

FACTORS INFLUENCING REPRODUCTIVE SUCCESS IN MALE SPOTTAIL DARTERS (*ETHEOSTOMA SQUAMICEPS*, PISCES, PERCIDAE)

James H. Bandoli
Department of Biology
University of Southern Indiana
Evansville, Indiana 47712

ABSTRACT: The mating system of spottail darters is a form of resource defense polygyny in which females deposit eggs on the undersurfaces of benthic cavities defended by males. I investigated the (1) effect of nest site size on nest site defense by males and on brood size, the (2) timing and duration of nest site defense by males, the (3) effect of male size on nest site acquisition, and (4) female choice of nest sites and spawning partners. Field experiments with two sizes of artificial nest sites (tiles) conducted over two breeding seasons indicated that large tiles were defended more frequently by larger males and contained larger broods than small tiles. In both years, male size correlated positively with the total number of eggs defended, although in one year the relationship was not statistically significant. Some males defended nest sites for as long as 60 days, and six of 17 males that spawned in one year sequentially defended multiple broods. In laboratory experiments, male size was an important factor in the acquisition and defense of nest sites, and females chose the larger of two males as a spawning partner when nest site size was held constant.

KEYWORDS: *Etheostoma squamiceps*, female choice, male size, nest site defense, nest site size, Percidae, sexual selection, spottail darter.

INTRODUCTION

Resource defense polygyny occurs when a subset of the male breeding population is able to monopolize resources sought by females (Emlen and Oring, 1977). In such systems, males typically compete for resources, and intrasexual selection promotes characteristics that enhance resource acquisition and defense (Darwin, 1871). Male reproductive success may be influenced by the quality of the defended resource (Searcy, 1979; Alcock, 1987), the quality of the male (Cote and Hunte, 1989; Ryan, 1991), or both (Thompson, 1986), depending on the nature and extent of female choice.

Darters (Teleostei: Percidae) have a variety of reproductive modes, including broadcast, clumping, and clustering of gametes (Page, 1983). Page (1985) considered the most derived of these reproductive modes to be egg-clustering, a form of resource defense polygyny in which males defend cavities where females deposit eggs. This reproductive mode is ideal for studies of sexual selection because both competition among males and female choice can occur.

Aspects of sexual selection have been investigated in several egg-clustering percids, including the tessellated darter, *Etheostoma olmstedi* (Constantz, 1979,

1985), the johnny darter, *E. nigrum* (Grant and Colgan, 1983, 1984), the fantail darter, *E. flabellare* (Knapp and Sargent, 1989), and the waccamaw darter, *E. perlongum* (Lindquist, *et al.*, 1984). Mating strategies of the spottail darter, *Etheostoma squamiceps*, an egg-clustering species found in southern Illinois, western Kentucky, and southwestern Indiana (Page, *et al.*, 1992), have received limited attention. Information on the natural history of *E. squamiceps* comes largely from population studies in Illinois (Page, 1974). The sexes are of approximately equal size during their first year; thereafter, males become 5-15% larger than females. Females spawn at 1 year, while males generally become sexually mature in their second year; the maximum age of both sexes is 3+ years. During the breeding season, males defend cavities under solid benthic structures, usually rocks. Females attach a single layer of eggs to the ceilings of these structures. Clutch size (eggs spawned by a female at a specific time and location), based on counts of four aquarium spawnings, averaged 60 eggs (range 20-120; Page, 1974). Fractional spawning by *E. squamiceps* females has not been documented, but other members of the genus show this trait (Gale and Deutsch, 1985; Weddle and Burr, 1991), and fractional spawning may be widespread in the *Etheostomatini* (Hubbs, 1985). For example, the mean number of mature ova in 18 breeding females was 110 (range 28-357; Page, 1974), which exceeds the average clutch size and supports the possibility of fractional spawning. Males remain with the eggs until they hatch (5-15 days, depending on water temperature); females leave the nest after spawning.

