

## INCIPIENT SECOND DORSAL FIN EGG MIMICS IN THE SPOTTAIL DARTER, *ETHEOSTOMA SQUAMICEPS*?

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**ABSTRACT.** In five of the 10 species in the spottail darter species group, breeding males develop white or yellow knobs on the second dorsal fin. In those species with more well-developed knobs, female spawning decisions may be influenced by these knobs, which are presumed to be egg mimics. In the spottail darter (*Etheostoma squamiceps*), the knobs are small and club-shaped and may represent an early stage of evolutionary development. We tested the hypothesis that female choice drives knob evolutionary development by looking for evidence that male spottail darters with larger or more obvious knobs had larger broods or shorter pre-spawning intervals. Males with more well-developed knobs (as judged from photographs reviewed by human observers) were not guarding larger broods than males with less well-developed knobs. Similarly, knob size (measured from photographs as height above the fin margin) did not correlate with brood size. Finally, during a two day interval, males guarding eggs did not have significantly larger knobs than males without eggs. These results suggest that female choice is weak or absent in early stages of knob evolutionary development, and that another mechanism such as genetic drift or an alternate function for knobs may be necessary to produce the larger knobs found in other species.

**Keywords:** *Catonotus*, dorsal fin knob, breeding tubercle, female choice, behavior

In many fish species in which the male defends the nest site, a female is more likely to spawn with a male that already has eggs in his nest (for example, see Ridley & Rechten 1981; Marconato & Bisazza 1986; Unger & Sargent 1988; Knapp & Sargent 1989; Sikkil 1989; Kraak & Groothuis 1994; and Goulet 1998). This finding has prompted several studies that attempt to identify the strategies males use to increase reproductive success. One of the strategies thus far revealed is egg mimicry (Knapp & Sargent 1989; Bart & Page 1991; Porter et al. 2002).

Darters of the subgenus *Catonotus* practice egg clustering in which males defend a nest cavity where females deposit eggs in a monolayer on the ceiling (Page 1985). In several species in this group, breeding males develop enlargements on the distal spines or rays of the first or second dorsal fins (Page & Swoford 1984). These structures, ranging from small, white club-like enlargements to larger,

orange fleshy knobs, are hypothesized to be egg mimics that increase the chance that a female will spawn with a nest-guarding male (Page & Bart 1989; Bart & Page 1991). Subsequent studies have shown that such structures may influence female spawning decisions. For example, Knapp & Sargent (1989) showed that female fantail darters (*Etheostoma flabellare*) prefer to spawn with males with intact fleshy knobs and trailing orange ocelli on the first dorsal fin compared to males from which the knobs and ocelli had been removed. In a similar experiment, Strange (2001) tested female preference for males in three species of the spottail darter species group (*Etheostoma oophylax*, *E. pseudovulatum*, and *E. neopterum*) with well-developed knobs. Females preferred males with intact knobs over conspecific males with the knobs removed. Purported egg mimics are not limited to the dorsal fins, as Porter et al. (2002) have shown a positive correlation between the

