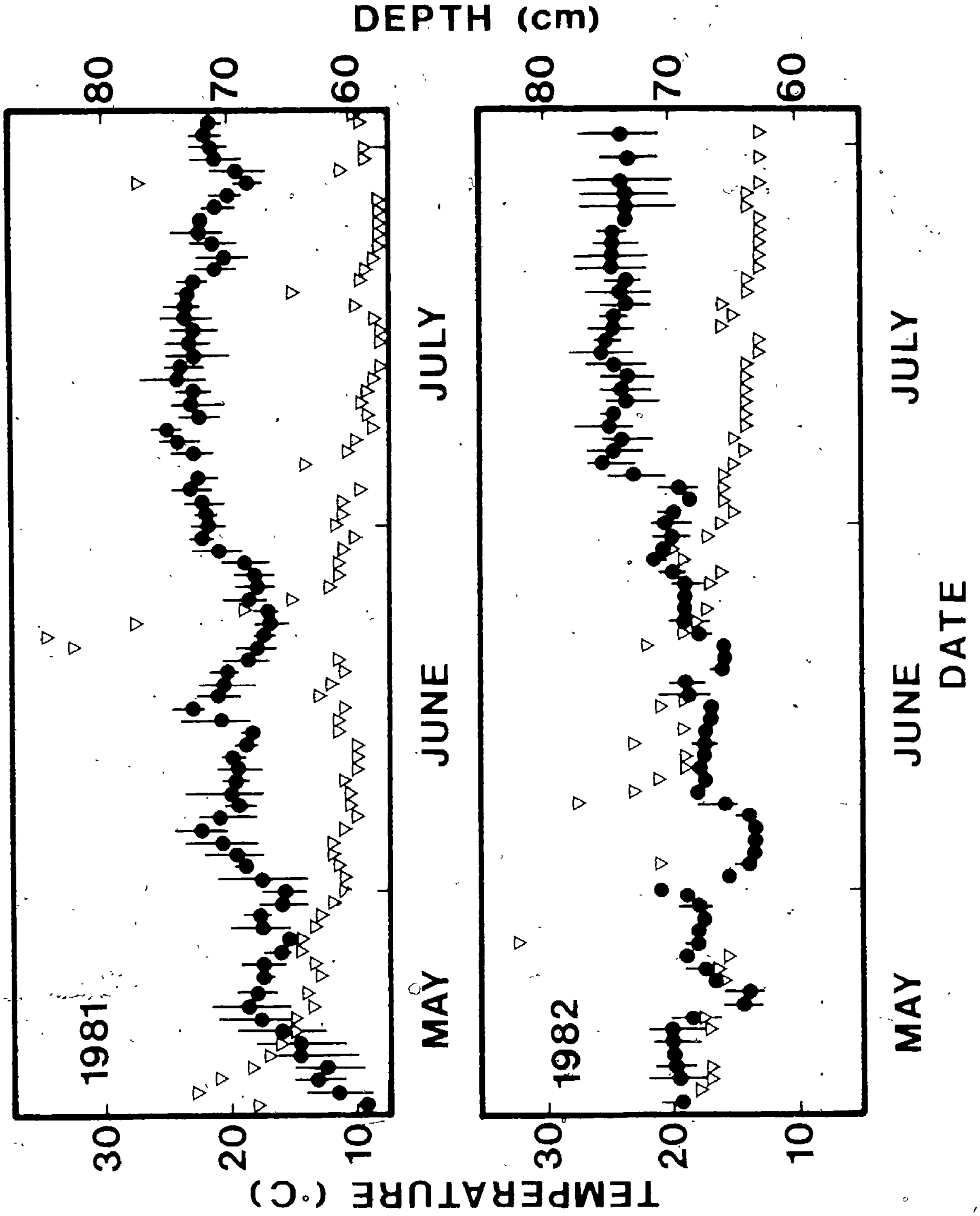


Figure 2.1 Depth and mean water temperature (± range) at a fixed location in the river (● =T°; ▽ =depth).

Table 3.4 Discriminant Function derived from the 1982 predictors (excluding male size and age) of nest success (n=121; $p=3.74 \times 10^{-5}$, Wilk's Lambda) and correlation between each variable and the new function.

VARIABLE	STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS	CORRELATION COEFFICIENT
Solitary	-0.405	0.201
Central	-0.240	-0.145
Nesting Day	-0.347	-0.278
Nest Diameter	0.428	0.258
Group Size	-0.268	-0.505
Spawning Period	0.919	0.768

Data were collected, beginning on June 5, 17 and 29, from three groups composed of 60, 13 and 43 nesting males respectively, yielding a total sample size of 116. However, one male was deleted from subsequent analyses because an overhanging branch precluded complete observations on his activities.

Table 2.1 lists the variables measured for each group member and their transformation, where appropriate (Zar, 1974 : 182-188). Group size is the total number of males nesting in the group. A centrality score was calculated for each male by summing the inverses of the distance between his and every other nest in the group (from Warntz, 1964, in Bietz, 1980). I then ranked these scores, and any male whose score was below the median was classified as peripheral (=0) and the remaining males were classified as central (=1). This method of defining centrality was found to be functionally equivalent to several other procedures (see section 4.2.1). Nesting day refers to whether a male initiated his nest on the first, second or third day of nesting activity during the spawning period. Nest diameter was estimated from the group maps, by taking the average of the longest and shortest axes of the nest. Males who had fared poorly during the spawning period deserted their nests soon afterward and were therefore not tagged and measured; this resulted in many missing values in the size and age variables (Table 2.1). The remaining variables represent totals for the entire two or three day spawning period. The number of intrusions received by a male is the sum of fertilization stealing attempts from

Table 2.1 Variables measured for the nesting males studied in 1981 (male length, weight and age, n=57; all other variables, n=115). See text for complete definitions.

VARIABLE	DESCRIPTION	TRANSFORMATION
Predictor:		
Group Size	total # males in the group	----
Centrality	central vs peripheral	----
Nesting Day	day of nest initiation within a spawning period	----
Nest Diameter	(long + short axes) x $\frac{1}{2}$	ln (x)
Male Length	total length (cm)	ln (x)
Male Weight	(g)	ln (x)
Male Age	# annuli on scales	----
Spawning Success:		
Females Entering Nest	total # for the spawning period	$(x + 0.5)^{\frac{1}{2}}$
Females Spawning	"	$(x + 0.5)^{\frac{1}{2}}$
Spawning Time	total time (s) for the spawning period	$(x + 0.5)^{\frac{1}{2}}$
Fertilization Stealing:		
Intrusions Received	total # for the spawning period	$(x + 0.5)^{\frac{1}{2}}$
Intrusions Performed	"	$(x + 0.5)^{\frac{1}{2}}$

nesting neighbours and satellite males. Technical difficulties precluded the collection and <u>in situ</u> enumeration of larvae.

2.1.1 Spawning Success

A) Analysis excluding male size and age

Missing values in the male variables were nonrandom consequences of the males' poor spawning performances. Recommended methods of estimating missing data were therefore inappropriate (Tabachnick and Fidell, 1983 : 68-72). The preferred solution was to delete these variables from the list of predictors before analyzing the data set. The other approach (section 2.1.1.B) was to consider only those males for which size and age data were available.

A Principal Components Analysis was performed on the correlation matrix of group size, centrality, nest date and nest diameter (predictors of spawning success) to determine which variable(s) accounted for most of the structure in the data set (Jeffers, 1978). Male scores on the first component axis (PC-1) were correlated with their counterparts from the first component of spawning success variables (number of females entering and spawning, and spawning time). A significant correlation coefficient would indicate a noteworthy relationship between one or more predictors and male spawning success.

B) Analysis including male size and age

The 57 cases for which male length, weight and age were obtained were subjected to the same procedures as described above, having included the male variables in the list of predictors.

In addition, Brian Bietz generously offered some unpublished 1978 data consisting of centrality scores and male size (Bietz, 1980) for comparison with my results. The relationships between centrality and male length and weight were examined with one-way ANOVAs.

2.1.2 Nest Intrusions

A) Analysis excluding male size and age

The relationships between the set of predictor variables and the number of intrusions received and performed were determined by two separate multiple regressions. However, highly correlated predictors, such as length, weight and age, can seriously affect the validity of the results (Wonnacott and Wonnacott, 1981 : 438). To avoid difficulties with such multicollinearity, I used the PC-1 derived from the set of predictors in section 2.1.1.A as the sole predictor in the regression equations.

B) Analysis including male size and age

The 57 cases for which male length, weight and age data were available were subjected to the same procedure as above except that the PC-1 from section 2.1.1.B was used as the predictor.

2.2 1982 Reproductive Success

I made no behavioural observations in 1982, to allow data collection on many groups as well as solitary nesters, and to collect and count the larvae from as many nests as possible. I surveyed the entire study site daily, mapped all nests and examined their contents to verify the progeny's developmental stage. As time permitted, I measured and tagged males guarding eggs, as described in section 2.1, except that the scales were taken from the left side of the fish. Two or three days after no more eggs could be seen in a nest, the presence or absence of longear larvae was determined by suction of interstices in the gravel with a kitchen baster. If larvae were present, and if time permitted, the entire contents of the nest, to a depth of at least 5cm, were scooped out with a fine mesh dipnet. This material was quickly sorted, removing the largest pieces of gravel, and was transferred to 1-l jars containing approximately 100ml 37% formaldehyde. Subsequently, I washed the contents, in the laboratory, through a series of five sieves ranging from 250μ to 400mm in mesh size. The bottom two were then emptied into an enamel tray and the larvae were removed as they were counted.

Table 2.2 lists the variables measured, the sample sizes and the transformations used (Zar, 1974). Male nesting status was defined by two binary dummy variables, solitary and central. Peripheral males scored a zero for both variables. Centrality was determined using the

Table 2.2 Variables measured for nesting males in 1982 (male length, weight and age, n=43; number of larvae, n=109; all other variables, n=121). See text for complete explanations.

VARIABLE	DESCRIPTION	TRANSFORMATION
Predictor:		
Solitary	solitary (=1) vs social (=0)	----
Central	central (=1) vs other (=0)	----
Nesting Day	day of nest initiation <u>within</u> a spawning period	----
Nest Diameter	(long + short axes) x $\frac{1}{2}$	ln (x)
Group Size	# nests in the group	$(x + 0.5)^{\frac{1}{2}}$
Spawning Period	which spawning cycle of season	----
Male Length	total length (cm)	ln (x)
Male Weight	(g)	ln (x)
Male Age	# annuli on scales	----
Reproductive Success:		
Presence of Larvae	success (=1) vs failure (=0)	----
Number of Larvae	total # larvae in the nest	$(x + 0.5)^{\frac{1}{2}}$

method described in section 2.1. A more continuous range of group sizes was studied in 1982, as opposed to just three in 1981, so that a transformation suitable for count variables was appropriate. There were five spawning periods (or cycles) in 1982, the first one starting on June 28 and the last one being an isolated case on August 5.

2.2.1 Nest Success and Failure

A) Analysis excluding male size and age

A MANOVA was executed using SPSS (Cohen and Burns, 1977) to determine whether successful males (with 2- or 3-day-old larvae in the nest) differed, with respect to the predictor variables, from unsuccessful nesters (no larvae). Male length, weight and age were not included in this analysis. If significant differences between the two groups of males were found, a Discriminant Analysis (Klecka, 1975) would identify the variable(s) responsible for such differences.

Brian Bietz' 1979 data, including centrality score, nest date, group size and presence of larvae for 522 group nesters were available for comparison with my results. Successful and unsuccessful males were compared by MANOVA and Discriminant Analysis.

B) Analysis including male size and age

The subset of 43 cases for which male size and age measurements were obtained was analyzed following the same procedure as in 2.2.1.A above, having first added length, weight and age to the list of variables.

2.2.2 Larval Abundance

A) Analysis excluding male size and age

I obtained larva counts for 109 of the 121 nests inspected (section 2.2.1). The influence of each variable on reproductive success (number of larvae) was determined by regression analysis. To avoid problems with multicollinearity among predictors (Wonnacott and Wonnacott, 1981) a Principal Components Analysis was first performed on the predictor variables, excluding male length, weight and age. Only the first few interpretable components were to be included in the regression equation.

B) Analysis including male size and age

I applied the same procedure to the 37 cases for which size and age, as well as number of larvae, were available, having added male size and age to the list of predictors before executing the PCA.

2.2.3 Renesters

Twelve males tagged in 1982 were found renesting later in the season. I made an effort to collect complete data from such renesting attempts. Number of larvae for first and second attempts were compared by paired-sample t-test (Zar, 1974). No statistics were performed to compare nesting status during first and second attempts because of restrictive sample size.

2.3 Paternity Experiment

I designed a laboratory experiment to determine the success rate of fertilization stealing attempted by nesters and satellites. By electrophoretically typing muscle enzymes of several fish, identifiable males could be selected and allowed to spawn under continuous observation, and the proportion of fry fathered by various intruders could be determined for each nest.

In 1982 and 1983, fish brought back from the field were tagged using the same technique as in section 2.1. Several days later, muscle biopsies were taken from the dorsal musculature, having anesthetized each fish in a solution of tricaine methanesulfonate. All fish recovered from the operation, but a few died later. I assayed their tissue nonetheless. Samples were kept at -70°C until they were processed for starch gel electrophoresis.

All gels were run at 80mA and variable current for 3-4h, and slices were stained for different enzymes, following the recipes in Shaw and Prasad (1970). I first assayed the enzymes that are known to be polymorphic in other populations of longear or other sunfish (Avise and Smith, 1974a, b; Avise, 1977; Avise and Felley, 1979). The genetic variability detected in this population (section 3.3) was insufficient for the purposes of the experiment, which was therefore not executed.

2.4 Male Size Experiment

Because size and age measurements were obtained chiefly from successful nesters I decided to test female preference for male size under controlled laboratory conditions.

A large population of longears was found in the Ausable River near Exeter, Ontario, and approximately 200 fish were brought back from this site during the 1984 breeding season. They overwintered in two 830-l cement tanks under natural photoperiod. Water temperature dropped to 12°C in February and then gradually increased to 19°C. The fish were fed Purina^R trout chow every second or third day. In early March they were transferred to laboratory aquaria, where photoperiod was artificially increased to 16L:8D over two weeks and water temperatures were maintained at 22°C. The fish were fed flake food, trout chow or frozen <u>Artemia</u> two or three times a day.

Several females (Total Length 8.09 ± 0.085cm) were placed in a compartment of the experimental pool. The 0.64cm mesh plastic partition allowed them full view of the pool. Eight small (TL 9.08 ± 0.098cm) and eight large (TL 11.4 ± 0.087cm) males were introduced on opposite sides of a similar partition running perpendicularly to the females' compartment. A 5cm layer of gravel covered the bottom in all sections. Water depth was approximately 30cm. Periodically, the temperature was allowed to fluctuate by several degrees and the water was partially changed to induce gonadal maturation and nesting activity. The photoperiod was 16h long. Food was dropped in each section twice daily. Once nests were completed and mapped and females appeared ripe, I removed the partition between the two groups of males and released six females in the centre. I recorded all spawning activities for several hours with a cassette recorder. I then returned the females to their compartment. I compared nest diameter and spawning success of small and large males by Mann-Whitney tests (Zar, 1974). I tested the influence of nest diameter on spawning success and on intrusions by Spearman's rank correlations (Zar, 1974).

Chapter 3. Results

There were several spawning periods in a summer, the first one beginning in early or mid-June and the last ending in early August. An increase in water temperature apparently triggered synchronous nesting activity throughout the study site. Males moved into shallow waters and began nest construction solitarily (> 1m away from nearest neighbour) or in small groups (< 20 nests). Although nest excavation usually required less than 24h, new males joined these initiators, usually at the periphery, but sometimes between existing nests in the cluster, during the second and third day of nest initiation (second or third nesting day). Females began arriving before all nests had been completed. They were courted by several males as they swam through the cluster, and they often entered and circled in several nests before spawning. (I did not observe spawning behaviour in solitary nests). Refer to Breder (1936) and Huck and Gunning (1967) for a description of spawning behaviour. While a female spawned with a nesting male, several satellites hovering near the water surface darted simultaneously into the nest and quivered beside the female before being chased by the nest owner. Nesting neighbours also attempted fertilization stealing. The female usually remained in the nest during such interruptions, but occasionally left and entered one of the intruders' nest. Females were often seen spawning in more than one nest. Spawning activity lasted two or three days, during which nesting males guarded the eggs (which hatched in two or three days) and subsequently the larvae, until they dispersed four to six days after hatching. The males then usually abandoned the nest, although they occasionally swept out the accumulated silt, in preparation for the next spawning period.

3.1 1981 Behavioural Observations

3.1.1 Spawning Success

A) Analysis excluding male size and age

The first principal component from the set of predictor variables explained 40% of the structure in the data and described a gradient from nesting late in the spawning period, in a small peripheral nest to nesting early in a large, central nest (Table 3.1). The second component explained an additional 27% of the structure and represented a gradient from being in a large group and occupying a central, small nest to membership in a small group and occupying a peripheral and large nest. However, PC-2 did not appear to be biologically meaningful, since the proportion of central males was set at 0.5 for each of the three groups, and therefore any component showing joint variation in group size and centrality was obviously trivial. It therefore seemed advisable to omit PC-2 and subsequent components from further analyses. Ninety-four percent of the structure in the spawning

Table 3.1 Principal Components derived from the 1981 predictors (excluding male size and age) and the spawning success variables (n=115).