Etheostoma squamiceps is classified as Endangered in Indiana (Indiana Department of Natural Resources, 1993), where its distribution is limited to the extreme southwestern corner of the State. The breeding season lasts from mid-March through late May (pers. obs.). Bandoli, *et al.* (1991) found that *E. squamiceps* will readily use artificial nest sites with no significant difference in mean brood size (eggs defended by a male at a specific time; may include clutches from more than one female) compared to natural broods under rocks. In that study, the mean number of eggs per brood was 368, but nests containing over 1,000 eggs were not uncommon, ranging from 5% (Bandoli, pers. obs.) to 15% (Page, 1974) of all broods examined. The average brood/clutch size ratio indicates that larger broods may contain 10 or more clutches.

The results of field and laboratory studies on the reproductive biology of *E. squamiceps* in southwestern Indiana are reported in this paper with emphasis on factors that influence male reproductive success. Questions asked were: Do males that defend larger nest sites have larger broods? How long does a male defend a nest site? Does male size influence the acquisition and defense of nest sites? Can males defend multiple broods? Do females select males as spawning partners on the basis of either male size or nest site size?

FIELD STUDY—MATERIALS AND METHODS

Experiments on nest site selection and reproductive timing were conducted at Carpentier Creek, a first-order tributary of the Bayou Creek drainage in Van-

derburgh County, Indiana. Carpentier Creek drains suburban areas interspersed with bottomland hardwood woodlots. Siltation and debris have reduced the number of available nest sites, limiting *E. squamiceps* densities and promoting the use of artificial nest sites (Bandoli, *et al.*, 1991).

The purpose of the field experiment was to investigate the response of *E. squamiceps* to variation in nest site size. If nest site size is important in determining male reproductive success, larger nest sites should be defended more frequently, attract more females, and contain more and larger broods. If male size is important in nest site defense, larger males should defend larger nest sites. Moreover, if females choose males on the basis of size, male size should correlate positively with brood size when nest site size is held constant.

These predictions were tested using two different lengths of half-cylindrical ceramic field tile (10 cm inside diameter) as artificial nest sites. Large tiles ranged from 14.5 to 16.0 cm in length and provided an average of 170 cm² of undersurface area for egg deposition, an area large enough to accommodate over 1,400 eggs. Small tiles ranged from 7.0 to 9.5 cm in length and provided an average of 90 cm² of undersurface area, enough to hold approximately 700 eggs. Pairs of tiles (one large and one small marked for individual identification) were placed in the stream with roughly 3-m intervals between pairs. To encourage tile use, rocks near tiles were removed. Twenty and 24 pairs of tiles were placed in the stream in early March of 1990 and 1991, respectively. Tiles were checked biweekly (1990) or weekly (1991) from mid-March through late May for *E. squamiceps* nests and guarding males.

Darters were captured by placing an aquarium net over one end of a tile and flushing any occupants into the net. Standard lengths of captured fish were measured prior to returning individuals to their respective tiles. Eggs in small nests were counted in the field; large nests were photographed and eggs counted directly from projected slides. Since *E. squamiceps* females deposit new eggs around rather than over existing eggs, photographs of nests under the same tile on consecutive censuses could be compared to ensure that only eggs deposited since the last census were counted.

In 1991, the reproductive activities of individual males were monitored over time by marking males with unique combinations of fin clips and subcutaneous injections of permanent ink. These markings allowed the investigator to ask if males could defend multiple broods, how long a male would defend a nest site, and if males change nest sites during a breeding season. Comparisons of nest site defense, brood size, and use of nest sites by females between large and small tiles were performed on combined data from both years. Analyses involving male size were performed separately for each year because identification of individual marked males was done in 1991 only. Statistics were generated using ABSTAT (Anderson-Bell Corp.) and S-PLUS (Statistical Sciences, Inc.). Means reported in the text are \pm one standard error.

Table 1. Artificial nest site selection by *Etheostoma squamiceps*. The numbers in parentheses are standard errors.