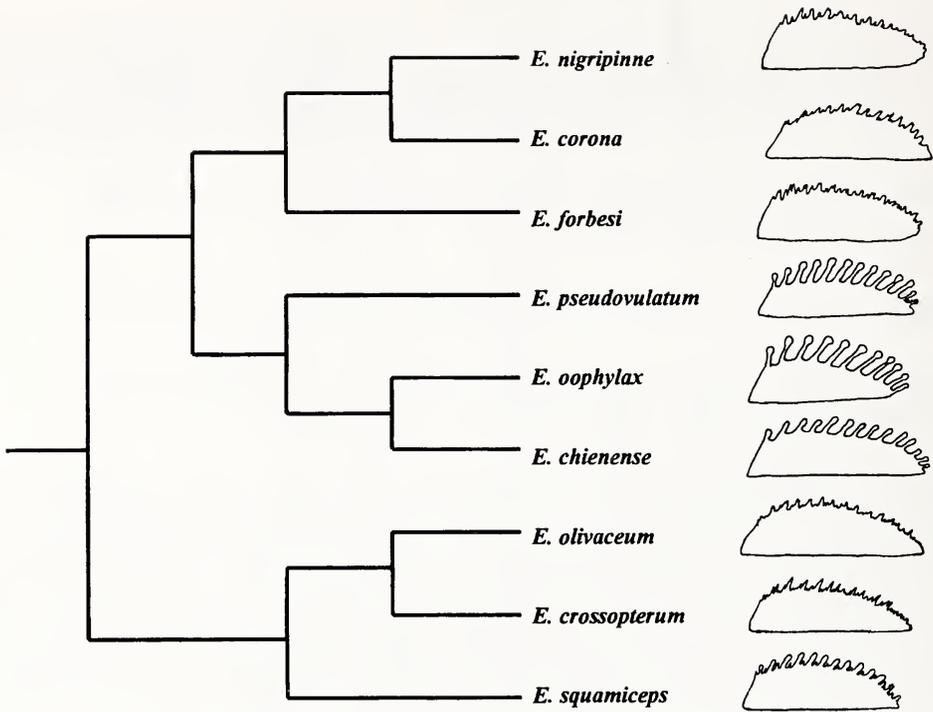


Figure 1.—Phylogenetic affinities of members of the spottail darter species group based on Porterfield et al. 1999. Drawings show a lateral view of the second dorsal fin of breeding males (based on drawings in Page et al. 1992). The phylogenetic status of *Etheostoma neopterum* (not shown), a species with large knobs similar to *Etheostoma oophylax*, is currently unresolved.

number of white spots (presumed egg mimics) on the pectoral fins of male striped darters (*Etheostoma virgatum*) and the estimated minimum number of female spawning partners.

Fleshy knobs occur to varying degrees on the second dorsal fin in breeding males in five of 10 species in the spottail darter species group (*Etheostoma oophylax*, *E. chienense*, *E. neopterum*, *E. pseudovulatum*, and *E. squamiceps*; Page et al. 1992). A phylogenetic analysis of darters in the subgenus *Catonotus* using both morphological and molecular characters suggests these knobs may have evolved more than once. White or yellow second dorsal fin knobs occur in a clade comprising the guardian darter (*E. oophylax*), the relict darter (*E. chienense*), and the egg-mimic darter (*E. pseudovulatum*; Porterfield et al. 1999; Fig. 1). The lollypop darter (*E. neopterum*), which also has relatively large yellow knobs on the second dorsal fin, may belong to the above clade (Page et al. 1992); however, cytochrome *b* data place it in a clade with species lacking knobs (Porterfield et al. 1999),

which if true would represent a separate evolution of these knobs. The spottail darter (*E. squamiceps*) is most closely related to *E. olivaceum* and *E. crossopterus*, two species lacking enlargements of the second dorsal fin (Fig. 1). The small, white club-like enlargements of the distal rays of the second dorsal fin in *E. squamiceps* (Fig. 2) may therefore be an incipient second (or third depending on the status of *E. neopterum*) independent development of a second dorsal fin egg mimic in this species group.

In order for an egg mimic to be an effective signal, the mimic must be both conspicuous and generally similar to actual eggs. The initial appearance of a dorsal fin knob may be due to pleiotropy, since fleshy white “breeding tubercles” associated with spines and rays of pectoral, pelvic, or anal fins of breeding males are common in darters (Bart & Page 1991). These structures do not seem to function directly in nest cleaning (Bart & Page 1991), although they may decrease damage to eggs due to contact with spines. Their evolu-



Figure 2.—Breeding male spottail darter with well-developed, club-like knobs on the second dorsal fin. The darter was collected in a tributary of the Bayou Creek drainage in southwestern Indiana. The standard length of the fish is 68 mm.

tionary elaboration as egg mimics would theoretically begin when they are detected by females and elicit an increased tendency to spawn, but at what point does this happen? If females are biased toward any structure resembling eggs, then even small, white club-like enlargements such as those found in *E. squamiceps* may elicit a response from females. Alternatively, incipient knobs may need to reach a (1) minimum size and/or (2) appropriate color (eggs in *Etheostoma* are typically orange; Page 1983) before females respond. If this is the case, then factors other than female choice may be necessary to maintain and enlarge the initial fin ray breeding tubercle.

We examined the possibility that knob size influences female choice by looking at knob development and reproductive success (indicated by brood size) in male spottail darters (*Etheostoma squamiceps*). Compared to knobs in other species in this group, those in *E. squamiceps* males are small and club-shaped (Figs. 1, 2), and possibly at an early stage of evolutionary development. Egg mimics may enhance male reproductive success in two

ways: first, they may signal the presence of eggs when in fact the male has not yet spawned, reducing the pre-spawning interval in males with more well-developed knobs. Second, they may increase the apparent number of eggs a male is defending, such that males with larger knobs may attract more females, increasing brood size. We examined both of these possibilities using spottail darters in southwestern Indiana. *Etheostoma squamiceps* is a state-endangered species in Indiana (Indiana Department of Natural Resources 1993), which precluded studies involving the removal or modification of existing knobs on males. Therefore, we used direct measurements of knobs, measurements of knobs from photographs, and human observer evaluation of knob development from photographs of males captured while guarding nests, and compared knob development with reproductive success (brood size).