VARIABLE	PC-1	PC-2	PC-3	PC-4
Predictor:				
Group Size	-0.130	-0.696	-0.704	0.055
Centrality	0.363	-0.627	0.583	0.368
Nesting Day	-0.697	0.094	0.090	0.705
Nest Diameter	0.605	0.336	-0.396	0.603
Eigenvalue	1.59	1.09	0.89	0.43
Variance Explained	39.7%	27.3%	22.3%	10.7%
Spawning Success:				
Females Entering	0.574	-0.669	-0.472	
Females Spawning	0.587	-0.066	0.807	
Spawning Time	0.571	0.740	-0.354	
Eigenvalue	2.83	0.13	0.04	
Variance Explained	94.2%	4.4%	1.4%	

variables was summarized by their PC-1 (Table 3.1), which represents a gradient from low to high spawning success.

The correlation between a male's score on the first predictor component and that on the spawning success component was significant at the 0.001 level (Figure 3.1). The conclusion I draw from this relationship is that late-nesting males occupying small and usually peripheral nests tended to fare poorly compared to early-nesting males who owned large and usually central nests. This is supported by the bivariate relationships depicted in Figure 3.2. These are selected representatives of equivalent relationships; for example, a trend similar to that shown in Figure 3.2A is evident whether the criterion variable is number of females entering the nest or total spawning time.

B) Analysis including male size and age

When male size and age were included in the list of predictors, the first principal component explained 42% of the structure (Table 3.2) and was mainly an increasing size and age gradient. PC-2 accounted for an additional 20% of the data structure and represented a gradient from small central nests to large peripheral ones. However, I discarded PC-2 and subsequent components because they provided little information (with purely random data each component would explain about 15% of the variation), and furthermore a scree test (Cattell, 1966) indicated that only the first eigenvalue was meaningful. Ninety-two percent of the structure in the spawning success variables (Table 3.2)

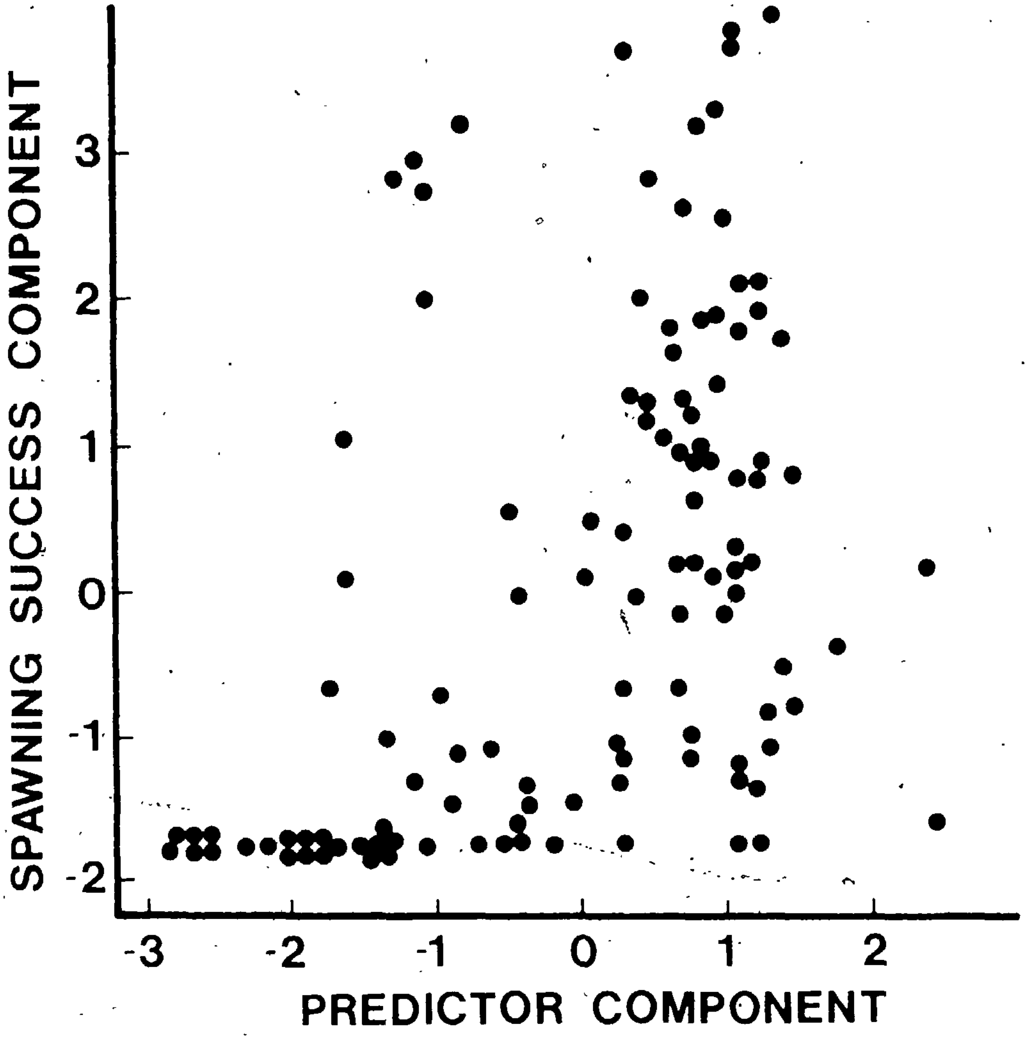


Figure 3.1 Relationship between scores on the first predictor component (excluding male size and age, Table 3.1) and the first spawning success component (Table 3.1) for males nesting in 1981 : $r = 0.447$, $p < 0.001$, $n=115$.

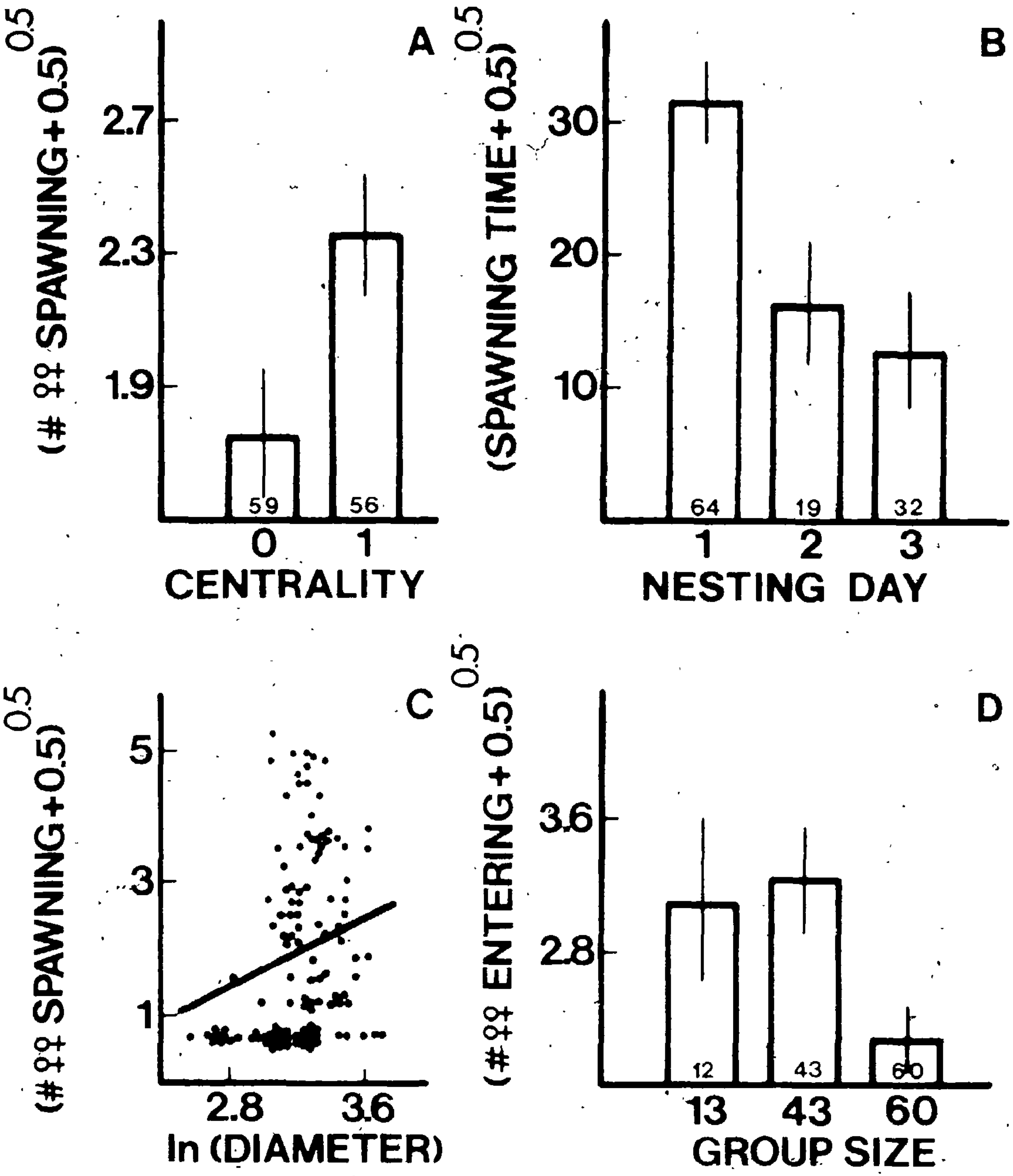


Figure 3.2 Relationship between predictor variables (excluding male size and age) and spawning success in 1981 ($n=115$). A) $p < 0.025$; B) $p < 0.0005$; C) $Y = -2.15 + 1.29 \ln(\text{DIAMETER})$, adjusted $r^2=3.3\%$, $p \le 0.05$, 1 and 113 df; D) $p < 0.025$; F-tests (numbers in bars: sample sizes; error bars: 1 Standard Error (SE)).

Table 3.2 First four Principal Components derived from the 1981 predictors (including male size and age) and spawning success variables (n=57).

VARIABLE	PC-1	PC-2	PC-3	PC-4
Predictor:				
Group Size	0.282	-0.106	-0.578	-0.652
Centrality	0.228	-0.700	0.144	0.084
Nesting Day	-0.297	0.147	-0.725	0.267
Nest Diameter	0.249	0.622	0.123	0.178
Male Length	0.523	0.148	0.037	-0.077
Male Weight	0.551	0.148	-0.029	-0.023
Male Age	0.375	-0.215	-0.318	0.676
Eigenvalue	2.94	1.39	1.09	0.75
Variance Explained	42.1%	19.9%	15.5%	10.7%
Spawning Success:				
Females Entering	0.575	-0.621	-0.532	
Females Spawning	0.591	-0.135	0.796	
Spawning Time	0.566	0.772	-0.290	
Eigenvalue	2.76	0.19	0.06	
Variance Explained	91.8%	6.3%	1.9%	

was summarized by its first component, a gradient from low to high spawning success.

No significant correlation was found between PC-1 from the predictors and PC-1 from the spawning success variables (figure 3.3), and therefore male size and age could not be linked with spawning success. The prediction that larger or older males would occupy central nests and enjoy greater spawning success was therefore not entirely supported. Figure 3.4 shows pertinent bivariate plots. Bietz' 1978 data on central and peripheral male sizes indicate a significantly greater size for central males (Figure 3.5). The similar trend in my data not being significant (Figure 3.4A) leads me to suggest that a less biased sampling of male size would have yielded stronger support for my prediction.

3.1.2 Nest Intrusions

A) Analysis excluding male size and age

The number of intrusions received and performed by a nesting male were related to his score on the predictor PC-1 (Table 3.1) in the following way:

$$(\text{Intrusions Received} + 0.5)^{0.5} = 4.26 + 1.120\ (\text{PC-1});$$

$$p < 0.0025;\ 1 \text{ and } 113 \text{ df};$$

$$(\text{Intrusions Performed} + 0.5)^{0.5} = 3.82 + 0.604\ (\text{PC-1});$$

$$p < 0.0025;\ 1 \text{ and } 113 \text{ df}.$$

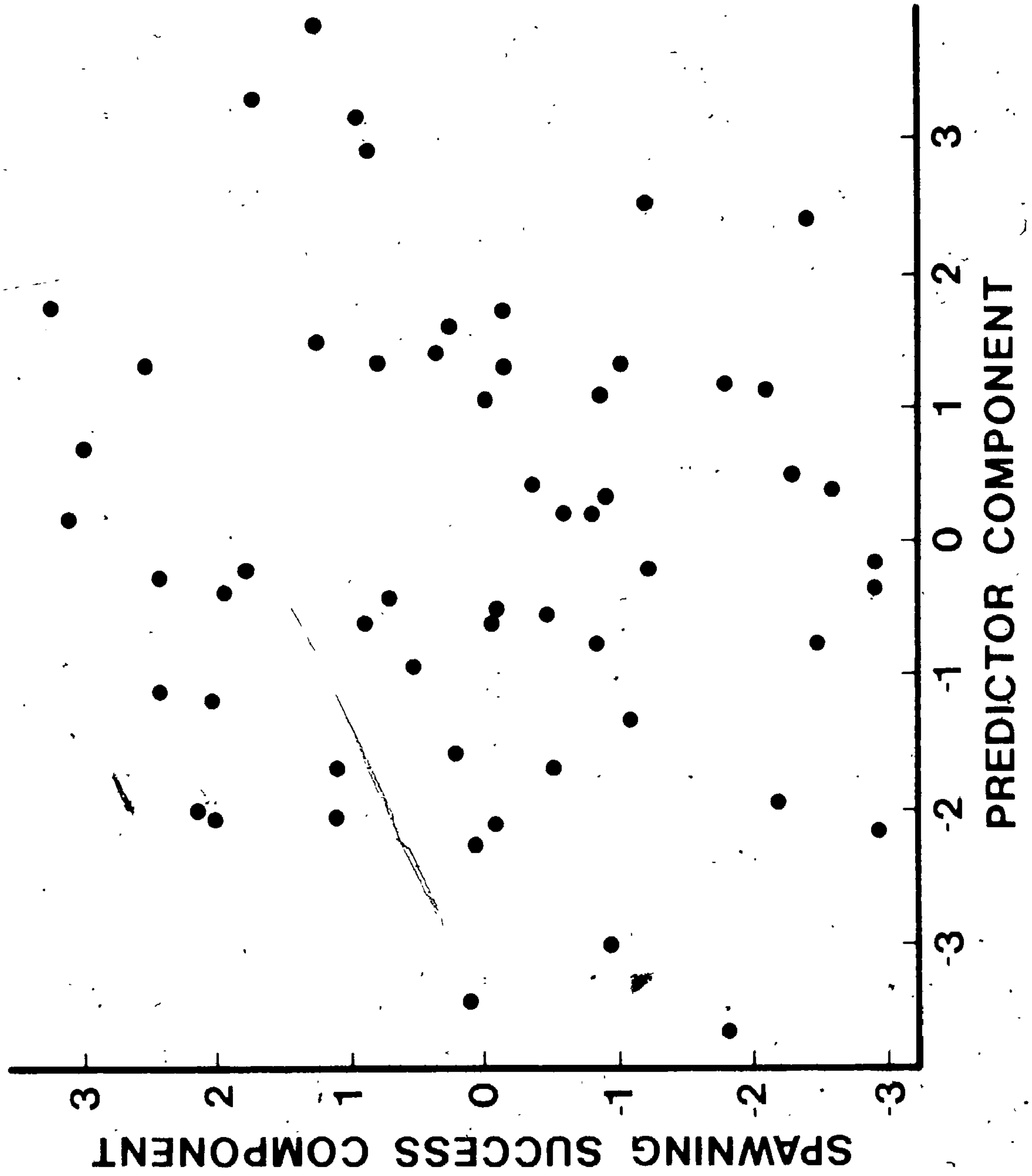


Figure 3.3 Relationship between scores on the first predictor component (including male size and age, Table 3.2) and the first spawning success component (Table 3.2) for males nesting in 1981 : r = 0.112, p > 0.2, n=57.