Parameter	1990		1991	
	Large tile	Small tile	Large tile	Small tile
Mean number of tiles available per census ¹	15.8 (1.8)	14.6 (2.9)	21.1 (1.4)	20.4 (1.5)
Number of observations	77	73	231	220
% of tiles guarded at least once during the reproductive season	100	63.2	90.5	65
Mean % of tiles guarded per census	32.6 (7.1)	16.9 (8.2)	32.5 (3.6)	8.2 (2.7)
% of tiles with one or more broods during the reproductive season	44.2	16.4	66.7	25
Number of broods	23	11	21	5
Mean brood size	575.9 (77.8)	335.4 (34.0)	597.1 (56.8)	473.0 (134.9)
Number of guarding males captured (with and without broods)	31	16	25	11
Mean standard length of guarding males (mm)	70.4 (0.8)	66.4 (0.8)	72.7 (1.2)	67.2 (2.4)
Number of females captured	10	5	17	6

¹ Twenty and 24 pairs of tiles were placed in the stream in 1990 and 1991, respectively.

FIELD STUDY—RESULTS

In both years, the availability of large and small tiles was similar despite temporary losses due to flooding and disturbance by raccoons and humans (Table 1).

Are Larger Nest Sites Defended More Frequently? Males guarded large tiles more frequently than small tiles, with over 95% of the large tiles defended at least once during the breeding season. Across both years, a mean of $32.5 \pm 3.2\%$ of the large tiles were defended on each of 16 census dates, significantly more than the $10.9 \pm 3.2\%$ defense frequency for small tiles (paired *t*-test: $t = 6.17$, $df = 15$, $P < 0.001$).

Are Females Attracted to Larger Nest Sites? More females were captured under large tiles than under small tiles in each year (Table 1); combined data from both years showed this pattern to be significantly different from the equal use of large and small tiles expected by chance ($\chi^2 = 5.9$, $df = 1$, $P < 0.025$).

Do Larger Nest Sites Contain Larger Broods? Of the 60 broods found during the two breeding seasons, 44 (73.3%) were located under large tiles. Brood size was significantly larger for large tile nests ($\bar{X} = 586.0 \pm 48.3$, range 85-1632) than for small tile nests ($\bar{X} = 378.4 \pm 48.2$, range 134-781; two sample t -test: $t = 2.43$, $df = 58$, $P < 0.02$).

Do Larger Males Defend Larger Nest Sites? Males captured while defending tiles ranged from 55-81 mm in standard length; females captured under tiles ranged from 34-70 mm in standard length. Age estimates based on standard length (Page, 1974) place most of the males in the three year old cohort, whereas females ranged from one to three years. Two sample t -tests showed that the mean standard length of males captured under large tiles was significantly larger than that of males captured under small tiles in both 1990 ($t = 3.23$, $df = 45$, $P < 0.002$) and 1991 ($t = 2.34$, $df = 34$, $P < 0.02$; Table 1).

Do Larger Males Defend More Eggs? In 1990, 19 males were captured while guarding eggs under large tiles. For these males, standard length correlated significantly with the number of eggs defended (Spearman's rank correlation: $r_s = 0.67$, $P < 0.005$). A similar but nonsignificant trend was seen in 1991 (broods combined for males with multiple broods: $r_s = 0.40$, $P < 0.18$, $n = 13$).

Do Males Defend Multiple Broods? Of 35 males marked in 1991, 18 did not defend broods. Seventeen of these males were captured only once and may have spawned outside the study area. One male was captured on three different census dates and never had any eggs in his nest. Eleven males each defended one brood in the study area; two broods were defended by each of three males; and three males each defended three broods. All multiple broods were defended sequentially rather than simultaneously, and three males with multiple broods changed tiles between broods. Males with multiple broods defended nests from 30 to 60 days. Among spawning males, fitness (total number of eggs guarded during the breeding season) ranged from 134 (smallest single brood) to 2,580 (three sequential broods).

Do Males Change Nest Sites? Seven of 14 males with multiple captures in 1991 changed tiles at least once during the breeding season, although two of these males defended the same tiles for four and five consecutive weeks, respectively. The other seven males were consistently found under the same tiles, and three were among the six males known to have defended multiple consecutive broods. No significant difference existed between the mean standard length of changers ($\bar{X} = 72.4 \pm 2.5$) and nonchangers ($\bar{X} = 71.3 \pm 2.6$; two sample t -test: $t = 0.40$, $df = 12$, $P < 0.69$), and the mean number of observations per darter was similar for each group (4.4 and 3.5 captures/male for changers and nonchangers, respectively).