This study rests on a critical assumption—that most or all of the males were guarding eggs that they had sired. Alloparental care, in which males guard eggs they did not sire (Unger & Sargent 1988), has thus far been doc-

umented in two species of darters—the tessellated darter (*Etheostoma olmstedii*) and the striped darter (*E. virgatum*). Constantz (1985) observed that male tessellated darters frequently moved between nest sites (rocks), with larger males displacing smaller males from limited breeding sites and abandoning them when most of the available surfaces for egg deposition were filled. These abandoned nests were then frequently occupied by smaller males that tended the eggs and attempted to attract additional females. Alloparental care in the striped darter was documented by genetic analysis of guarding males and eggs; however, the extent of alloparental care varied, as some foster eggs were found in four of eight nests in one population but only in one of 11 nests in another (Porter et al. 2002).

Alloparental care probably occurs opportunistically in most species in the subgenus *Catonotus* as males compete for limited nest sites. In a laboratory experiment, Bandoli (2002) found that male *E. squamiceps* given their original nest sites and eggs spent significantly more time defending them and consumed fewer eggs than did males given a foreign nest site with foster eggs, a distinction expected if alloparental care occurs in the field. However, in a field study, Bandoli (1997) found limited movement of breeding males between nest sites. Nine of 14 uniquely-marked *E. squamiceps* males in southern Indiana were consistently found at the same nest sites for several weeks. Three of these males defended multiple consecutive broods without changing nest sites (Bandoli 1997). Further, there was no evidence that any of the five males that changed nest sites abandoned eggs or inherited foster eggs (Bandoli unpubl. data).

We believe that while alloparental care probably occurs in *E. squamiceps*, the available evidence suggests that it occurs too infrequently to invalidate the assumption that the number of eggs in a nest can be used as an indicator of the fitness of the guarding male.

## METHODS

All spottail darters used in this study were collected in tributaries of the Black River (Posey County, Indiana) or Bayou Creek (Vanderburgh County, Indiana). Males were collected by placing artificial nest sites (sections

of ceramic field tiles; Bandoli et al. 1991) in streams in late March. During the subsequent two-month breeding season, males guarding tiles were easily captured by hand net. All fish were handled in the field, marked with a small caudal fin clip, and released at their places of capture. Standard lengths (SL) were measured to the nearest mm, and any broods found were photographed so that eggs could be counted from projected slides.

The relation between knob size and reproductive success (number of eggs guarded) was examined in three ways. The first two involved the use of photographs taken of 35 males captured in April and May of 1998 and 1999. All males were guarding nests with eggs at the time they were captured and photographed. Males that had been captured previously (indicated by the clipped caudal fin) were excluded. Males were photographed in a 23 cm × 16 cm × 6.5 cm glass aquarium. We used a black 17 × 21 cm acrylic plastic sheet (Plexiglas®) as a background and to force the male against the front of the aquarium. At least two photographs (ISO 400 slides using natural light) were taken of each male with the camera positioned so that the entire male was visible and filled the frame. We asked 29 human observers to assess the overall appearance of the knobs by having them rate knob development from projected slides of the male spottail darters. The degree of knob development varies among breeding male *E. squamiceps* in Indiana (pers. observ.), ranging from well-developed and obvious (as shown in Fig. 1-F in Page et al. 1992) to poorly-developed and more similar to *E. crossopterum* (Fig. 1-E in Page et al. 1992). To prepare the observers for the task of assessing variation in the second dorsal fin, we provided copies of the drawings of second dorsal fins of *E. squamiceps* and *E. crossopterum* taken from Page et al. 1992. Observers were first shown all of the slides without scoring. They were then asked to view the slides again and to rate knob appearance as most similar to *E. crossopterum* (score of 0 – no obvious swelling of distal tips of rays), most similar to *E. squamiceps* (score of 2 – club-like knobs present as distinct swellings of distal rays) or intermediate (score of 1). Slides were shown in random order, and 10 of the darters had one additional slide placed randomly in the tray to test for consistency of ratings. Only ratings from observers

who gave the same scores on both the first and second photo of the same male at least 8 of 10 times were used in this analysis ( $n = 10$ ). Mean knob development scores between 1.5–2 were categorized as strongly developed; means between 0.5–1.4 were intermediate, and those from 0–0.4 were labeled weakly developed. The relation between knob development and reproductive success was assessed by comparing the mean number of eggs guarded by males in each category.