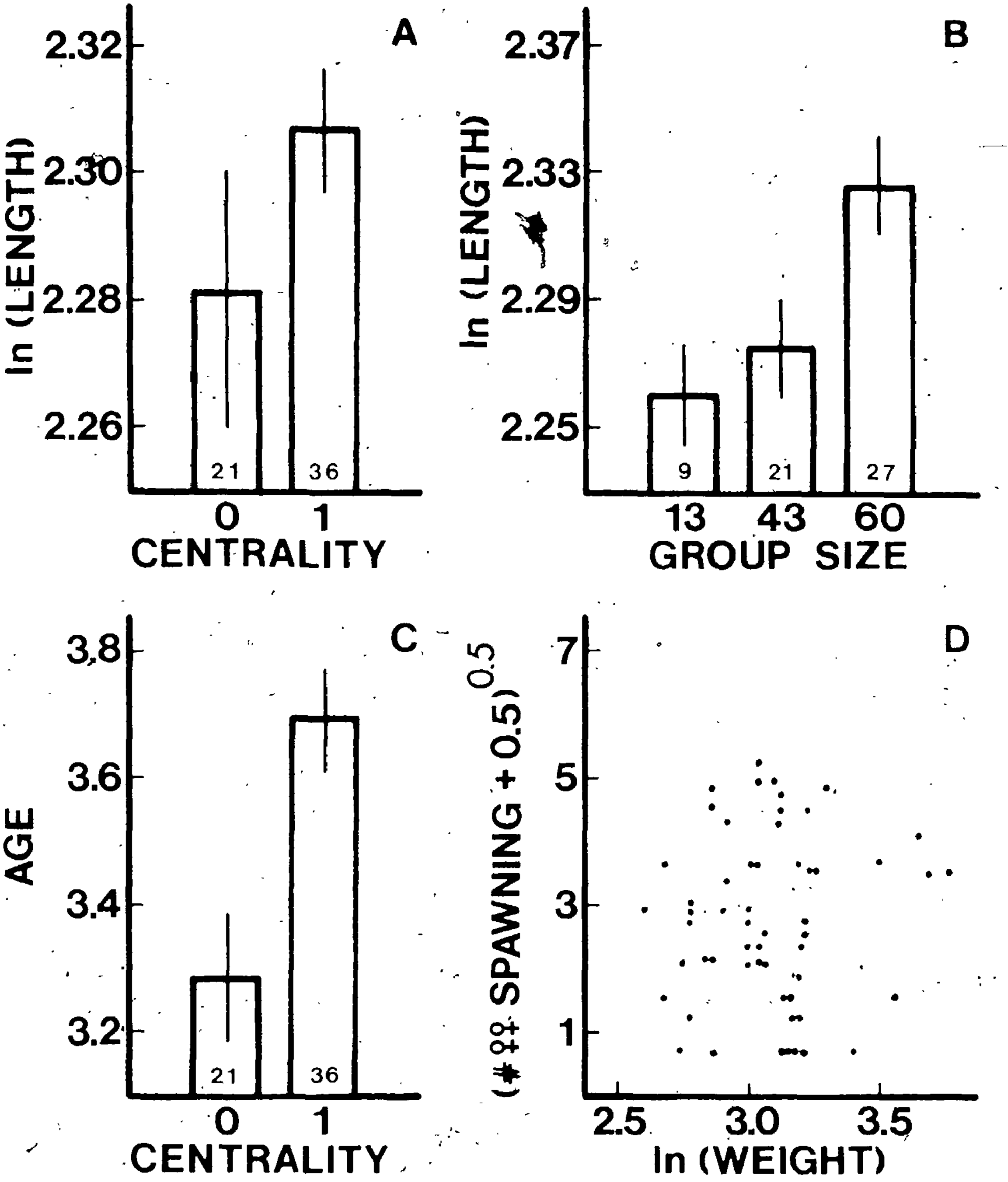


Figure 3.4 Relationship between male size, other predictor variables and spawning success in 1981 (n=57). A) $p > 0.1$; B) $p < 0.0025$; C) $p < 0.0025$; D) $p > 0.25$, 1 and 55 df; F-tests (numbers in bars: sample sizes; error bars: 1 SE).

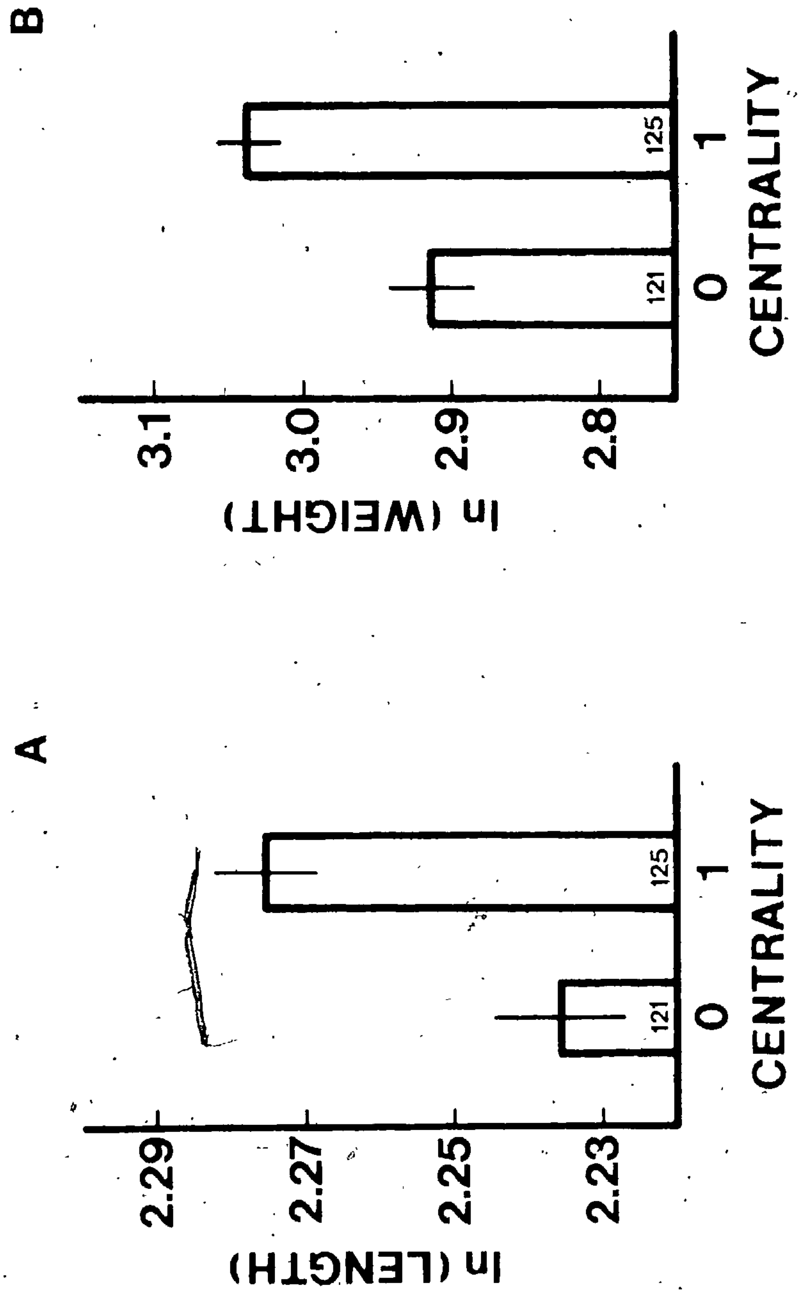


Figure 3.5 Relationship between centrality and male size, Bietz' 1978 data ($n=246$). A) $p < 0.0005$; B) $p < 0.001$; F-tests (numbers in bars: sample sizes; error bars: 1 SE).

The coefficients of determination (r^2), adjusted for degrees of freedom (Zar, 1974: 260), were 8.3% and 7.5% respectively (Figure 3.6A and B). It can be concluded that, all else being equal, males who nest late in small and usually peripheral nests receive and also perform fewer intrusions than males nesting early in large and usually central nests. This conclusion is supported by the bivariate plots shown in Figure 3.7, although there was no significant relationship between nest diameter and intrusions.

B) Analysis including male size and age

The subset of cases for which male size and age were available produced non-significant relationships between the predictor PC-1 (Table 3.2) and number of intrusions received ($p > 0.1$, F-test) and performed ($p > 0.25$, F-test). The adjusted coefficients of determination (r^2) were 0.9% and 0.0% respectively. Therefore a male's size and age cannot be used to predict the number of intrusions he receives or performs, as illustrated in Figure 3.8 (the relationship shown in Figure 3.8B is the only significant one of six possible combinations between number of intrusions received or performed and male size or age).

The overall conclusion from the 1981 data is that males who nest early, in large nests located in the centre of the group enjoy high spawning success, and also perform many fertilization stealing attempts into each others' nests. Although the analyses failed to identify male size as an important determinant of spawning success and rate of

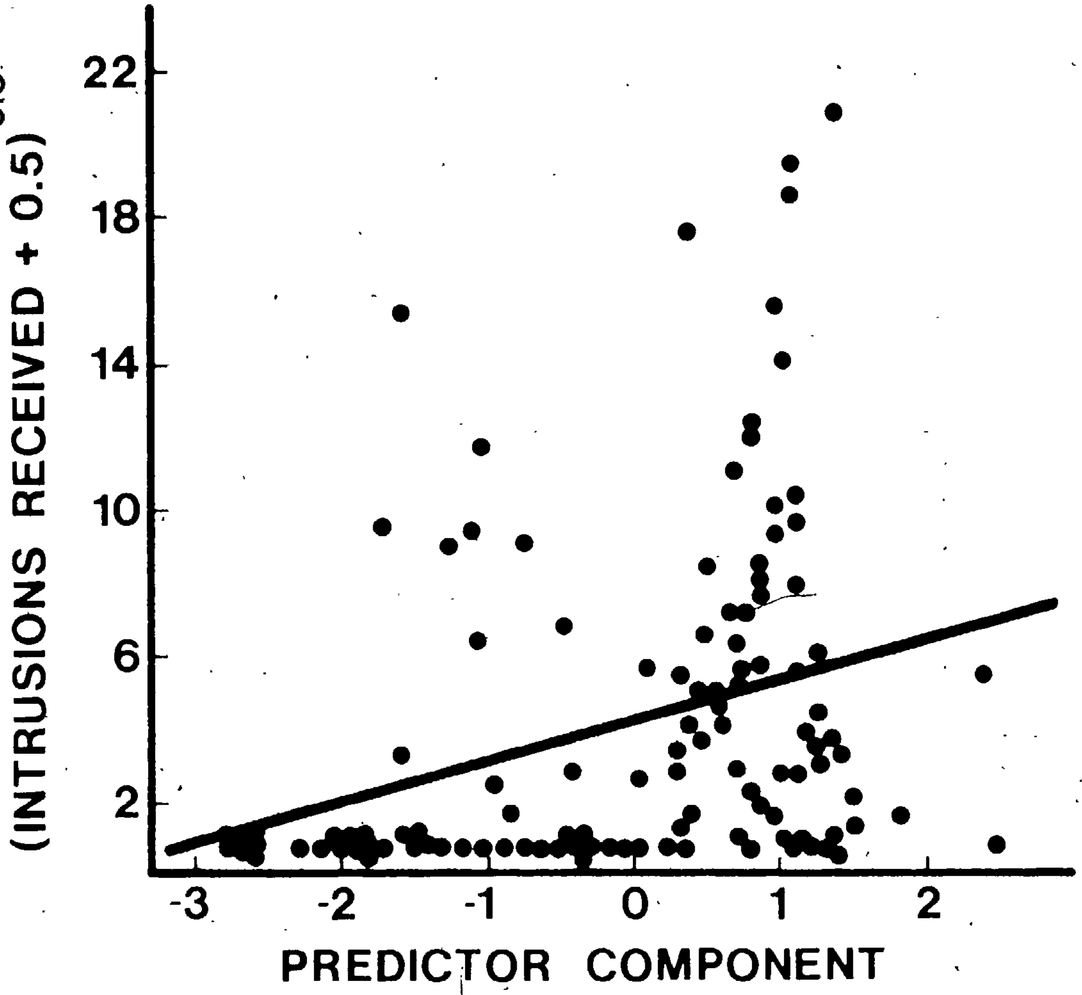


Figure 3.6 A Relationship between scores on the first predictor component (excluding male size and age, Table 3.1) and the number of intrusions received by males nesting in 1981 (n=115) : $Y = 4.26 + 1.12$ (PC-1), adjusted $r^2=8.3\%$, $p < 0.0025$, F-test, 1 and 113 df.

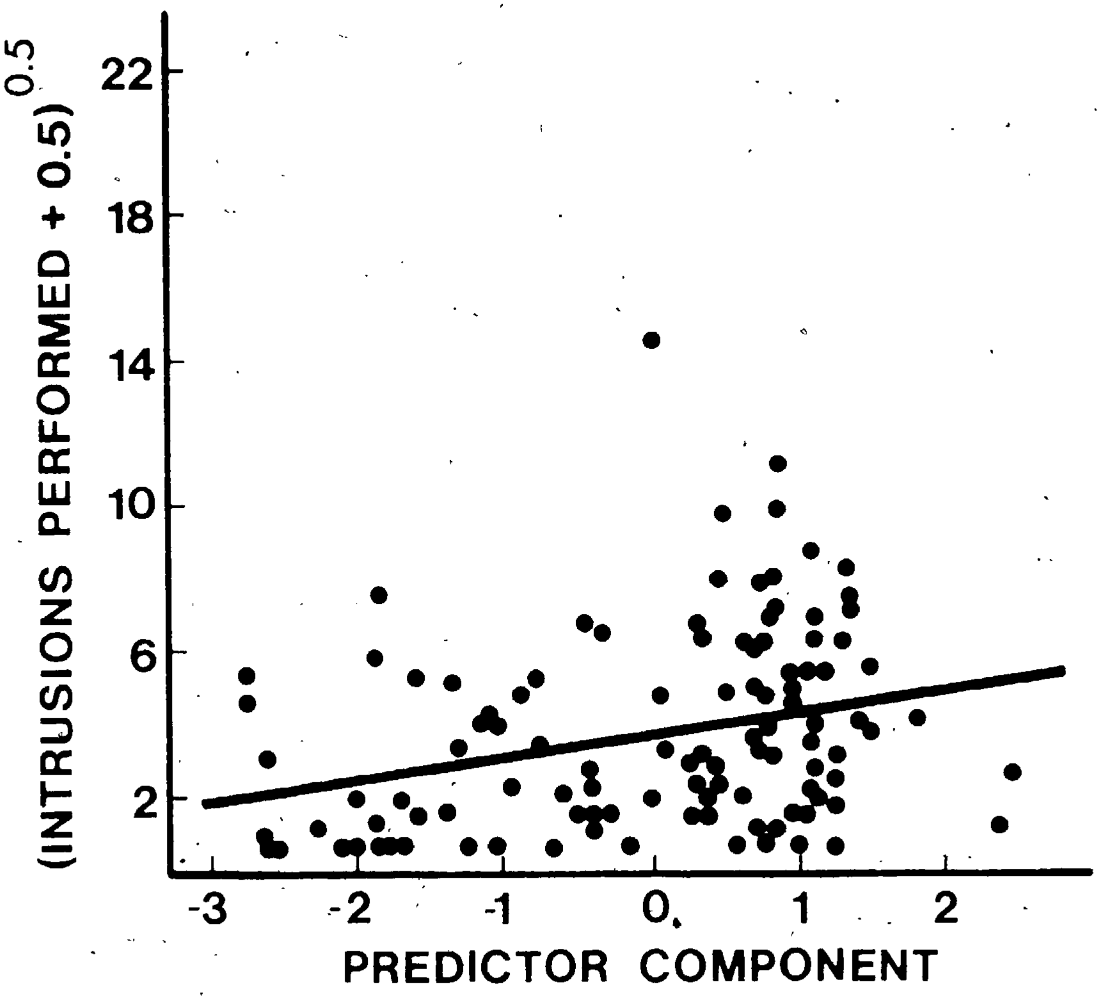


Figure 3.6 B Relationship between scores on the first predictor component (excluding male size and age, Table 3.1) and the number of intrusions performed by males nesting in 1981 : $Y = 3.82 + 0.604\ (PC-1)$, adjusted $r^2=7.5\%$, $p<0.0025$, F-test, 1 and 113 df.