Table 2. Standard lengths (mm) of spottail darters during the first half (15 March - 16 April) and second half (23 April - 28 May) of the 1991 breeding season. The numbers in parentheses are standard errors.

Parameter	n	Mean	Range
Males first seen defending tiles			
First half of season	20	73.9 (1.0)	63-80
Second half of season	17	67.6 (2.1)	55-81
Males first seen defending eggs			
First half of season	6	76.2 (1.3)	71-80
Second half of season	13	69.2 (2.0)	59-81
Females captured under tiles			
First half of season	11	54.5 (1.9)	40-62
Second half of season	12	46.8 (3.0)	34-70

An unanticipated finding was that males first seen during the first half of the 1991 breeding season (early March through mid-April) were significantly larger in standard length than those first seen in the second half (two sample *t*-test: $t = 2.87$, $df = 35$, $P < 0.007$; Table 2). Similarly, the mean standard length of males which first spawned during the first half of that breeding season was significantly larger than that of males which first bred during the second half (two sample *t*-test: $t = 2.21$, $df = 17$, $P < 0.05$). Additionally, the mean standard length of females caught under tiles during the first half of the breeding season was significantly larger than that of females caught after this period (two sample *t*-test: $t = 2.11$, $df = 21$, $P < 0.05$).

LABORATORY STUDY—MATERIALS AND METHODS

Three sets of laboratory experiments were conducted during the 1990-1992 and 1995 breeding seasons in 38-L aquaria (50 cm by 25 cm; 30 cm deep) with natural substrate and tiles for nest sites. Darters were maintained on a 13L:11D photocycle and fed frozen brine shrimp augmented with live benthic invertebrates from local streams. Water temperature varied from 18°-22° C.

Male *E. squamiceps* used in laboratory experiments were determined to be in breeding condition based on coloration (Page, 1974) and had a mean standard length of 72.1 mm (range 60-83 mm). Females had distended abdomens indicating the presence of mature eggs and a mean standard length of 56.7 mm (range 35-72 mm). Standard lengths of most males were in the range expected for age 3+ (> 64 mm; Page, 1974). All females and most males were used in one trial only; any male used more than once was always paired with a different male.

Experiment 1: Is Male Size Important in Nest Site Defense? In each of 13 trials, two males (one 5-29% larger in standard length than the other) were placed in an aquarium containing a single large tile positioned to the right or left

of center by a coin toss. Trials lasted 10 days (1990) or 6 days (1995) with a total of 29-30 observations per trial. Observations were made at least twice per day (weekends) up to a maximum of six per day between 0730 and 2100 h with at least 1 h between observations. At each observation, the position of each male was scored as under the tile or on the substrate outside the tile (non-swimming darters rest on the bottom). The percent of observations each male was observed alone under the tile was determined for each trial; these observations were averaged across all trials, and a paired *t*-test was used to compare the mean tile defense frequencies of large to small males. In addition, the percent size difference between males for each trial was compared to the percent of time the larger male spent defending the tile using Spearman's rank correlation statistic.

Experiment 2: Does Nest Site Size Influence Female Choice of Spawning Site When Male Size is Held Constant? In each of 16 trials conducted in 1991 and 1992, two breeding males of similar size (less than 3% difference in standard length) were placed in an aquarium with one large tile (15 cm long) and one small tile (8 cm long). A gravid female was introduced within 24 hours. A coin toss determined whether the large tile was placed to the right or left of center, and the small tile was placed on the opposite side. Previous experiments showed that spawning in the laboratory occurred from 4 h to several days following introduction of the female, making constant monitoring impractical. Therefore, all trials were conducted by periodically examining all tiles for eggs and noting the positions of all darters in each aquarium. Observations were made at least twice daily (weekends and days on which experiments began or ended) up to a maximum of five per day. Observations were conducted between 0730 and 2100 h with at least 1 h between successive observations. Trials varied in length (mean duration 4.1 d) and ended 24 h after a female spawned or after 5 days without a spawn. The number of observations per trial ranged from 8-26 with a mean of 13.3. Darter positions were scored as under a specific tile or on open substrate. The percent of observations during which each tile was defended by a male was determined for each trial, and these values were used to calculate mean tile defense frequencies for large and small tiles across all trials. These defense frequencies were compared using a paired *t*-test. The tile under which spawning occurred was used to indicate female choice. A chi-square goodness of fit test was used to compare the observed distribution of spawning locations with the equal spawning under large and small tiles expected by chance.