We used the same slides described above to measure knob height. We measured SL and the height above the fin margin of the second, third and fourth full knobs on the second dorsal fin to the nearest mm on projected slides of each male. Only males that had at least one slide in which the fish was positioned such that SL and at least two of the three knobs could be accurately measured were included. We also attempted to measure anterior-posterior knob width, but found the precision to be too low to be reliable. For each male, the ratio between actual SL measured in the field and the SL measured from the projected slide was used to convert mean projected knob height to actual size. Since body size may influence mate choice in *E. squamiceps* (Bandoli 1997), we used partial correlation to control for standard length and compare mean actual knob height to brood size.

Finally, to investigate the possibility that the primary value of knobs is as egg mimics that increase the probability that a female will spawn with a male with an empty nest, we captured an additional 25 nest-guarding males in a 100 m stretch of a tributary of the Black River on 13–14 April 2001. Seventeen of the males were guarding eggs, while the remaining eight males guarded empty nest sites. Using the largest intact knob (usually the 4<sup>th</sup>), knob height above the fin margin and anterior-posterior knob width at the widest point were measured to the nearest 0.1 mm in the field using a stereoscope fitted with an ocular micrometer. Measurements were made while males were briefly anesthetized using MS 222® (ethyl 2-aminobenzoate, methanesulfonic acid salt); all males were allowed to fully recover before being returned to their nests. To compensate for the possibility that larger males may have larger knobs, relative knob height and width were determined by dividing knob height and width by SL. We used  $t$ -tests

to compare (1) mean knob height and knob width and (2) mean relative knob height and width between males with and without eggs.

## RESULTS

The 13 males captured in 1998 were not significantly different in either SL ( $t = 0.08$ ;  $P = 0.93$ ) or brood size ( $t = 1.75$ ;  $P = 0.09$ ) from the 22 males captured in 1999. Data from both years were therefore combined. The mean SL of the 35 photographed males was 74.2 mm (range 62–85 mm); brood size ranged from 95–1754 eggs ( $\bar{x} = 786.9$ ).

Only five of the males were judged by human observers to have well-developed knobs on the second dorsal fin (mean score  $\geq 1.5$ ); 14 were judged as poorly developed (mean score  $\leq 0.4$ ). Males with well-developed knobs guarded an average of 593 eggs; males with poorly-developed knobs guarded an average of 755.8 eggs. To improve sample sizes, males were divided into two categories—those with mean knob scores  $> 1.0$  (mean score = 1.39;  $n = 14$ ) and those with mean scores  $< 1.0$  (mean score 0.38;  $n = 21$ ). Males with more well-developed knobs guarded an average of 772.5 eggs; those with less well-developed knobs guarded an average of 796.5 eggs. The difference was not significant ( $t = 0.16$ ;  $P = 0.88$ ). Therefore, males with more well-developed knobs as judged by human observers were not guarding more eggs. Interestingly, males judged to have more well-developed knobs were significantly smaller (mean SL = 71.6 mm) than males with less well-developed knobs (mean SL = 76.0;  $t = 4.4$ ;  $P = 0.02$ ).

For 22 of the 35 males photographed, there was at least one slide on which both SL and knob height above the fin margin could be accurately measured. Most of those excluded were due to either the tip of the nose being obscured by the corner of the aquarium or lateral flexion of the tail preventing an accurate measure of SL. Mean actual knob height was 2.1 mm (range 1.1–3.2 mm); this was not significantly different from the mean of 2.02 mm for 25 breeding males measured directly in the field in 2001 (see below;  $t = 0.57$ ;  $P = 0.57$ ). Mean actual knob height correlated weakly but significantly with SL (Spearman rank correlation,  $r_s = 0.43$ ;  $P = 0.047$ ), indicating that knob size increases with body size. Partial correlation analysis controlling for SL found

no relation between knob height and brood size ( $r = 0.18$ ;  $P = 0.44$ ).

The 25 males guarding nests on 13–14 April 2001, ranged from 52–71 mm in SL ( $\bar{x} = 61.4$  mm). The mean knob height above the fin margin was 2.02 mm (range = 1–3 mm); knob width ranged from 0.3–1 mm ( $\bar{x} = 0.65$  mm). Males that were guarding eggs had a mean knob height of 2.09 mm, which was not significantly different from that of males guarding empty nests (1.88 mm;  $t = 1.13$ ;  $P = 0.13$ ). Knob width was also not significantly different (0.64 and 0.68 mm, respectively;  $t = 0.09$ ;  $P = 0.46$ ). Relative knob height was not significantly different (0.034 and 0.031 for males with and without eggs, respectively;  $t = 1.20$ ;  $P = 0.12$ ). Similarly, relative knob width (0.010 for males guarding eggs, 0.011 for males without eggs) was also not significantly different ( $t = 0.70$ ;  $P = 0.25$ ). Knob height had a significant positive correlation with SL ( $r = 0.40$ ;  $P = 0.05$ ); knob width also correlated positively but non-significantly with SL ( $r = 0.38$ ;  $P = 0.059$ ). There were no significant correlations between SL and either relative knob height ( $r = 0.08$ ;  $P = 0.72$ ) or relative knob width ( $r = 0.01$ ;  $P = 0.99$ ), indicating that knob size increases proportionately with male size.