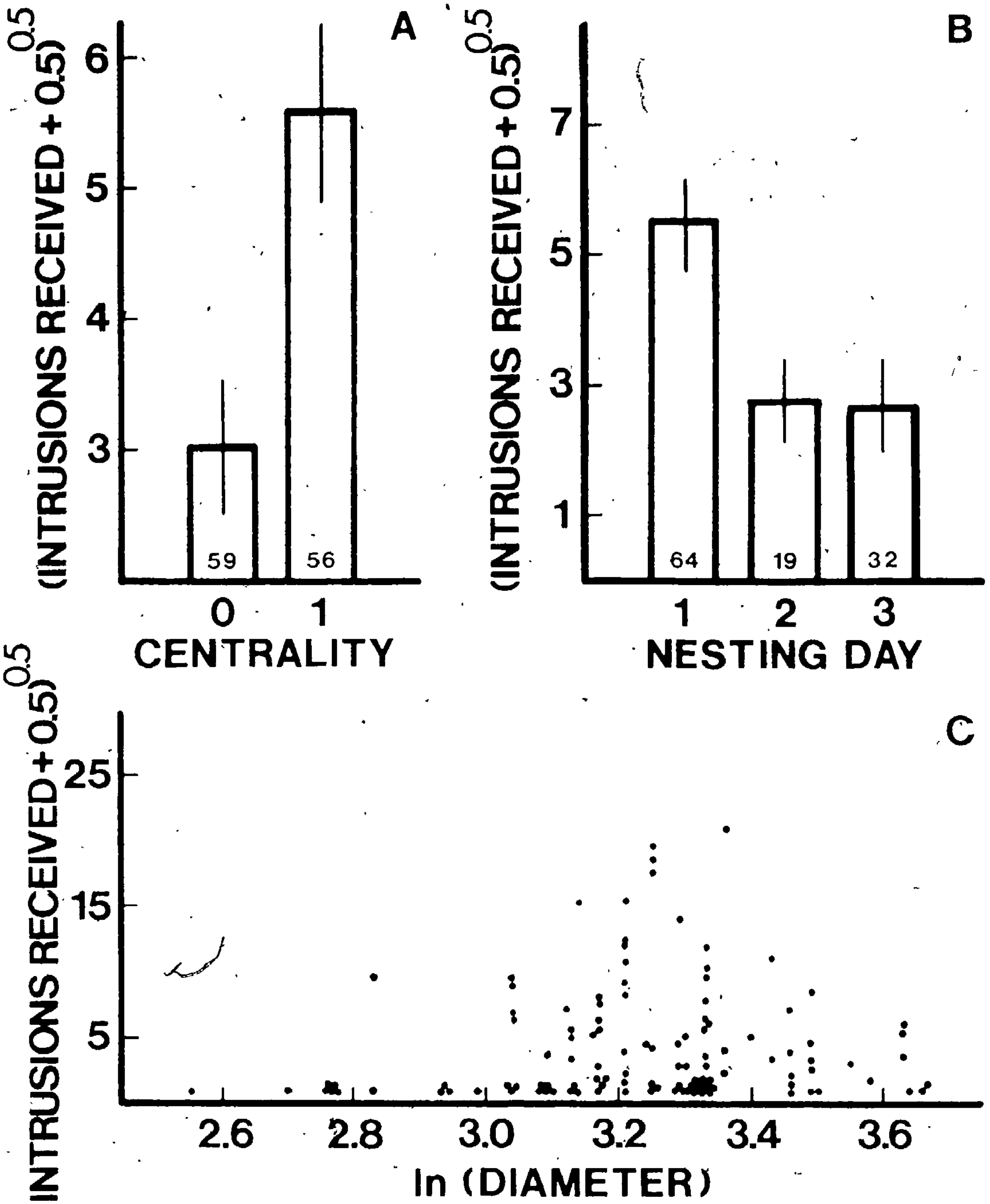


Figure 3.7 A-C Relationship between predictor variables (excluding male size and age) and the number of intrusions received by males nesting in 1981 ($n=115$). A) $p \approx 0.005$; B) $p < 0.005$; F-tests; C) $r = 0.110$, $p > 0.2$ (numbers in bars: sample sizes; error bars: 1 SE).

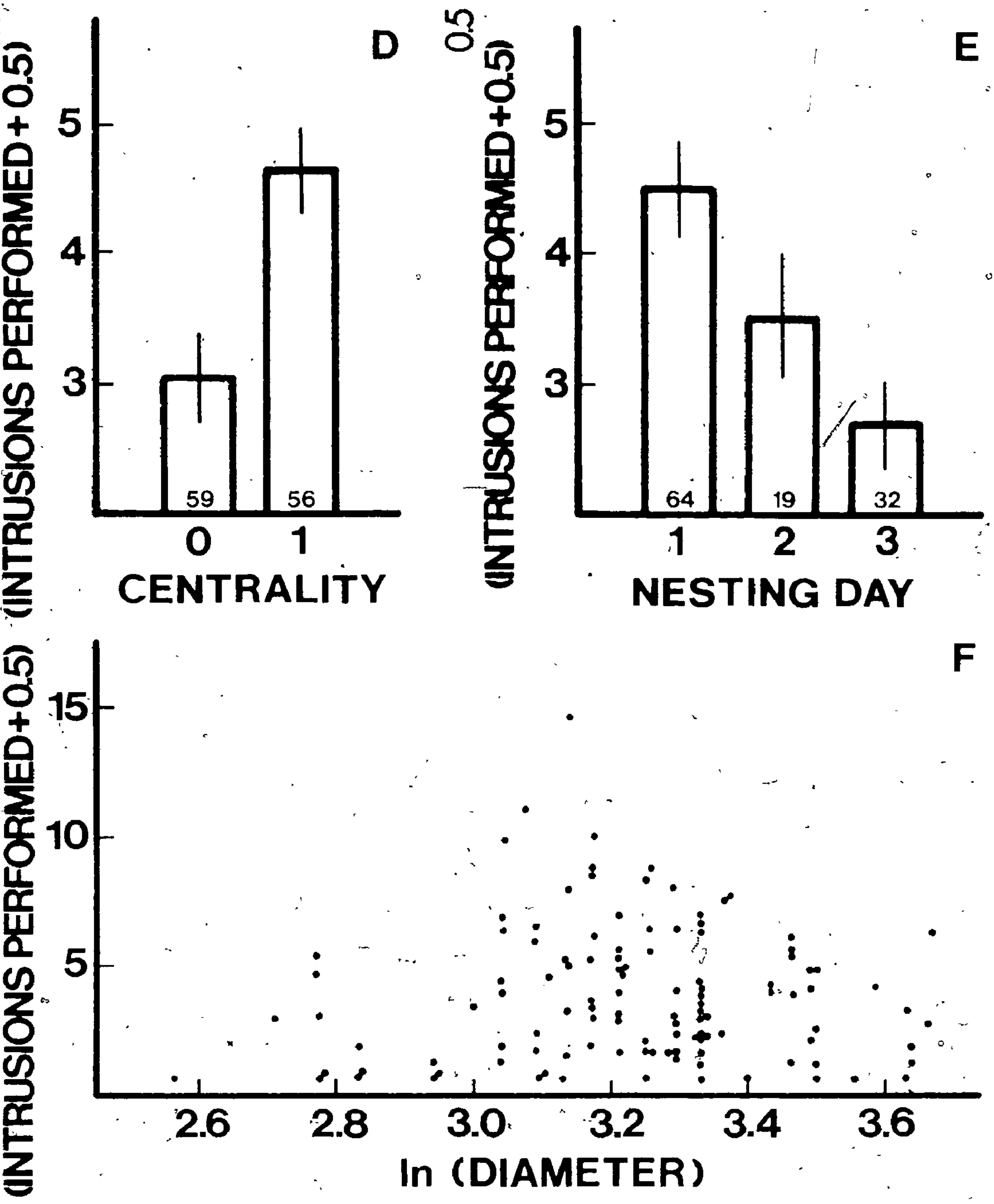


Figure 3.7 D-F Relationship between predictor variables (excluding male size and age) and the number of intrusions performed by males nesting in 1981 (n=115). D) $p < 0.001$; E) $p < 0.005$; F-tests; F) $r = 0.032$, $p > 0.5$ (numbers in bars: sample sizes; error bars: 1 SE).

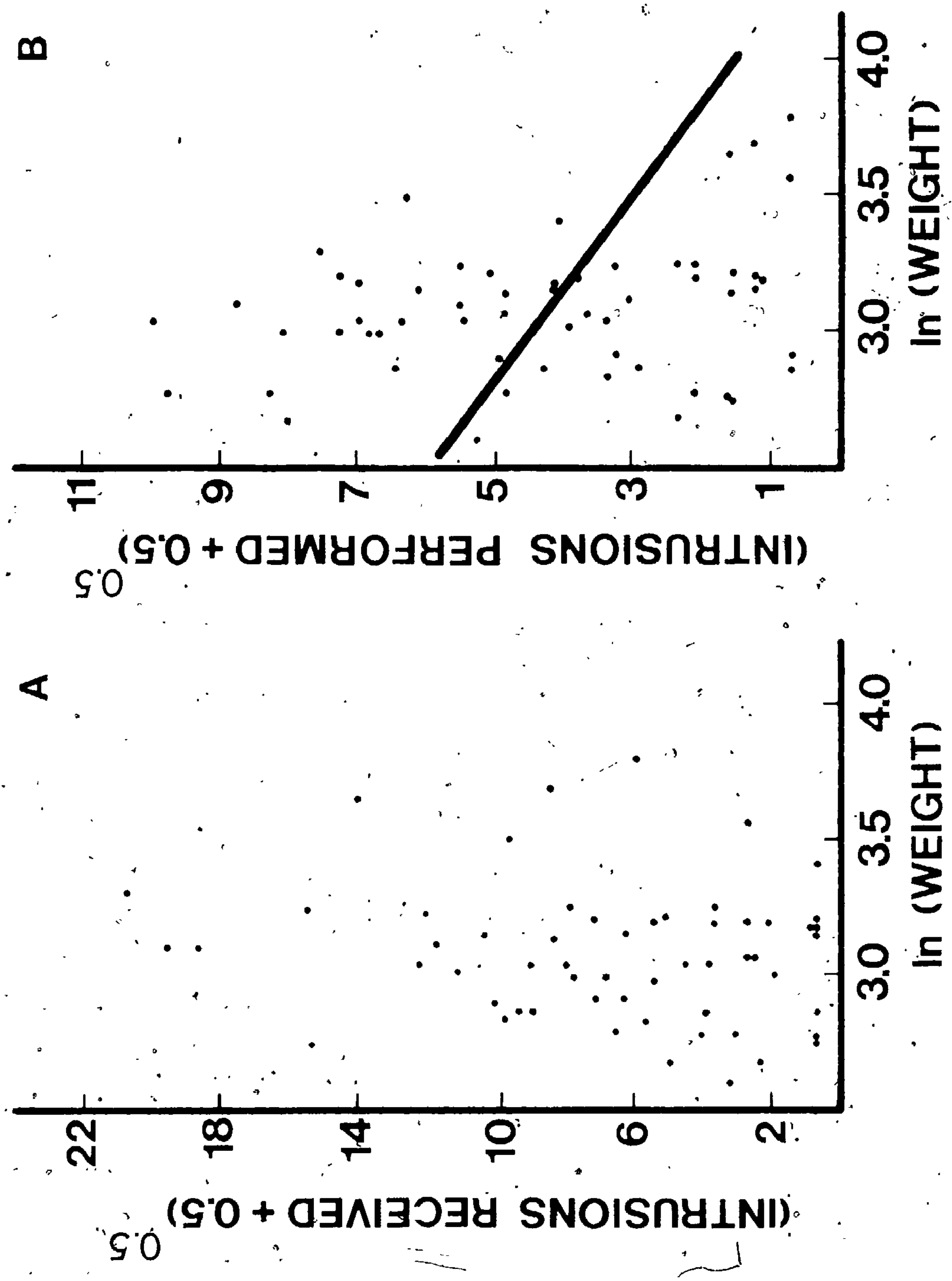


Figure 3.8 Relationship between male size and number of intrusions received and performed by males nesting in 1981 (n=57). A) $p > 0.5$; B) $Y = 13.4 - 2.97 \ln(\mathrm{WEIGHT})$, adjusted $r^2 = 8.9\%$, $p < 0.025$; F-tests, 1 and 55 df.

intrusions, Figure 3.4 suggests that early nesting, central males are in fact larger than late, peripheral nesters, and Bietz' data (Figure 3.5) clearly confirm this trend. Because the success rate of intrusions is unknown, it is impossible to determine whether central males enjoy greater overall reproductive success than peripheral males, who attract fewer females but also receive fewer intrusions.

3.2 1982 Reproductive Success

3.2.1 Nest Success and Failure

A) Analysis excluding male size and age

The MANOVA executed on the all cases revealed highly significant differences, with respect to the predictor variables, between successful (larvae in the nest) and unsuccessful males (Wilk's Lambda, $p=3.74 \times 10^{-5}$, 6 and 114 df). Preliminary F-tests (Table 3.3) suggested that spawning period and group size might be responsible for the differences.

When actual group membership was concealed, the Discriminant Function correctly classified 67.7% (82 of 121) of the males as either successful or unsuccessful. Figure 3.9 shows the separation between the two groups of males achieved with this function. The loadings of the variables onto the Function (Table 3.4) suggested that spawning period, and also nest diameter and 'solitary', were important determinants of nest success. However, not all of these variables were

Table 3.3 Means and standard errors of predictor variables (excluding male size and age), for 1982 successful and unsuccessful males (univariate F-tests, 1 and 119 df).

VARIABLE	MALES WITH LARVAE (n=51)	MALES WITHOUT LARVAE (n=70)	P
Solitary	0.294 ± 0.064	0.200 ± 0.048	>0.1
Central	0.392 ± 0.069	0.500 ± 0.060	>0.1
Peripheral	0.314 ± 0.066	0.300 ± 0.055	>0.25
Nesting Day	1.373 ± 0.097	1.600 ± 0.094	>0.1
Nest Diameter	3.478 ± 0.031	3.421 ± 0.023	>0.1
Group Size	1.978 ± 0.108	2.454 ± 0.110	0.003
Spawning Period	2.650 ± 0.161	1.800 ± 0.106	<0.0005

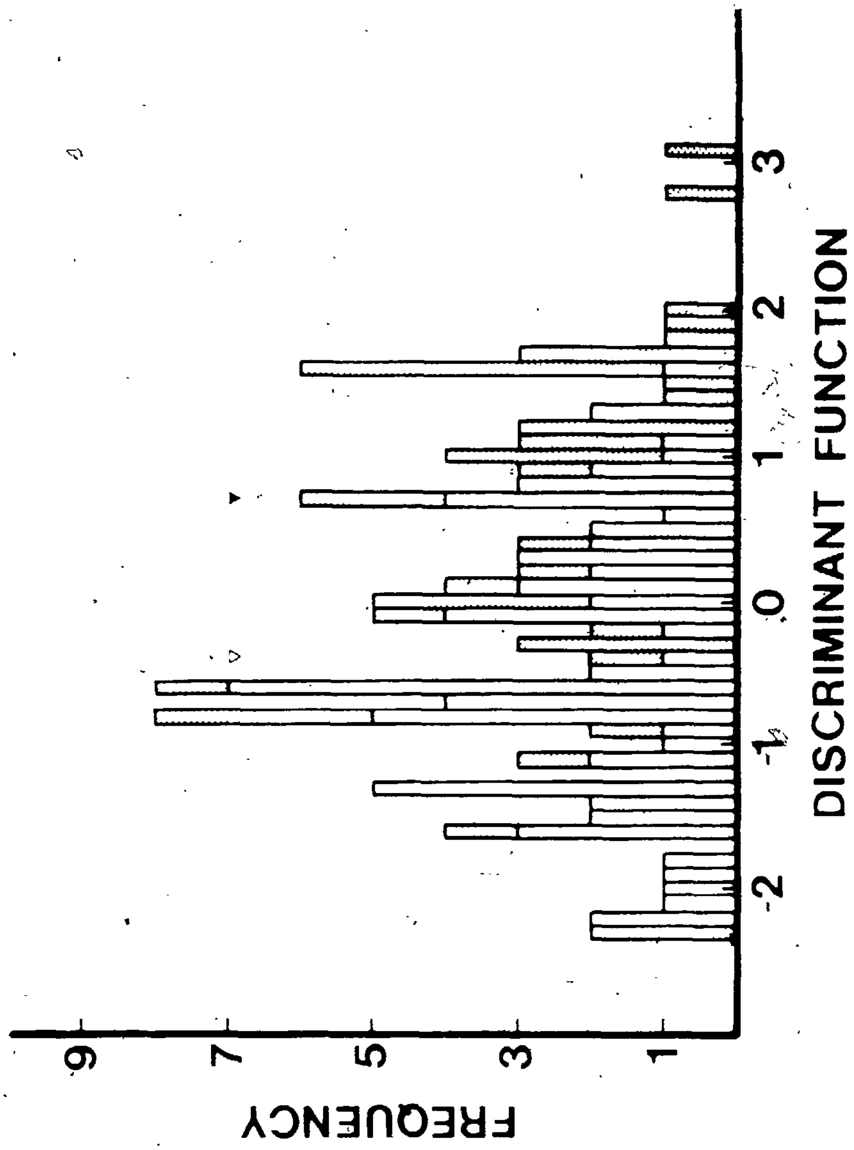


Figure 3.9 Distribution of 1982 successful and unsuccessful males on the Discriminant Function (Table 3.4) derived from the predictor variables (excluding male size and age; n=121) (triangles: group centroids; open bars and triangles: unsuccessful males).

Table 3.4 Discriminant Function derived from the 1982 predictors (excluding male size and age) of nest success ($n=121$; $p=3.74 \times 10^{-5}$, Wilk's Lambda) and correlation between each variable and the new function.

VARIABLE	STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS	CORRELATION COEFFICIENT
Solitary	-0.405	0.201
Central	-0.240	-0.145
Nesting Day	-0.347	-0.278
Nest Diameter	0.428	0.258
Group Size	-0.268	-0.505
Spawning Period	0.919	0.768

well correlated with the Discriminant Function (Table 3.4), and in fact, a higher correlation was found for group size, which did not load heavily. This would suggest that the loadings for 'solitary' and nest diameter are not very meaningful, an interpretation supported by univariate F-tests (Table 3.3). Note that peripheral nests are presented as a separate category in Table 3.3 to facilitate comparisons among nest types. I did not include 'Peripheral' in the Discriminant Analysis (see section 2.2). Spawning period seems to be the main discriminator of nest success, with perhaps a slight influence from group size. The conclusion I draw from this analysis is that a male's success is mainly determined by the spawning period (the probability of getting larvae increases over the summer) but membership in a small group is also advantageous.

The MANOVA on Bietz' 1979 data (which consist exclusively of social nesters) revealed that successful and unsuccessful nests differed significantly with respect to the variables recorded (Wilk's Lambda, $p = 1.63 \times 10^{-6}$, 3 and 518 df). The preliminary univariate F-tests (Table 3.5) suggested that nesting day (day of nest initiation within the spawning period) and centrality were important discriminating variables.