Experiment 3: Does Male Size Influence Female Choice of Spawning Partner When Nest Site Size is Held Constant? In each of 26 trials conducted in 1991 and 1992, two males of different sizes (large males averaged 14.8% greater in standard length than small males) were placed in an aquarium with two large tiles, one on each side of the aquarium. A gravid female was introduced within 24 h. The duration of the trials varied as in Experiment 2 with a mean trial duration of 5.1 d. Observations were performed as in Experiment 2 with a mean of 19.1 observations per trial (range 8-28). The percent of observations individual darters were under tiles was determined for each trial, and these values

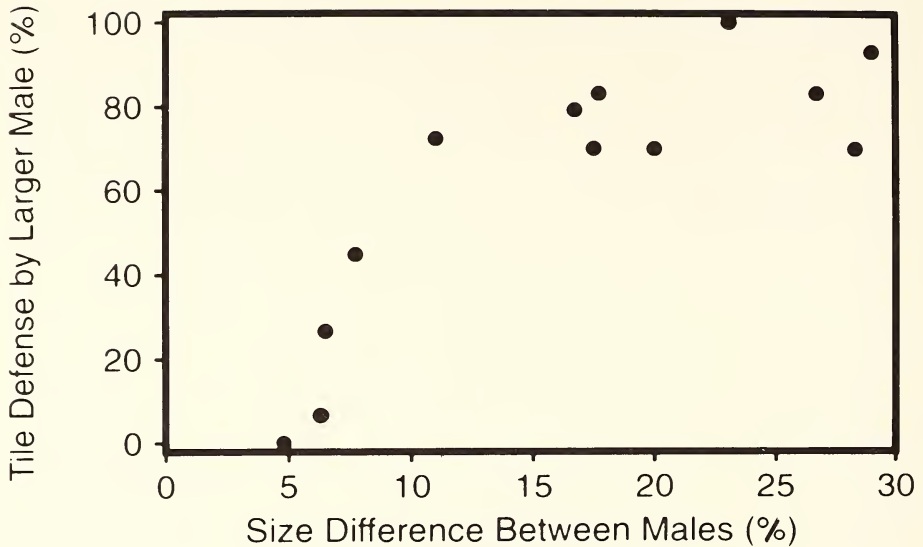


Figure 1. The relationship between male size (standard length) and nest site defense in 13 laboratory trials. Each trial had 29 or 30 observations of two males in an aquarium with a single nest site (tile). The horizontal axis is the difference in size between the two males expressed as a percent of the standard length of the smaller male. The vertical axis is the percent of the observations in which the larger male was alone under the tile.

averaged across all trials for large and small males. Mean tile defense frequencies of large and small males were compared with a paired *t*-test. When spawning occurred between observations, the male spawning partner was determined by noting which male defended the tile before and after spawning. A chi-square goodness of fit test was used to compare the observed distribution of spawning partners with the equal spawning with large and small males expected by chance.

LABORATORY STUDY—RESULTS

Experiment 1: Is Male Size Important in Nest Site Defense? Tiles were defended by males on 77% of the observations. The large male was alone under the tile $61.5 \pm 8.9\%$ of the time, significantly more than the mean for small males (15.0 ± 5.0 ; paired $t = 3.48$, $df = 12$, $P < 0.003$). Moreover, the greater the size difference between the males, the greater the percent of observations the larger male spent alone under the tile ($r_s = 0.78$, $P < 0.005$; Figure 1).

Experiment 2: Does Nest Site Size Influence Female Choice of Spawning Site When Male Size is Held Constant? Females spawned in 9 of the 16 trials. Eight clutches were deposited under large tiles; in one trial, two clutches were deposited by the same female, the first under the small tile (12 eggs) and the second 2 h later under the large tile (37 eggs). Overall, female choice of nest

site was significantly different than expected by chance ($\chi^2 = 4.9$, $df = 1$, $P < 0.05$).