## DISCUSSION

The results of this study do not support the hypothesis that the size of the second dorsal fin knobs in *E. squamiceps* males influences spawning decisions by females. There is indirect evidence that female spottail darters prefer to spawn with males already defending eggs (Bandoli 2002); however, the results of this study provide no evidence that males with taller or larger knobs have a shorter pre-spawning period, which is predicted if these knobs function as egg mimics. There were no significant correlations between brood size and knob size, implying that females choosing among males already defending eggs are not influenced by the presence of larger knobs. Finally, males with knobs rated by human observers as well-developed did not have larger broods than males with knobs rated as poorly-developed.

It may be argued that there is insufficient variation in the small knobs in *E. squamiceps* to allow females to discriminate. In *E. oophylax*, a species with well-developed knobs and

similar to *E. squamiceps* in SL, the maximum anterior-posterior diameter of mimics of 35 males collected in Ledbetter Creek in April 1999 ranged from 0.8–1.8 mm (Page & Knouft 2000), which is greater than the range of variation in knob widths measured in this study (0.3–1.0 mm). However, knob height above the fin margin in this study ranged from 1–3 mm, which is a greater range of variation than in anterior-posterior knob diameter in *E. oophylax* and may be more important as a potential signal. In *E. oophylax*, knobs and the fin rays that support them have a “lollypop” appearance, and the knobs alone may constitute the presumed egg mimic, with the rays functioning only to elevate the knobs. In contrast, knobs in *E. squamiceps* are club-shaped (see Fig. 1), such that there is no distinct “beginning” to the knob as the ray projects above the fin margin. Hence, if knobs in *E. squamiceps* are functioning as a signal, the entire structure above the fin margin may be important.

Knob height correlated weakly but significantly with male size in both the 1998–1999 sample and the 2001 sample, suggesting that the effect of knob size may be difficult to separate from body size, which influences reproductive success in *E. squamiceps* (Bandoli 1997). However, the fact that males rated by human observers as having more well-developed knobs were significantly smaller in SL suggests that, despite larger males having slightly larger knobs, they may be more conspicuous in smaller males.

The results of this study do not support the hypothesis that female choice is the initial force driving the evolutionary enlargement of second dorsal fin breeding knobs in spottail darters. However, there are several factors that may have obscured the predicted relationship between knob size and reproductive success. It is possible that the observed lack of response by females to variation in male knob size may be a local effect, and that female *E. squamiceps* in Illinois or Kentucky may be more discriminating. It is also possible that there may be more variation in knob size (and therefore more discrimination) in this species in other locations; geographic variation in knob size has been demonstrated in *E. oophylax* (Page & Knouft 2000). Environmental factors such as turbidity and photic conditions may decrease female sensitivity to subtle cues.

Additionally, variation in nest site availability and the resulting male competition (Bandoli 1997) may also influence female choice, temporally or geographically masking their use of other cues. Finally, any relation between knob size and reproductive success would be masked if males with larger knobs had higher rates of filial cannibalism, or if the frequency of alloparental care is substantially higher than we assume.

This study uses indirect evidence of female choice of males based on knob development, and it can be argued that a more direct approach, such as a knob-removal study (e.g., Strange 2001) may be more appropriate. However, even if females do prefer males with small knobs over males lacking them, it still would not explain their evolutionary elaboration into larger, more egg-like structures unless females also preferred males with more well-developed knobs over males with smaller knobs. To date, no study has examined the relationship between knob size and fitness in any of the strongly-knobbed species in the spottail darter species group. Moreover, Strange's (2001) study looked at the three species of *Catonotus* with yellow knobs. It is possible that knobs don't function as egg mimics until they develop a color similar to the orange typical of darter eggs. This could be tested by looking at female choice in *E. chienense*, which has distinct but relatively small white knobs.

Presumed egg mimics influence female spawning decisions in several species in the *Catonotus* subgenus; however, the results of this study imply that female choice may not drive the initial enlargement of male second dorsal fin knobs. This suggests that other factors, such as genetic drift, or an as yet unidentified function for small enlargements of dorsal fin rays may be involved.

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