Figure 3.10 shows the separation between successful and unsuccessful males on the Discriminant Function, which correctly classified 60.0% of the cases. The loadings of the variables onto this Function (Table 3.6) indicated that nesting day and centrality were

Table 3.5 Means and standard errors of predictor variables, for Bietz' 1979 successful and unsuccessful males (univariate F-tests, 1 and 520 df).

VARIABLE	MALES WITH LARVAE (n=259)	MALES WITHOUT LARVAE (n=263)	P
Group Size	6.748 ± 0.126	7.058 ± 0.113	>0.05
Centrality	0.568 ± 0.031	0.414 ± 0.030	<0.0005
Nesting Day	1.243 ± 0.030	1.445 ± 0.033	<0.0005

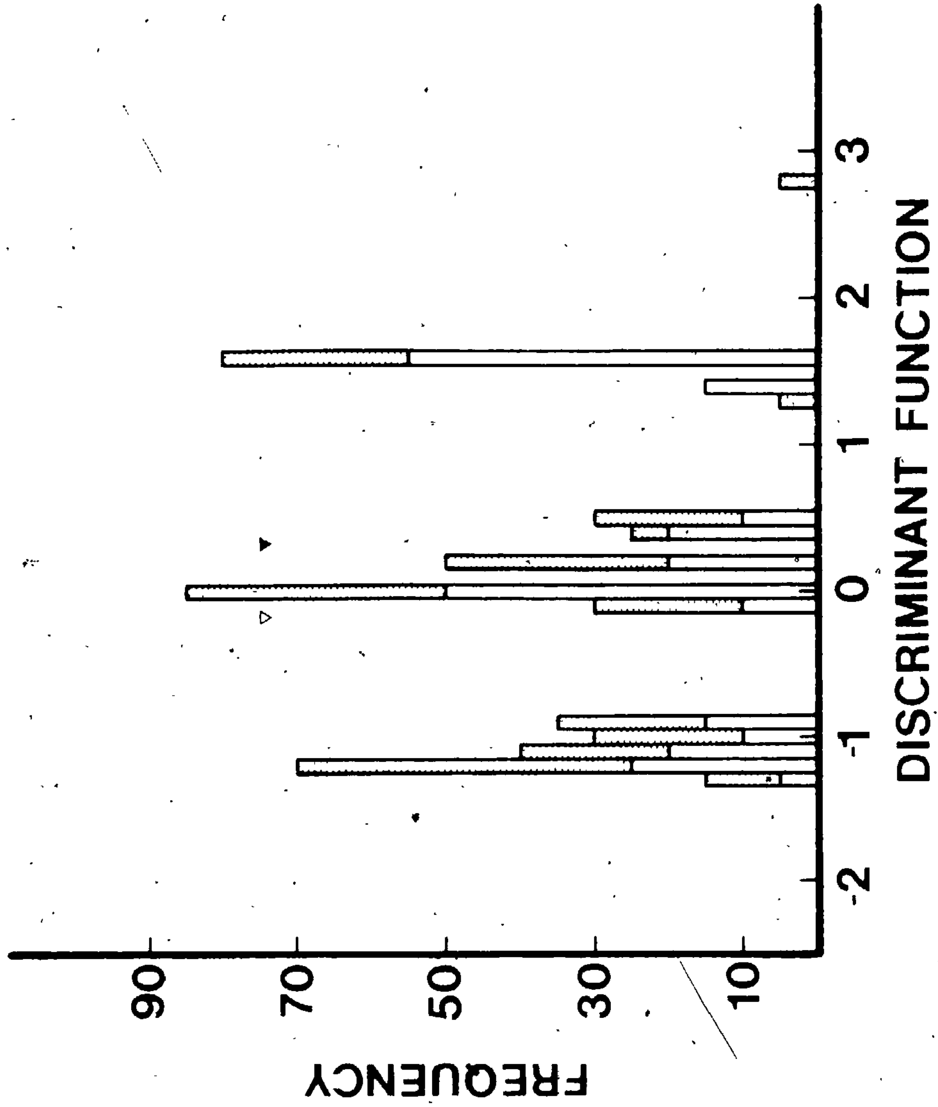


Figure 3.10 Distribution of Bietz' 1979 successful and unsuccessful males on the Discriminant Function (Table 3.6) derived from the predictor variables (n=522) (triangles: group centroids; open bars and triangle: unsuccessful males).

Table 3.6 Discriminant Function derived from Bietz' 1979 predictor variables of nest success (n=522; $p = 1.63 \times 10^{-6}$, Wilk's Lambda) and correlation between each variable and the new function.

VARIABLE	STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS	CORRELATION COEFFICIENT
Group Size	0.192	0.332
Centrality	-0.574	-0.639
Nesting Day	0.706	0.806

important determinants of a male's success, and these variables were also well correlated with the Discriminant Function (Table 3.6). The conclusion drawn, supported by univariate F-tests (Table 3.5), is that successful males tended to initiate their nest early in the spawning period and were more likely to occupy a central nest.

B) Analysis including male size and age

The MANOVA on the 43 cases with male size and age detected no significant overall difference between successful and unsuccessful males (Wilk's Lambda, p=0.177, 9 and 33 df). The univariate F-tests indicated significant differences in nesting day, male length and weight (Table 3.7), but obviously these cannot be used to implicate male size in nest success. It should be noted that, as was the case in 1981, the size and age data are biased samples of the male population, being mainly representative of successful males (see Figure 3.14 for size distribution of 1982 males).

The overall conclusion I draw from the nest success analyses is that spawning period is the main determinant of nest success, with perhaps an additional benefit to nesting in a small group. Bietz' more extensive data on group nesters show a definite advantage for males initiating their nest early in the spawning period, in a central position.

Table 3.7 Means and standard errors of predictor variables (including male size and age), for 1982 successful and unsuccessful males (univariate F-tests, 1 and 41 df).

VARIABLE	MALES WITH LARVAE (n=35)	MALES WITHOUT LARVAE (n=8)	P
Solitary	0.343 ± 0.082	0.125 ± 0.125	>0.1
Central	0.457 ± 0.085	0.625 ± 0.183	>0.25
Peripheral	0.200 ± 0.069	0.250 ± 0.164	>0.25
Nesting Day	1.314 ± 0.114	2.125 ± 0.351	0.008
Nest Diameter	3.510 ± 0.039	3.365 ± 0.088	>0.1
Group Size	1.919 ± 0.138	2.348 ± 0.296	>0.1
Spawning Period	2.686 ± 0.158	2.500 ± 0.189	>0.5
Male Length	2.351 ± 0.018	2.226 ± 0.046	0.007
Male Weight	3.261 ± 0.065	2.872 ± 0.159	0.017
Male Age	3.657 ± 0.099	3.375 ± 0.263	>0.25

3.2.2 Larval Abundance

A) Analysis excluding male size and age

The first principal component derived from the correlation matrix of the predictors of larval abundance explained 39% of the structure in the data (Table 3.8). It represented a gradient from being in a large group and initiating nest construction late in the spawning period, in a central nest, to nesting alone or in a small group, early in the period, and not occupying a central nest. The second component accounted for an additional 22% of the structure and was mainly a gradient from a male occupying a large nest constructed early (with respect to both the particular spawning period and the entire breeding season) to occupying a small nest started late. A scree test (Cattell, 1966) recommended the retention of the first one or two components for further analyses.

The number of larvae obtained by a male was related to his scores on the first two components in the following way:

$$(\text{Number of Larvae} + 0.5)^{0.5} = 10.5 + 3.180\ (\text{PC-1}) + 0.643\ (\text{PC-2});$$

$$p < 0.0005,\ 2 \text{ and } 106 \text{ df.}$$

However, the influence of PC-2 was not significant (t-test, $p > 0.5$), whereas that of PC-1 was significant at the 0.001 level. The adjusted coefficient of determination, R^2, was 9.6% (Figure 3.11A). Thus, a male in a large group, initiating his nest late in the period, in a

Table 3.8 First four Principal Components derived from the 1982 predictors of number of larvae (excluding male size and age; n=109).

VARIABLE	PC-1	PC-2	PC-3	PC-4
Solitary	0.579	0.003	0.128	-0.097
Central	-0.357	-0.217	-0.656	0.462
Nesting Day	-0.362	0.538	-0.146	-0.505
Nest Diameter	-0.042	-0.700	-0.230	-0.675
Group Size	-0.551	0.081	0.319	-0.142
Spawning Period	0.318	0.409	-0.614	-0.215
Eigenvalue	2.36	1.33	1.03	0.63
Variance Explained	39.3%	22.2%	17.2%	10.5%

central position, is expected to obtain fewer larvae than a male nesting solitarily or in a small group, and nesting early in a non-central position. The implied higher success of 'non-central' nesters is not due to peripheral males doing better than central males, but rather, to the inevitable inclusion of solitary males in the 'non-central' category by the artificial dummy variables used in the multivariate analysis to specify nesting status (see section 2.2). Figure 3.11B shows explicitly the respective success of the three types of nesting males. Figure 3.11C-E depicts some additional bivariate relationships relevant to the conclusions drawn from the regression analysis.

B) Analysis including male size and age

When male size and age were added to the list of predictors of larval abundance, the first principal component accounted for 45% of the data structure (Table 3.9). It represented a gradient from small, younger males initiating their nest late in the period and in large groups, to large, older males nesting early in the period and in small groups or solitarily. The second component explained an additional 23% of the structure in the data and was a gradient from a male occupying a large nest early in the season, in a central location to a male occupying a small nest late in the summer, in a non-central location. Again, the artificiality of the dummy variables (see sections 2.2 and 3.2.2.A) should be kept in mind when interpreting these results. A scree test advised the retention of the first one or two components for

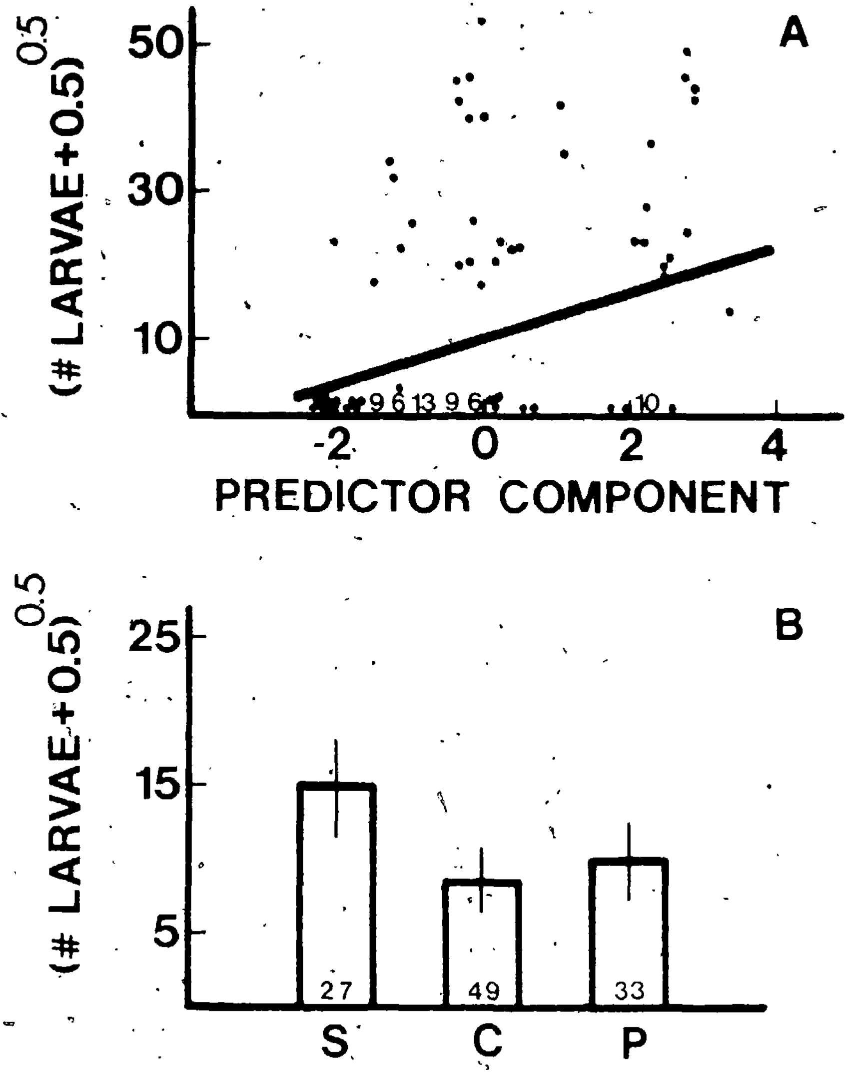


Figure 3.11 A-B A) Relationship between scores on the first predictor component (excluding male size and age, Table 3.8) and larval abundance in 1982 nests (n=109) : $Y = 10.5 + 3.18$ (PC-1), adjusted $r^2=9.6\%$, $p < 0.001$, 1 and 107 df; B) Relation of larval abundance to nesting status (n=109), $p > 0.1$, 2 and 106 df; F-tests (S: Solitary; C: Central; P: Peripheral; numbers in bars: sample sizes; error bars: 1 SE).

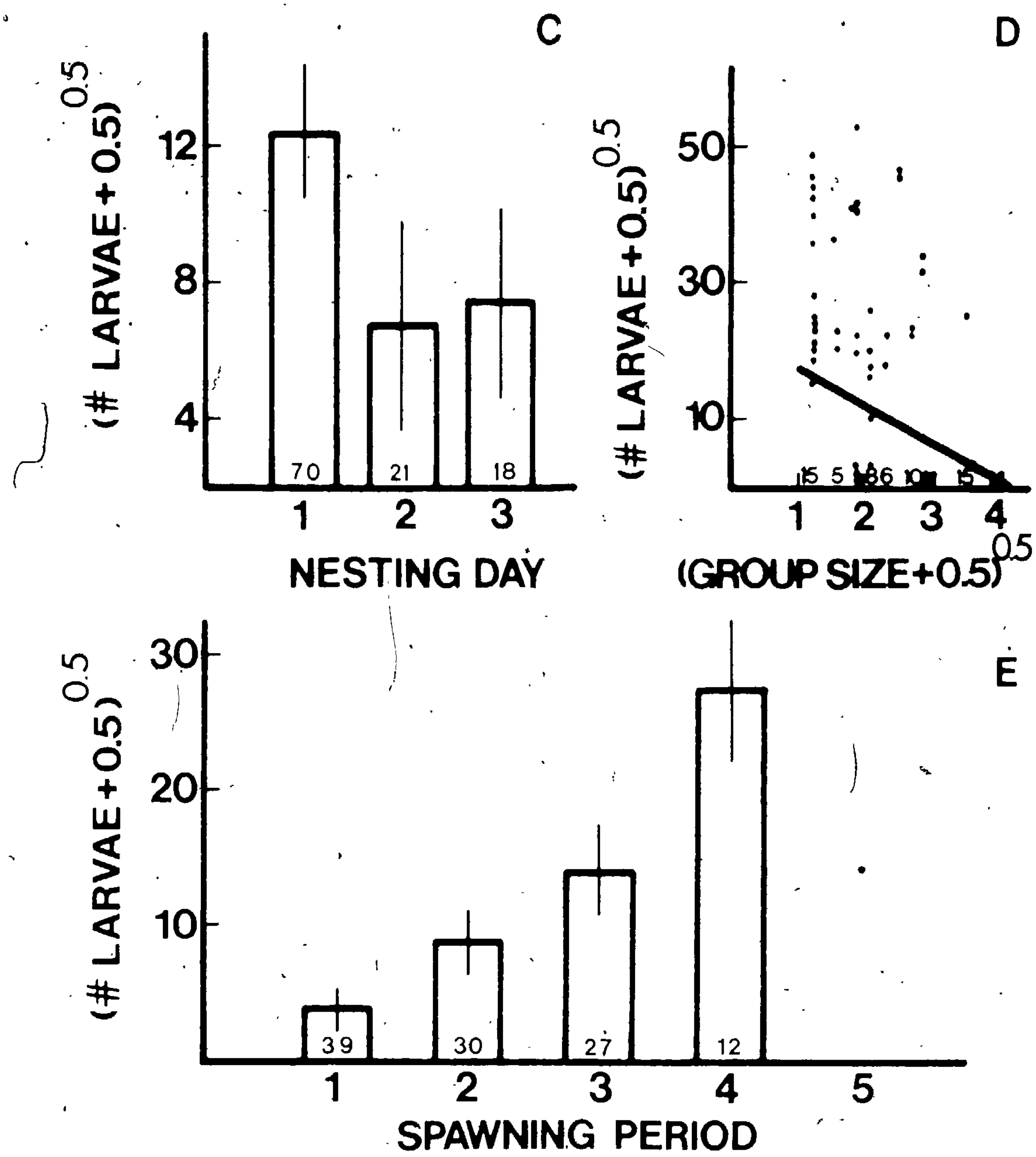


Figure 3.11 C-E Relationship between predictor variables (excluding male size and age) and larval abundance in 1982 nests (n=109). C) $p > 0.1$; D) $Y = 22.7 - 5.41 (\text{GROUP SIZE} + 0.5)^{0.5}$, adjusted $r^2 = 9.1\%$, $p < 0.001$, 1 and 107 df; E) $p < 0.005$; F-tests (numbers in bars: sample sizes; error bars: 1 SE).