Large tiles were defended by a male in $68.4 \pm 6.1\%$ of the observations, significantly more than the small tiles ($36.8 \pm 5.5\%$; paired $t = 3.77$, $df = 15$, $P < 0.002$). In trials where spawning occurred, this difference was also apparent before eggs were deposited. During this period, males defended the large tiles for $53.5 \pm 10.8\%$ of the observations versus $22.0 \pm 7.6\%$ for the small tiles, a significant difference (paired $t = 5.57$, $df = 8$, $P < 0.0006$). When the expectation of spawning site choice was altered from uniform (1:1) to one based on the observed defense frequencies prior to spawning (1:2.3 for small and large tiles, respectively), female choice of spawning site did not differ from expectations based on observed tile defense frequencies ($\chi^2 = 1.07$, $df = 1$, $P < 0.5$).

Experiment 3: Does Male Size Influence Female Choice of Mates When Nest Site Size is Held Constant? Females spawned in 13 of 26 trials. Eleven spawnings occurred with the larger male, one with the smaller male, and one female spawned with both (160 eggs with the smaller male, three with the larger male). Female choice of spawning partner was significantly different than expected by chance ($\chi^2 = 5.8$, $df = 1$, $P < 0.025$).

Large males defended tiles during $63.8 \pm 4.8\%$ of the observations compared with $45.8 \pm 5.5\%$ for small males, a significant difference (paired t -test: $t = 3.05$, $df = 25$, $P < 0.006$). Prior to spawning, the difference in tile defense frequencies of large and small males was not significant ($66.3 \pm 8.8\%$ and $56.0 \pm 10.4\%$, respectively; paired $t = 1.03$, $df = 11$, $P < 0.33$). However, females chose the larger male as a spawning partner significantly more than expected even when the expectation was modified by the observed before-spawning male defense frequency from 1:1 to 1:1.2 for small and large males, respectively ($\chi^2 = 5.04$, $df = 1$, $P < 0.025$).

DISCUSSION

The results from the field experiments indicated that nest site selection does affect male reproductive success as measured by the number of eggs defended. Large tiles contained both more broods and larger broods than did small tiles. In both field and laboratory experiments, males preferred large tiles as nest sites despite the fact that small tiles were capable of holding more eggs (at least 700) than the average brood found under large tiles (586 eggs). However, *E. squamiceps* broods can be much larger than 700 eggs, occasionally exceeding 1000 eggs (Page, 1974; Bandoli, *et al.*, 1991). The value of larger nest sites may be that they permit an occasional large brood and associated higher fitness.

The finding that larger males generally guard larger tiles suggests that male size is important in nest site acquisition and defense, a pattern also seen in the fantail darter (Seifert, 1963) and the johnny darter (Grant and Colgan, 1984). This finding was further supported by the laboratory experiments which showed that, when two males competed for the same tile, the larger male spent

more time defending the tile than did the smaller male, and exclusive tile defense by the larger male increased as the size difference between the males increased.

Field and laboratory observations indicated that females also prefer large tiles as spawning sites. However, these observations may be confounded by the fact that, before spawning, large tiles are more likely to be defended by males than are small tiles. Therefore, females may select the large tiles based on the frequency of tile defense by males rather than tile size.

When nest sites were of equal size, females preferred those defended by the larger male. This result was not confounded by unequal nest site defense frequencies before spawning and, therefore, may represent a real choice. In field experiments, male size varied directly with brood size among males defending large tiles, although the correlation was significant in one year only.