Table 3.9 First four Principal Components derived from the 1982 predictors of number of larvae (including male size and age; n=37).

VARIABLE	PC-1	PC-2	PC-3	PC-4
Solitary	0.348	0.415	0.008	0.188
Central	-0.224	-0.412	-0.430	-0.144
Nesting Day	-0.411	0.127	0.350	-0.025
Nest Diameter	0.053	-0.548	-0.285	-0.106
Group Size	-0.399	-0.136	0.456	-0.072
Spawning Period	-0.065	0.506	-0.512	-0.404
Male Length	0.440	-0.182	0.086	0.108
Male Weight	0.441	-0.176	0.138	0.160
Male Age	0.323	-0.059	0.341	-0.852
Eigenvalue	4.01	2.07	0.84	0.63
Variance Explained	44.5%	23.0%	9.4%	7.0%

inclusion in the regression equation. The number of larvae that a male obtained depended on his PC-1 and PC-2 scores in the following way:

$$(\text{Number of Larvae} + 0.5)^{0.5} = 23.3 + 2.906\ (\text{PC-1}) + 1.172\ (\text{PC-2});$$

$$p > 0.05;\ 2 \text{ and } 34 \text{ df}.$$

Although this relationship was not significant, the PC-1 coefficient differed from zero (t-test, $p < 0.05$). When PC-1 was used as the sole predictor, the equation became significant at the 0.025 level (F-test, 1 and 35 df), with an adjusted r^2 of 11.6% (Figure 3.12A). This indicated a weak tendency for large, older males initiating their nest early in the spawning period, in small groups or solitarily, to obtain more larvae than small, young males nesting late and in large groups. Figures 3.12B and 3.13 do not support this conclusion in its entirety, however.

The overall conclusion from the 1982 data is that nest success or failure depends primarily on the spawning period, and perhaps also on group size. Bietz' data suggest that nest initiation day (within the spawning period) and centrality are important determinants of nest success, whereas group size is not. The number of larvae that a male obtains depends on group size, on whether he is solitary or social, on nesting day, and to a very slight extent, on his size.

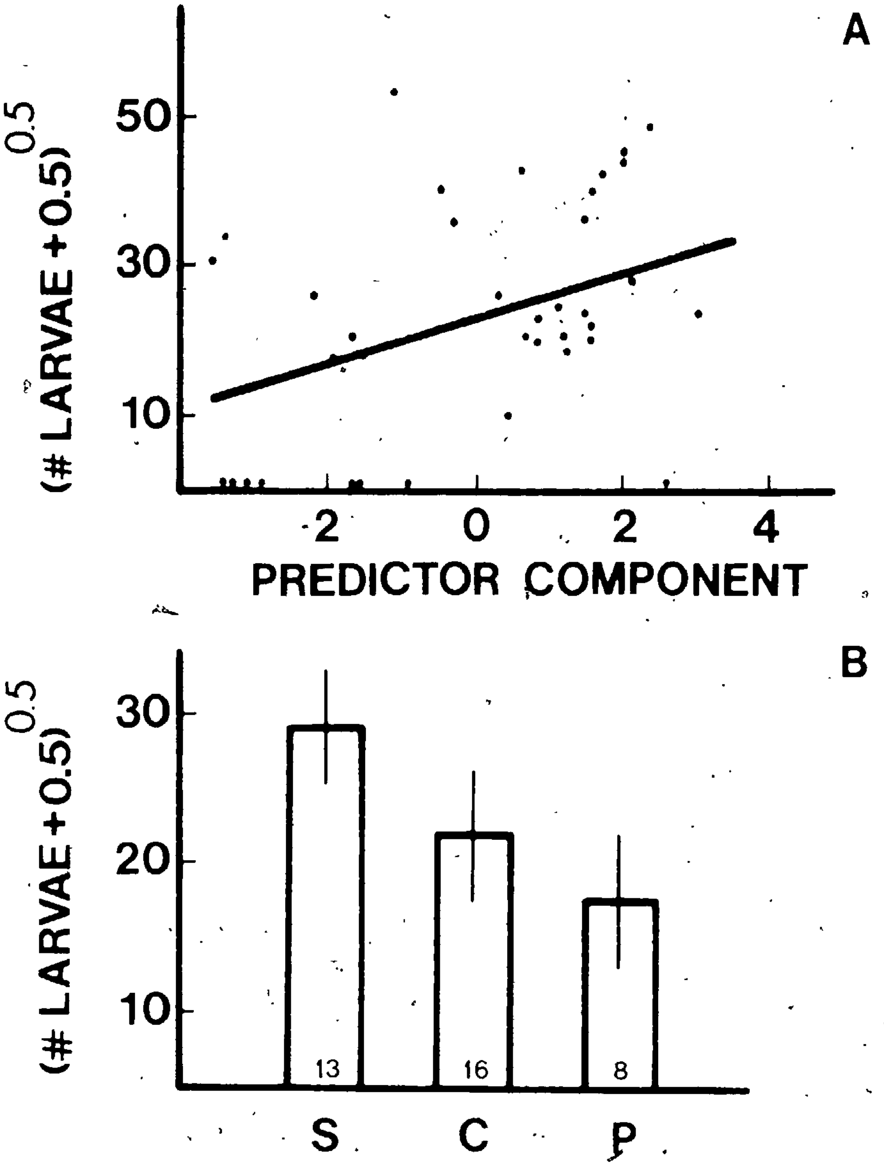


Figure 3.12 A) Relationship between scores on the first predictor component (including male size and age, Table 3.9) and larval abundance in 1982 nests (n=37) : Y = 23.2 + 2.91 (PC-1), adjusted r^2=11.6%, $p <$ 0.025, 1 and 35 df; B) Relationship between nesting status and larval abundance in 1982 nests (n=37) : $p > 0.1$, 2 and 34 df; F-tests (S: Solitary; C: Central; P: Peripheral; numbers in bars: sample sizes; error bars: 1 SE).

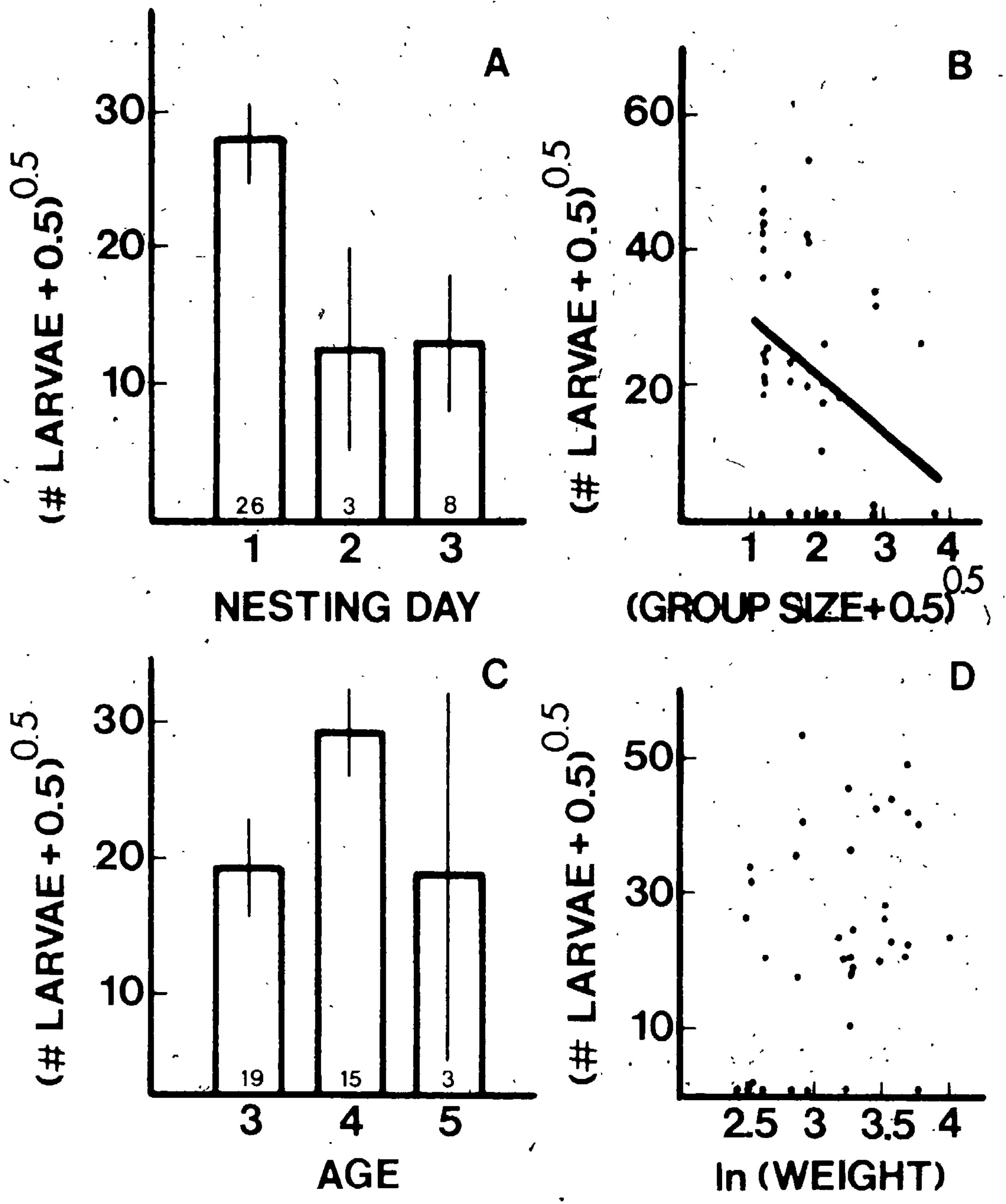


Figure 3.13 Relationship between predictor variables (including male size and age) and larval abundance in 1982 nests (n=37). A) $p < 0.025$; B) $Y = 38.5 - 8.13 (\text{GROUP SIZE} + 0.5)^{0.5}$, adjusted $r^2 = 11.1\%$, $p < 0.025$, 1 and 35 df; C) $p > 0.1$; D) $p < 0.05$, 1 and 35 df; F-tests (numbers in bars: sample sizes; error bars: 1 SE).

3.2.3 Renesters

Figure 3.14 depicts the size distribution of all nesting males tagged in 1982 and that of the 12 who were found renesting later in the season. The mean age (±SE) of the renesters was 3.67 ± 0.188 years. Table 3.10 describes first and second nest characteristics, for comparison with Table 3.3. Renesters' nests were more similar to those of successful males than to unsuccessful nests (Table 3.3). Males who renested apparently shifted from peripheral and central positions to central and solitary nests (Table 3.11), although the sample size precludes a statistical evaluation of this trend. Eleven of the twelve males were successful with their first attempt, although I collected the larvae from nine of these nests. Their second nesting attempt was equally successful (Table 3.10).

3.3 Paternity Experiment

Appendix I summarizes the genetic variability detected in male and female longears sampled from the Thamesford population. Based on the 11 loci examined, the average heterozygosity (H ± SE) for this population is 0.03 ± 0.012. The low individual heterozygosity and the scarcity of rare-allele homozygotes in the Thamesford sample severely restricted the number of identifiable males available. Whether intrusions performed by different males all have an equal probability

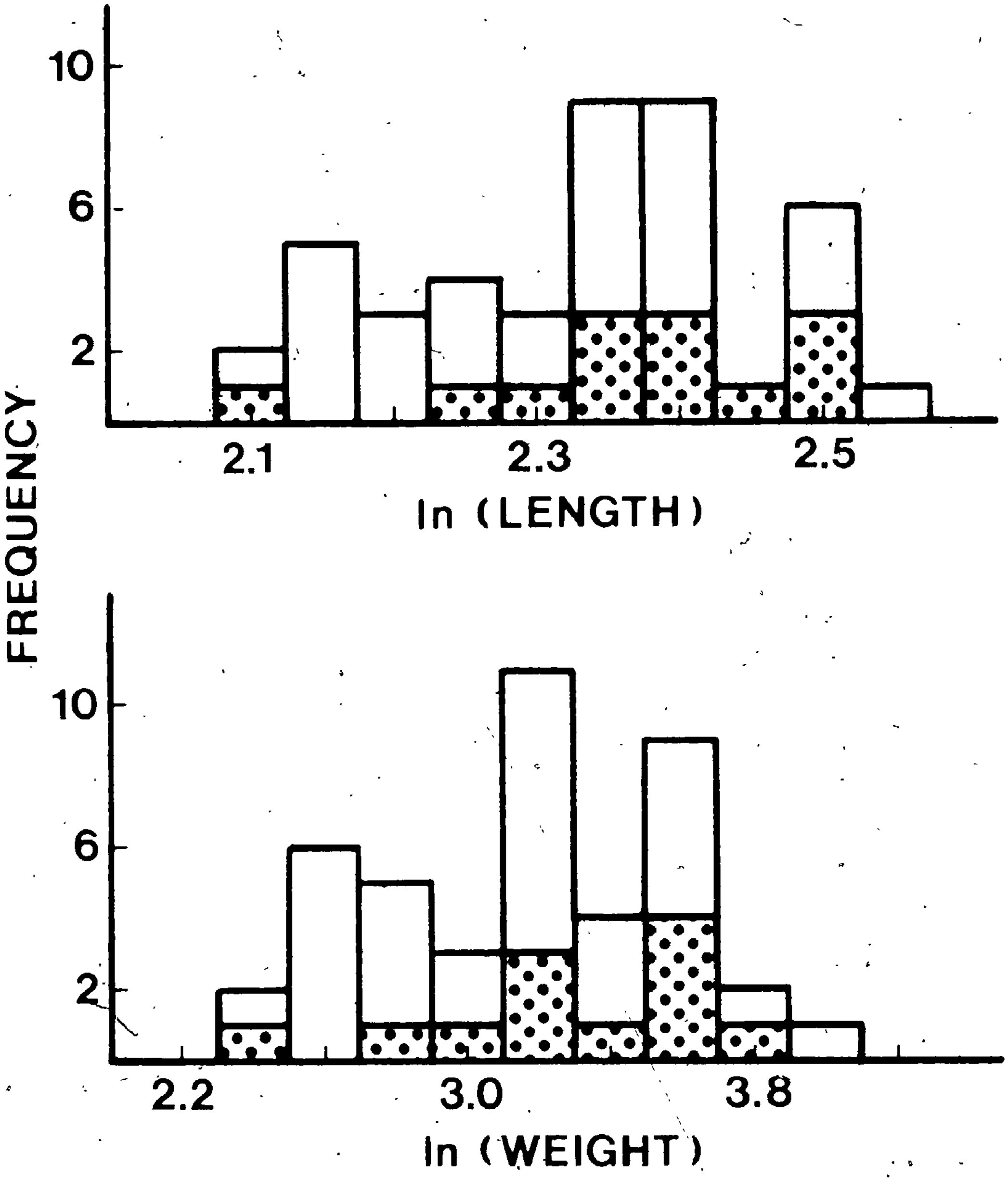


Figure 3.14 Size distribution of tagged 1982 nesting males (n=43); stippled bars, renesters (n=12).

Table 3.10 Means and standard errors of first and second nest variables for the 1982 tagged males found renesting later in the season (n=12; Number of larvae: n=9; paired-sample t-tests).

VARIABLE	FIRST NEST	SECOND NEST	P
Solitary	0.167 ± 0.112	0.500 ± 0.151	>0.1
Central	0.500 ± 0.151	0.333 ± 0.142	>0.2
Peripheral	0.333 ± 0.142	0.167 ± 0.112	>0.2
Nesting Day	1.333 ± 0.188	1.417 ± 0.229	>0.5
Nest Diameter	3.619 ± 0.062	3.413 ± 0.059	<0.05
Group Size	1.945 ± 0.240	1.581 ± 0.124	>0.2
Spawning Period	1.917 ± 0.193	3.167 ± 0.207	<0.001
Number of Larvae	25.4 ± 4.267	23.2 ± 4.417	>0.2

Table 3.11 Nesting status of tagged renesters during their first and second attempts in 1982 (n=12).

		SECOND NEST			
		Peripheral	Central	Solitary	TOTAL
	Peripheral	0	2	2	4
FIRST	Central	1	2	3	6
NEST	Solitary	1	0	1	2
	TOTAL	2	4	6	12

of success, and whether they are in fact successful, therefore remains unknown.

3.4 Male Size Experiment

Five small and eight large males nested. There was no difference in nest diameter between the two size classes ($p > 0.5$, Mann-Whitney test), and no relationship between nest diameter and any of the spawning success variables ($p > 0.05$ all cases, Spearman's rank correlation) or intrusions received ($p > 0.1$) or performed ($p > 0.5$). The males' spawning activities are summarized in Table 3.12. Two of the small males spawned, as did six of the eight large ones. Spawning occurred sporadically throughout the observation period. Although large males attracted more females into their nest than did small males, they did not enjoy a significantly greater spawning success. Predictably, the number of intrusions received was proportional to the amount of spawning achieved ($r = 0.902$, $p < 0.001$, Spearman's rank correlation). The males who fared poorly did not compensate by performing more intrusions ($r = -0.178$, $p > 0.5$). In summary, the results of this experiment could not falsify the null hypothesis that females show no mate size preference.

Table 3.12 Male spawning success and intrusion frequency in the male size experiment (Mann-Whitney tests).

VARIABLE	SMALL MALES (n=5)	LARGE MALES (n=8)	P
Females Entering	1.83 ± 0.541	4.91 ± 0.428	<0.01
Females Spawning	1.04 ± 0.228	2.57 ± 0.643	>0.1
Spawning Time	3.16 ± 1.507	12.08 ± 4.320	>0.2
Intrusions Received	1.16 ± 0.295	2.00 ± 0.845	>0.5
Intrusions Performed	0.91 ± 0.125	2.22 ± 0.714	>0.2

Chapter 4. Discussion

4.1 The Thamesford population

The longear population has declined dramatically in the Middle Thames during the last 20 years. In 1969, the daily number of active nests within my study site peaked at more than 2000 nests (Keenleyside, 1978). The daily number in the same area peaked at less than 400 active nests in 1979 (Bietz, 1980) and at 43 occupied nests in 1982 (this study). Whereas "typical" clusters range in size from a few to more than 100 nests (Keenleyside, 1972; Bietz, 1980; this study, 1981), the largest 1982 group consisted of 16 nests, with most clusters containing fewer than 10 nests. The range of group sizes was therefore rather restricted and the distinction between central and peripheral nests was perhaps not very meaningful in this case. Solitary males comprised a greater proportion of the 1982 nesting population than usual (24% as opposed to Bietz' value of 3% (Bietz, 1980)). These facts lead me to suggest that 1982 was probably not "typical" for longear reproduction, and therefore the results should be interpreted with caution. The reduced population size and atypical cluster formation may have mitigated male competition and female choice and accentuated other factors affecting male fitness.

The genetic variability in this population is lower than published estimates for longear and other sunfish (Avise and Smith, 1974a, b; Avise, 1977). Avise reported an average heterozygosity (±SE) of 0.122 ± 0.012 for another longear population sampled at 14 loci, which is considerably higher than my value of 0.03 ± 0.012. This is perhaps linked to the recent population decline, its location near the northern limit of its range (Gruchy and Scott, 1966; Scott and Crossman, 1973), the 50-year-old dam 1.8km downstream restricting gene flow with other populations, or a possible previous population bottleneck (Nei et al., 1975; Gyllensten et al., 1985). For non-monomorphic loci, only homozygotes for the common allele and a very few heterozygotes were ever discovered, thus imposing a severe limitation on sample sizes and number of unique male phenotypes available for the paternity experiment. The necessity of relying on heterozygotes as experimental males would yield, at best, a conservative estimate (rather than an exact value) of fertilization stealing success, for identical males as a group. Experimentation with only two or three unique males would create a highly unrealistic situation, given that several neighbours and satellites may intrude in a particular nest. Sperm competition would be greatly reduced, which would yield inflated estimates.

4.2 Reproductive success of group nesters

4.2.1 Spawning success

I have drawn primarily on the 1981 and Bietz' data to evaluate each of the factors hypothesized to influence the reproductive success of social nesters.

Although the 1981 multivariate analyses did not point to group size as an important factor, differences in spawning success among the three groups are apparent (Figure 3.2D). This is true even after the influence of other predictor variables on spawning success is removed : for example, the partial correlation coefficient between group size and spawning time is -0.272 ($p<0.005$, 110 df). Males from the largest group were less successful than others, despite being larger, on average, than members of the other two groups (Figure 3.4B; weight: $p<0.005$; age: $p>0.05$, F-tests with 2 and 54 df). Female choice need not be invoked since these groups were sequential, the largest representing the first spawning attempt of the season. Perhaps ~~fewer~~ females, and only the larger males, ripen early in the summer. Members of the other two groups in 1981 enjoyed, on average, equal success. Bietz' 1979 data show no group size difference between successful and unsuccessful males, the measure of success being in this case the acquisition of larvae rather than the amount of spawning (Tables 3.5 and 3.6). Bietz (1980) reached different conclusions with an analysis of covariance on the same data, but including solitary nesters as well. He regressed number of successful males against their group size, for each spawning period and found all slopes to be less than 1.0, indicating a decreasing proportion of successful males with increasing group size. I suspect that these differences stem from the inclusion of solitary males in the analysis, most of whom were successful and would therefore lower the estimated slopes. Whichever interpretation is adopted for Bietz' data, it is clear that females do not prefer larger groups. Within the restricted range of group sizes in 1982, successful males tended to nest solitarily or in small groups (Tables 3.3 and 3.4), and the number of larvae that a male obtained was negatively related to his group size (Tables 3.8 and and 3.9; Figures 3.11D and 3.13B). However, the largest groups were found early in the season (spawning period 1 and 2), so that once the influence of spawning period is extracted, the partial correlation between group size and larval abundance is no longer significant ($r = -0.149$; $p > 0.1$, 106 df). Taken together, these results fail to support the prediction, stemming from a sexual selection hypothesis, that females should prefer large groups, whether it be for the wider range of males, minimized searching and selection time, or simply greater conspicuousness (Wilson, 1975).

I transformed the original centrality scores into a binary variable (section 2.1) for two reasons. First, scores are not comparable between groups, be[illegible] a function of group size. This would require a separate analysis for each group, which the sample-size-to-variable ratios, particularly in 1982, clearly precluded. Second, the centrality scores often formed a nearly linear hierarchy among nests in a group, with very few nests assigned equal ranks. I thought that this was a too fine-grained measure of centrality. I arbitrarily selected the median score of each group as the cut-off value, with no a priori reason for selecting alternatives. Nonetheless, I subsequently experimented with several other methods of defining centrality. I tried using standardized centrality scores, partitioning centrality into three (rather than two) categories, varying the proportion of central males in the group, and finally, standardizing map coordinates of all nests in a group (to improve circularity of the cluster) before superimposing rings of various thicknesses on the map to delimit peripheral nests. I then repeated the PCA on the predictors of spawning success (Table 3.1), successively replacing the original definition of centrality (section 2.1) by each of the new classification schemes listed above. There were no detectable differences in results among analyses, indicating that the definition of centrality adopted in this thesis was suitable. Central males enjoyed greater spawning success than peripheral males in 1981 (Table 3.1, Figure 3.2A). This is true even once the influence of other predictor variables on spawning success is removed : for example, the partial correlation between centrality and spawning time is significant at the 0.05 level (r = 0.210; 110 df). Bietz' 1979 data clearly show that central males were more likely than peripheral males to obtain larvae (Tables 3.5 and 3.6). Again, his interpretation of the importance of centrality, based on his data, differs from mine since he concluded that probability of spawning bore no relation to position in the group. He retained the original centrality scores, however, and therefore examined each group separately. In some groups, successful males averaged a higher score than unsuccessful males. In others, there was no difference, and in others still, the relationship was reversed. Undoubtedly this is partly explained by the substantial reduction in the degrees of freedom associated with comparisons within individual groups, but more importantly, by the continuous distribution of the scores themselves. In 1982, no reproductive advantage was conferred upon central males (Tables 3.3, 3.4, 3.7; Figures 3.11B, 3.12B) but I acknowledge that such a distinction may seem unreasonable when considering very small groups of loosely aggregated nests. It can be concluded that, all else being equal, centrality is a significant determinant of a social male's reproductive success, and intrasexual competition for the acquisition of central nests is therefore likely.

Some late nesters became central by filling the spaces among existing nests whereas others expanded the colony from its periphery, but generally, central males began nesting on the first day of a spawning period, and peripheral males arrived later ($r = -0.308$, $p < 0.001$). Males initiating their nest on day 1 of a spawning period obtained more spawnings than late nesters in 1981 (Table 3.1, Figure 3.2B). For instance, even once the influence of other predictor variables is removed, the correlation between nesting day and spawning time is significant (partial r = -0.235; $p < 0.01$, 110 df). The analyses on the 1982 data failed to reveal a significant difference in nesting day, within the spawning period, between successful and unsuccessful males (Tables 3.3 and 3.4; but see Table 3.7). The PCAs on the 1982 predictors of larval abundance accorded moderate importance to nesting day (Tables 3.8 and 3.9) but the univariate F-tests were not significant (Figures 3.11C and 3.13A), indicating only a weak reproductive advantage, in 1982, to nesting early in the period. Furthermore, the partial correlation coefficient between nesting day and 1982 larval abundance was only -0.135 ($p > 0.1$, 102 df). Bietz' 1979 data suggest that nesting day is the most important difference between successful and unsuccessful males, with males obtaining larvae having initiated their nest significantly earlier (Tables 3.5 and 3.6). My overall conclusion is that males nesting on the first day of a spawning period enjoy greater reproductive success than late nesters. Certainly such males are available to visiting females for the greater portion of a spawning period, whereas males still preparing a nest must relinquish several spawning opportunities and may even miss them altogether.

To avoid disturbing the owners by collecting nest measurements, I used maps to estimate nest diameters. These were probably most accurate for group nesters, for whom mapping grids were erected. Inaccuracies may have contributed to the scatter and low coefficients of determination associated with this variable, particularly in 1982, where a sizeable portion of the nesters were solitary. The 1981 data, which consist entirely of group nesters, indicated that nest diameter is an important determinant of spawning success (Table 3.1, Figure 3.2C). All else being equal, however, the correlation between nest diameter and spawning time is not significant (partial $r = 0.039$; $p > 0.5$, 110 df). The 1982 data revealed no relationship between nest diameter and reproductive success either (Tables 3.3, 3.4, 3.7 and 3.8). The partial correlation coefficient between nest diameter and larval abundance is 0.113 ($p > 0.2$, 102 df). I therefore conclude that, all else being equal, females show no discrimination among males with respect to the size of their nest. Rather, nest diameter influences spawning success only indirectly, through its covariation with other predictors of success. Perhaps females evaluate other unrecorded nest variables, such as depth or particle size of the substrate, which may affect egg and larval conspicuousness and viability.

The correlations between male length or weight and male age are lower than expected (length: $r = 0.428$, $p < 0.001$; weight: $r = 0.527$, $p < 0.001$, 55 df), with the size distributions of three- and four-year-old males broadly overlapping. The correlation between the 1981 spawning success component and the predictor component incorporating size and age was not significant (Figure 3.3), nor were the bivariate relationships between size or age and spawning success variables (e.g. Figure 3.4D). However, the partial correlation coefficients between male length (but not weight or age) and each of the spawning success variables were significant and positive ($p < 0.02$ in all cases, 49 df). The MANOVA on 1982 successful and unsuccessul males with size and age data found no overall difference between the two groups of males, although univariate tests suggested that length and weight were greater for successful males (Table 3.7). Regressing larval abundance against the first predictor component from Table 3.9 indicated that male size influenced a male's reproductive success, but bivariate relationships did not support this (Figures 3.13C and D). None of the partial correlation coefficients between male length, weight or age and larval abundance were significant ($p > 0.2$ in all cases, 29 df). The laboratory experiment also failed to demonstrate a reproductive advantage for large males (Table 3.12), probably due to minimal sample size and spawning activity. This study fails to corroborate the prediction that females should prefer larger or older males. However, because size measurements were obtained mostly from successful males (49 of 57 in 1981, 35 of 43 in 1982), the conclusi[illegible] that size has no significant impact on a male reproductive success should be restricted to successful nesters, and the unbiased comparison of successful and unsuccessful male sizes has yet to be accomplished. Although the null hypothesis cannot be rejected, trends in the predicted direction were usually discernible and sometimes approached statistical significance. Furthermore, size and age tended to correlate with the predictor variables shown to exert a significant influence on reproductive success, namely centrality (Figures 3.4A and C) and nesting day (Table 4.1). In addition, Bietz' data clearly show that central males were larger than peripheral males (Figure 3.5) and that such males tended to reproduce successfully (Tables 3.5 and 3.6). Moreover, the partial correlation coefficients between male length and 1981 spawning success (mentioned above) suggested a tendency for larger males to enjoy greater reproductive success. I therefore propose that greater sample sizes and unbiased sampling would disclose a convincing relationship between male size and reproductive success.

The possibility remains, of course, that females are not evaluating male quality, or that they do so by assessing other phenotypic traits such as colouration, aggression or courtship intensity. Behavioural cues in particular might reflect not only competitive but also parental abilities. Some authors (Loiselle and Barlow, 1978; Kodric-Brown, 1981) have compared teleost breeding aggregations to bird leks, arguing that paternal care, where it occurs, arose as a coincidental extension of maintaining territoriality to attract additional mates. Kodric-Brown, for instance, does not consider incidental protection of the brood to be parental investment. Whether or not such a view is justifiable should not derogate the possibility that females evaluate parental abilities of potential mates, using behavioural cues as well as physical traits, in lekking fish species that have extended paternal care, presumably in response to predation pressure, beyond the spawning phase.

Table 4.1 Correlation between male size or age and nesting day (n=57, 1981; n=43, 1982).

	CORRELATION COEFFICIENT (P)	
VARIABLE	1981	1982
Length	-0.404 (≈ 0.002)	-0.619 (< 0.001)
Weight	-0.394 (< 0.005)	-0.595 (< 0.001)
Age	-0.059 (> 0.5)	-0.436 (< 0.005)

4.2.2 Fertilization stealing

I presumed when I collected data on reproductive success (spawning activities, presence and abundance of larvae) that I would later obtain estimates of fertilization stealing success, which would be taken into consideration when comparing the fitness of nesting males. This was not accomplished and I must therefore assume that all stealing attempts have equal probability of success, regardless of their author and number of concurrent intrusions. This probability may be insignificant if the owner's sperm saturates the nest and dilutes intruders' milt before fertilization occurs. In four species of sunfish, the functional life span of sperm was estimated at about one minute (Childers, 1967) and if longear sunfish sperm is equally viable, dilution is quite likely, provided that fertilization is not immediate. If, on the other hand, fertilization is instantaneous, stealing may be quite successful since intruders usually slip in between the spawning fish and therefore the sperm closest to the female's vent is likely to be the intruder's. I do not know which possibility is correct and I cannot ascertain whether males who spawn much but receive many intrusions are more successful than those who spawn little but receive few intrusions. Nonetheless, assuming that all intrusions are equally successful, the gains or losses incurred by nesting males can be compared, and Bietz' hypothesis that "unattractive" males increase their reproductive success by joining preferred males and stealing from them can be tested.

Late nesters within the spawning period who occupied small and peripheral nests accomplished very little spawning and yet did not compensate by stealing many fertilizations from more successful males. In fact, they generally performed fewer intrusions than successful males (Figure 3.6B). This in itself does not invalidate Bietz' hypothesis, especially if these males gain fertilizations, i.e. perform more than they receive. Only half of all 1981 nesters profited from fertilization stealing (Table 4.2) and only about half of these were peripheral males (who, in general, attract few females). Fifteen males performed as many intrusions as they received and the remaining nesters received more than they performed. Therefore, peripheral and central males enjoy a similar probability of gaining fertilizations, and this probability is only 0.5, meaning that on average, peripheral males neither benefit nor lose by joining successful males. However, if they cannot otherwise achieve any spawning, they certainly do no worse by joining a group, and in fact run a 0.5 chance of doing better. They may also gain valuable experience for future nesting attempts. Perhaps peripheral males are making the 'best of a bad situation' (Krebs and Davies, 1981) and Bietz' hypothesis remains plausible.

Central males, on average, neither gain nor lose from intrusions, which raises the question of why attractive males remain in nesting groups. As Bietz (1980) pointed out, the high spawning synchrony within the study site area may discourage central, early-nesting males from abandoning their nest when joined by "unattractive" males to

Table 4.2 Numbers of social males having gained or lost nest intrusions in 1981 (Gain = Intrusions Performed - Intrusions Received).

	NET INTRUSION GAIN			TOTAL
	+	0	-	
Central Males	26	6	25	57
Peripheral Males	32	9	17	58
TOTAL	58	15	42	115

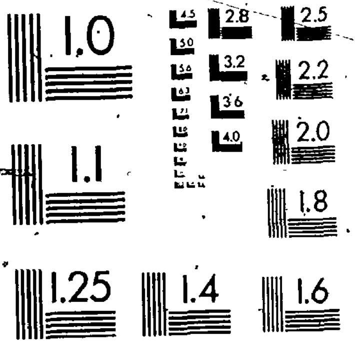
renest solitarily, because they would then become late nesters and run the risk of not spawning at all.

It seems curious that females should choose males nesting early and in central positions and remain in their nests despite fertilization stealing from neighbours and satellites, because these intrusions may effectively counteract female choice. However, if the ability or tendency to steal fertilizations successfully were heritable, a female might do equally well by investing in male offspring who would also be successful with this behaviour as she would by producing "attractive" males, or perhaps by balancing the proportion of each type with their relative fitness (Alcock, 1979a, b). She would do even better if successful intruders were also attractive to females for other reasons. This reasoning may explain the frequent instances in which females at last deserted a heavily intruded nest only to spawn with one (or more) of the intruders.