Male size has been shown to be an important parameter for female choice in a variety of fish species with breeding systems similar to *E. squamiceps*, including the redlip blenny (Cote and Hunte, 1989), river bullhead (Bisazza and Marconato, 1988), and mottled sculpin (Downhower and Brown, 1980). The value of male size as an object of choice by females has several potential correlates. First, larger males may be selected because they are better egg protectors (Cote and Hunte, 1989). *Etheostoma squamiceps* eggs in abandoned nests are quickly exploited by egg predators or lost to fungus (pers. obs.), and successful hatching may depend on the guarding behavior of the breeding male. Many *E. squamiceps* males showed a high degree of nest site fidelity, unlike *E. olmstedii* males, who abandon nests with large broods to seek new nest sites, leaving brood defense to smaller subordinate males (Constantz, 1985). Large males may be better at defending a nest, and females that choose them would be rewarded with higher fitness via increased egg survival, a pattern seen in the mottled sculpin (Downhower and Brown, 1980). Even if size is not a good indicator of the ability of a male to protect a brood, females may still gain from selecting large males if doing so results in a larger nest site. Large nest sites afford more room for egg deposition, an important factor when nest site availability is limited (Constantz, 1979). Further, large nest sites also contain larger broods. A female that adds eggs to a large brood may minimize the chance of losing her eggs to predators or filial cannibalism through the dilution effect (Kodric-Brown, 1983).

Finally, selection of large males may improve offspring quality. This hypothesis assumes that male size is an honest indicator of genetic quality (Kodric-Brown and Brown, 1984) with increased nutritional condition, better predator avoidance, and greater resistance to parasites as possible correlates. The first two correlates are difficult to quantify and cannot be addressed here. Resistance to parasites (Hamilton and Zuk, 1982) can be discussed. Strange (1992) found that 86% of 44 *E. squamiceps* examined from a southwestern Indiana stream were parasitized by enterogastric acanthocephalan worms (*Acanthocephalus dirus*) with the highest infection rate (100%) among the largest (oldest) darters. Additionally, the intensity of parasitism increased with age from 3.6 to 22.6 worms

per darter. Therefore, size alone appears to be an unlikely indicator of parasite resistance, although larger individuals might be better able to tolerate the unavoidable parasite load.

Male reproductive success in *E. squamiceps* is also influenced by the duration of nest site defense, a pattern seen in the egg-clustering johnny darter *Etheostoma nigrum* (Grant and Colgan, 1983). Some male *E. squamiceps* defended as many as three sequential broods, which required several weeks of nest guarding. The territorial mating system of *E. squamiceps* and *E. nigrum* imposes minimal mating costs on parental males (Gross and Sargent, 1985), making prolonged nest site defense advantageous. As new clutches are added to the brood, the time to complete hatching increases, and opportunities for additional spawnings occur.

In the field, the mean standard length of *Etheostoma squamiceps* males that bred early in the reproductive season was larger than those that bred later that season, a pattern also seen in the waccamaw darter (*E. perlongum*; Lindquist, *et al.*, 1984). Several potential benefits are associated with early reproduction. First, males that acquire nest sites early may have longer spawning periods, allowing them to recruit more females. Second, early spawning females had a larger mean standard length than those spawning later and may be able to produce larger clutches (Page, 1983). Third, early spawning may decrease competition for nest sites with bluntnose minnows, a sympatric cavity-nesting species that begins spawning midway through the spottail darter breeding season in southwestern Indiana (*pers. obs.*). Finally, water temperature influences egg development rate (Page, 1983), and temperatures of 20°-22° C have been found to maximize embryo survival in *Etheostoma lepidum* (Hubbs, *et al.*, 1969). Variable water temperatures in shallow streams make temperature prediction difficult, and males that acquire nest sites early are ready to spawn when stream temperatures become optimal. Females may also produce larger clutches at this time, a pattern seen in *Etheostoma rafinesquei* (Weddle and Burr, 1991).

The results of this study suggest that male reproductive success in the spottail darter is a function of (1) acquisition and defense of large nest sites, (2) early and prolonged nest site defense, and (3) female choice, all of which are influenced by male size. However, other factors not addressed in this study might also be important. These factors include the intensity of male breeding coloration (Kodric-Brown, 1983; Morris, *et al.*, 1995), the length and intensity of courtship and/or territorial displays (Grant and Colgan, 1984; Knapp and Warner, 1991), and the presence of eggs in the nest (Knapp and Sargent, 1989), any of which may influence female choice. These factors notwithstanding, size appears to be an important factor in determining fitness in males and may be a factor in the sex-specific differences in age at maturity. Growth curves for *E. squamiceps* are similar for males and females during their first year but separate thereafter as males become increasingly larger than females (Page, 1974). Males may be delaying reproduction in order to maximize growth.

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