In 1981, the 12 most successful males (10% of nesting males) garnered 40% of the spawnings, with the first six obtaining 22% of the females. Sixty-four percent of all nesters spawned at least once. The variance in male spawning success is therefore lower than that commonly seen in 'true' leks, where less than 10% of the males may perform over 75% of the copulations (Wilson, 1975). This discrepancy suggests that sexual selection may be less intense in social longear sunfish than in true lekking species, where the males invest nothing but sperm in their offspring and are therefore likely to be more stringently evaluated on their genetic quality (Borgia, 1979). It should be remembered, however, that the above statistics take neither satellites nor the possibility of bachelor males (reproductively inactive adults (Wirtz, 1981)) into consideration. The percentage of successful adult males may therefore be much lower than I estimated.

In summary, females discriminate among group members, often leaving a nest without having circled with the courting owner, and spawn more often with early-nesting males occupying central nests. Among these males, size has no prominent effect on reproductive success, but the unbiased comparison of successful and unsuccessful males was not achieved. There are, however, several indications that successful males are in fact larger, which suggests intrasexual competition for early occupancy of large central nests. Females may also evaluate other, unrecorded, male or nest characteristics. Although early- nesting males perform more intrusions than late nesters, both categories have an equal chance of gaining or losing fertilizations. However, intrusions may be the only possibility of success for "unattractive" males and therefore, despite the lack of net profit from fertilization stealing for these males as a group, I do not reject Bietz' hypothesis.

2 OF/DE 2



4.3 Reproductive success of solitary nesters

The multivariate analyses of the 1982 data indicated a reproductive advantage for members of small groups and for solitary nesters. An ANOVA nevertheless suggested that solitary males were no more likely than central or peripheral group males to obtain larvae ($p > 0.25$, 2 and 118 df) and the univariate comparisons presented in Chapter 3 (Tables 3.3 and 3.7, Figures 3.11B and 3.12B) all failed to demonstrate a significant reproductive superiority for solitary nesters, although the trend was consistently discernible. My conclusion is that solitary males enjoy a slight reproductive advantage over social nesters, albeit less striking than expected. Although I collected no behavioural evidence, this advantage may be the direct consequence of moderate female preference for large males: solitary males were significantly larger than social nesters (length: $p < 0.05$; weight: $p < 0.025$; age: $p > 0.1$; F-tests, 2 and 34 df). An SNK multiple range test (Zar, 1974) revealed that peripheral and central males did not differ in size ($p > 0.5$) but that both types were smaller than solitary nesters ($p < 0.05$ in both cases; 34 df). Incidentally, if purely stochastic events determined whether or not solitary males retain their nesting status throughout a spawning period, no size difference between solitary and central males should be apparent.

I did not record spawning activities of solitary males but I witnessed a few instances and never detected any satellites associating with these isolated nests. This, coupled with the absence of nesting neighbours, suggests that fertilization stealing attempts are rare or absent in isolated nests. All or nearly all larvae in such a nest would therefore be the owner's offspring, a most unlikely situation for social nesters. Even if larval abundance were no greater in solitary than in aggregated nests, the greater likelihood of paternity would still entail higher reproductive success for isolated nesters. It could of course be argued that because group members neither gain nor lose, on average, from nests intrusions, the enhanced certainty of paternity associated with solitary nesting is a disputable benefit. However, very few individual social nesters in fact balance the number of intrusions received with those performed, but instead run as great a risk of loss as of gain. In contrast, solitary males evade this risk (unless, of course, they occasionally suffer intrusions from satellites), and although they necessarily relinquish the opportunity to steal fertilizations to enhance their fitness, their attractiveness to females is apparently sufficient to procure them greater success than they might achieve within nesting aggregations.

In summary, my findings agree with the hypothesis that large males are attractive to females and that such males should nest solitarily to avoid spawning interference from other males. Solitary males are larger, they tend to obtain more larvae and probably enjoy greater certainty of paternity than do social males. This greater success was evident despite the "atypical" 1982 breeding season, where solitary nesters comprised an unusually large proportion of the breeding population. Individual solitary males would most likely have enjoyed an even greater differential in reproductive success had they been rarer relative to social nesters.

The 1982 data pointed to spawning period as the most important predictor of male reproductive success. This variable undoubtedly reflects climatic variations in water temperature or flow. A drastic drop in water temperature or increase in flow, resulting from cool weather and heavy rains, often promoted fungal growth on the eggs or washed out the nest contents of most longear nests. Such occurrences were common early in the summer, particularly during the first breeding attempt, and the likelihood of successfully rearing larvae therefore improved as the season progressed. Other stochastic environmental perturbations during either year of field work undoubtedly account for some of the variation in reproductive success left unexplained by the selected predictor variables.

4.4 Costs and benefits of group nesting

Grouped nesters unquestionably invest more time and energy in intraspecific territorial defence than do solitary males. Most of the time not channeled into nest preparation, courtship or spawning is spent circling in the nest, performing aggressive displays, butting or mouth-fighting with nesting neighbours. I never noticed any injuries that could have resulted from such interactions.

Competition for food resources is unlikely since males were never seen leaving their territory to feed. They occasionally nipped at the substrate between nests, probably ingesting small invertebrates, but seldom did so within the confines of their nest, in which case they presumably removed infertile or fungused eggs. I have not examined stomach contents to verify this.

I do not know whether competition for mates is intensified for group nesters because I have no data on frequency of female visits to solitary nests. Even if the average visit rates were identical for solitary and group nests, a female might conceivably reject an attractive social male, whom she would normally accept were he solitary, simply because she has simultaneously encountered an even better neighbour. This could represent a cost to all but the most attractive social nesters. On the other hand, if groups allured a disproportionate number of females, availability of the latter might be enhanced for social males, although the existing data do not support this possibility (Figure 3.2D).

Nesting aggregations are probably more conspicuous than isolated nests to predators, which may heighten the risk of predation for social adults or their broods. On the other hand, group defence mechanisms may counterbalance such a risk (see below). Although I did not investigate the importance of predation pressure, I never witnessed predation attempts during my observations, and very few males 'abandoned' their nest after having acquired eggs. Creek chub and common shiners continuously swam about longear nests but were never allowed within while the owner was present. If I removed a male from his territory, they invaded the nest within seconds and nipped repeatedly at the bottom for several minutes, nesting neighbours rarely attempting to evict them. The only egg predation I observed in occupied nests was by conspecific females who, as described by Keenleyside (1972), entered the nest, being courted by the owner, and suddenly snapped at the bottom instead of proceeding with spawning. The male promptly chased them away. Females probably cannibalized solitary nests as well. The minimal evidence of adult or egg predation does not allow its dismissal, however, as a significant cost of social nesting.

Finally, the risks of cuckoldry and nest parasitism were debated in sections 4.2.2 and 4.3 and can be summarized by stating that social males are as likely to lose as they are to gain fertilizations from nest intrusions, which connotes a substantial risk to males capable of attracting females, whereas males who would otherwise fail to reproduce can do no worse.

Before enumerating the potential benefits of nesting aggregations I must emphasize the remaining possibility that the existing breeding system may have resulted from limited habitat. Bietz' demonstration of presently unused yet suitable nesting habitat at the Thamesford site does not mean that ample habitat has always been available, especially if one acknowledges the recent population decline at Thamesford. Furthermore, the present breeding system may have evolved under different environmental circumstances and in more southern latitudes, where this species is relatively abundant, before it expanded its range to Canadian watersheds.

Benefits of group nesting are very unlikely to include enhanced foraging efficiency. Nesting males were never seen leaving their territory to feed. Males initiating nesting aggregations might conceivably select substrates harbouring an abundant invertebrate fauna, but solitary nesters certainly could do likewise.

Group members may benefit from efficient predator defence. Neither Bietz (1980) nor I observed any predation attempts on nesting males, which diminishes the plausibility of adult protection being a significant advantage of social nesting. I witnessed brood predation only when I removed or disturbed the nest owner, which suggests that males can effectively deter brood predators. This may, however, necessitate a substantial energy expenditure by solitary males, which can be efficiently reduced by cooperative defence. Social males in fact often combined their efforts in chasing cyprinids approaching their nests but tolerated them if they remained close to the water surface. Although I did not observe nesting groups continuously, I never saw other species known to consume longear eggs or larvae, such as snapping turtles or white suckers (Keenleyside, 1972; Bietz, 1980), approaching nests or being mobbed by nesting males. Although the economy of energy may be considerable for social males, predation does not, superficially, appear to be a pressing force favouring group nesting. In contrast, nesting bluegills decidedly gain protection by aggregating, since solitary males suffer the highest rates of brood loss, followed by peripheral males, who apparently shield central nests from many predators (Dominey, 1981a; Gross and MacMillan, 1981). Rigorous examination of predation intensity in longear sunfish is essential to resolve its importance in the evolution of group nesting. The argument presented with regard to possible habitat constraints during the evolutionary past of longears may also pertain to predation pressure. Perhaps predation was very influential, under the evolutionary circumstances of this species, in shaping its mating system, despite its present, apparently tempered, importance at Thamesford.

The amount of variation in male success explained by the chosen predictor variables (r^2) was minimal in all analyses, which could be construed as evidence that sexual selection is not the only, or perhaps not even the major, factor leading to social nesting. However, several points deserve mention. First, Goff (1984) correctly pointed out that coefficients of determination are expected to decrease when reproductive success is estimated late in the brood's development (instead of recording number of females, presence or number of eggs) because additional ecological, behavioural or stochastic factors may progressively come into play and alter offspring survival. Also, most studies that used multiple regression to examine reproductive success neglected to consider partial (and often considerable) correlations between the various predictors used, which can dramatically inflate the R^2 value (Wonnacott and Wonnacott, 1981). Furthermore, restricting the predictors to the first one or two, rather than all, principal components results in some loss of information, which can diminish the amount of variation explained. For example, PC-1 from Table 3.1 summarizes only 40% of the structure within the set of predictors, yet was used as the sole predictor of nest intrusions (Figure 3.6), because subsequent components did not appear to be interpretable (see section 3.1.1). Another plausible explanation for the low r^2 values is that other vital determinants of reproductive success, which could account for a significant portion of the unexplained variation, were not measured. The importance of climatic conditions, stochastic events, and predation has already been discussed, and the inclusion of these factors in the analyses might drastically improve analytical efficiency. Nonetheless, the meagre r^2 values do not necessarily imply that female choice has minimal consequences on male success. Female choice does not need to be extreme to operate. A slight reproductive advantage conferred upon the possessors of a certain trait is sufficient to result in directional selection on that trait. For example, female preference for slightly larger males, all else being equal, would lead to greater male size, provided that the preferred males enjoy at least a slight reproductive advantage.

The above arguments lead me to suggest that sexual selection, albeit less intense than expected, is operating, and at least partly responsible for the existence of nesting aggregations in longear sunfish. In this case, however, males may have been a relatively great driving force in shaping the mating system. Although Emlen and Oring (1977) state that female interests should weigh more heavily than those of males in the evolution of mating systems (because of their greater investment), this may not always be the case in species where males also invest heavily, by providing extended parental care, for example. In such cases, males may be major operators, females being ineffective in counteracting masculine input, in the development of the reproductive system. For example, if small longear males, ignored by females, were to join large males to enhance their fitness by stealing fertilizations as Bietz (1980) suggested, females might well be forced to comply with this system despite their preference for large, originally solitary males, because such males would become very rare or absent. The costs of searching for them would become prohibitive, and many females doing so would fare poorly or fail to reproduce altogether because of intense female competition. Females could instead compromise by spawning primarily with the largest, early-nesting central males and tolerating intrusions from less attractive males, yet spawning opportunistically with large solitary males. Relative frequencies of social and solitary nesters might fluctuate about an equilibrium point, maintained by a frequency-dependent mating advantage. This sexual selection scenario could conceivably explain the existence of nesting groups, the differential spawning success of their members, and the slight reproductive advantage discerned for solitary nesters. The self-interests of large, attractive males have been discussed previously and can be summarized by stating that they should endeavour to nest solitarily but should not abandon their nest if joined by less attractive males. As for the "unattractive" males nesting close to the preferred males, they could do no worse, and run the chance of doing better than by nesting alone (or not at all).

4.5 Alternative male reproductive behaviours

I had aspired to resolve whether satellites, social and solitary males belong to distinct factions of the population, each adopting a lifelong reproductive strategy, or whether the different behaviours represent alternate or sequential tactics employed by all adult males. I captured, tagged and measured only six satellite males, who were never recaptured. They were one or two years old and, as all satellites, distinctly smaller than any nesting male. This does not provide reliable evidence that satellites eventually become territorial. Perhaps they suffer severe mortality rates and never attain nesting size. Although the validity of this technique is questionable, scales from nesters never bore growth checks associated with reproductive effort between the origin and the second annulus, suggesting that they had not bred, as satellites or otherwise, until their third year. These observations provide (insufficient) evidence that satellite and territorial behaviours represent mutually exclusive reproductive pathways. The more reliable back-calculation of growth rates, used by Dominey (1980) and Gross and Charnov (1980) to demonstrate the existence of distinct pathways, could not be executed with this population: to do so requires the capture of both reproductively active and inactive young cohort males. The fate of satellites therefore remains unknown.

I have evidence (section 3.2.3) that nesting males breed more than once in a season and that they may switch nesting status between breeding attempts (Table 3.11). They probably do so between seasons as well, but tagged males were never seen in subsequent years. Table 3.11 invalidates the proposition that social and solitary nesting are mutually exclusive reproductive behaviours for individual males, despite the observation that solitary males are, on average, larger than social nesters (Table 3.9; section 4.3). These facts concur with Bietz' (1980) model, which predicts that attractive solitary males will not always succeed in maintaining their nesting status. I do not know what proportion of males normally renest during a breeding season. Only 12 of the 43 males tagged in 1982 were seen renesting. The others may have died, emigrated, or nested only once. Perhaps the renesters would not have attempted breeding again, had I not collected their larvae. On the other hand, second attempts may be feasible for males in good condition, although Figure 3.14 reveals no size difference between renesters and other tagged males. If renesting is in fact common, it seems odd that most males abandoned their first nest, particularly if their breeding attempt was reasonably successful. Renesters could save time by sweeping the silt off their old nest instead of excavating a new one. Perhaps they were relocating in an attempt to upgrade their nesting status, as the trend in Table 3.11 suggests.

I ultimately excluded satellites from my investigations, but a rudimentary comparison of social and solitary male seasonal success was fulfilled. However, without determining the success of fertilization stealing and the genetic basis of male behaviour, the comparison of average lifetime fitness for different male types is unattainable and discussions of plausible mechanisms maintaining their coexistence remain conjectural.

4.6 Conclusions

Solitary males tend to foster more larvae and probably enjoy greater certainty of paternity than do social nesters. Females exert some discrimination among the latter, spawning more often with males nesting early in the spawning period and occupying central nests.

These males also occupy large nests and tend to be large, although less so than solitary males. Females may also evaluate other unrecorded nest and male characteristics. Although late-nesting peripheral males perform fewer intrusions than successful nesters, males of both categories have an equal chance of gaining or losing fertilizations. For "unattractive" males, intrusions may represent the only possibility of success and therefore they may be making the best of a bad situation. For attractive males, intrusions represent a risk of reduced reproductive success, despite the absence of average net gain or loss, and these males should endeavour to nest solitarily to shun this risk. They should refrain from abandoning their nest, however, when joined by unattractive nesters, so as not to miss spawning opportunities.

Spawning period is an important determinant of reproductive success, probably because it reflects climatic perturbations, which stabilize as the season progresses. Other stochastic events may also affect egg and larval survival.

Intensified territorial defence undoubtedly represents a cost to social nesters. Reasonably attractive males may face detrimental mate competition simply because of the proximity of even more attractive neighbours. Nesting groups are probably more conspicuous than solitary nests to predators, but members may profit from efficient predator defence. No data were collected to elucidate this point, but predation may have been a significant force in the evolution of social nesting in longear sunfish, as has been suggested for bluegills. The possibility of previously limiting habitat having forced nesting males to aggregate should not be discarded.

Sexual selection remains a plausible explanation for the existence of nesting aggregations, but not because of female preference for group members. In fact, females apparently prefer solitary males and members of small groups. Rather, males may have exerted a greater influence in shaping the present mating system, as proposed by Bietz. Nesting males who are insufficently attractive to reproduce successfully nest around attractive males, thereby creating aggregations, to enhance their fitness by stealing fertilizations from spawning males. This may represent a cost to males capable of attracting females, but the high local spawning synchrony may prevent them from relocating their territory. Females are apparently forced to comply with these pervasive circumstances, perhaps due to constraints on searching time, while persevering in opportunistic spawnings with attractive males who were able to remain solitary. Without determining intrusion success and the genetic basis of male behaviour, the lifetime fitness of different males cannot be compared. Whether or not the relative frequencies of each type are at equilibrium and are maintained by frequency-dependent mating advantages remains conjectural.

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Appendix I

Genetic variability detected in male and female longears collected at Thamesford in 1982 and 1983.

ENZYME	N	NUMBER OF ALLELES	FREQUENCY OF COMMON ALLELE	% HETEROZYGOUS
Es	71	2	0.95	4%
Got	79	2	0.94	9%
Pgi	93	2	0.94	11%
6-Pgd	20	2	0.98	5%
Pgm	79	2	0.98	4%
Adh	20	1	1.00	0
Alk. Ph.	30	1	1.00	0
α-Gpdh	42	1	1.00	0
G-6-Pdh	21	1	1.00	0
Mdh	60	1	1.00	0
Pep	14	1	1.00	0

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