

## The influence of brood loss on nest abandonment decisions in largemouth bass *Micropterus salmoides*

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Largemouth bass *Micropterus salmoides* broods were experimentally reduced in size to test whether brood size (BS) and simulated brood depredation affect the decision by a male to continue providing care for its brood or to abandon that brood prematurely before its offspring reach independence. The highest ranked of the generalized linear models predicting brood abandonment was based on the number of offspring remaining in a nest following brood devaluation, indicating that parental male fish reassess the value of a brood following perturbation. Paternal *M. salmoides* were more likely to abandon their broods if initial BS was small before devaluation, and if there was a greater decrease in BS, indicating a threshold for both the amount of brood loss and remaining BS. Larger, older males were also less likely to abandon their brood than smaller, younger conspecifics. These results have broad implications for determining drivers of parental care trade-offs and how individuals assess the value of a brood.

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Key words: fitness; life history; parental care; recruitment; reproductive success; reproductive value.

### INTRODUCTION

Parental care evolved as a strategy to maximize fitness of the care-providing parent by increasing the likelihood of offspring survival, particularly *via* the defence of their brood from predation. Parental care decisions are based on trade-offs between current and expected future reproductive outputs, *i.e.* the investment of finite resources into the care of a current brood comes at an immediate and direct cost to the parent *via* energetic expenditure and risk of physical harm, as well as at a delayed and indirect cost *via* reduced potential for future offspring (Williams, 1966). As a result, parental investment varies based on the perceived value of a brood (*i.e.* the potential contribution of a brood to an individual's fitness), the energetic requirement to raise that brood, the parent's expected reproductive success and potentially, past investment into a brood (Williams, 1966; Trivers, 1972; Gross, 2005; Zuckerman & Suski, 2013). When the fitness contribution of a brood is outweighed by the perceived cost of providing

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care, or the value of a brood becomes reduced through depredation, individual parents may reduce their level of investment into the brood (Williams, 1966; Sargent & Gross, 1986; Gross 2005). Ultimately, if reproductive value of a brood is reduced below a particular threshold, parental individuals may abandon their offspring in favour of investing towards future reproductive output. Such parental decisions have been observed in the bi-parental care-providing cichlid *Aequidens coeruleopunctatus* (Kner 1863). Following a reduction in brood size (BS), females were observed to partake in less risky brood defence (Carlisle, 1985) and paternal males to abandon their brood in favour of attempting another bout within the same reproductive season (Jennions & Polakow, 1998). Patterns of brood abandonment are observed across other taxa, with water fowl, passerine birds and centrarchids all exhibiting a tendency towards offspring abandonment following brood depredation (Verboven & Tinbergen, 2002; Ackerman & Eadie, 2003; Steinhart *et al.*, 2008). For iteroparous species that are limited to a single reproductive event within a given season, the decision to abandon a brood may be more risky from a fitness standpoint owing to uncertainties in future survival, somatic growth and future reproductive opportunities (Wingfield & Sapolsky, 2003; Gross, 2005; Steinhart *et al.*, 2008).

Largemouth bass *Micropterus salmoides* (Lacépède 1802) are an ideal model species for studies involving parental care decisions (Gross, 2005). Native to North America, *M. salmoides* begin reproductive behaviour in spring as water temperatures approach 15° C, with males constructing shallow bowl-shaped nests in littoral substrata (Heidinger, 1975). Upon completion of nest construction, male *M. salmoides* court females and subsequently fertilize eggs as they are deposited into the nest. Following egg deposition, the female departs the nest, leaving the male to provide sole parental care for the next 3–5 weeks, until offspring reach independence. During this time, paternal *M. salmoides* partake in energetically costly parental care (Cooke *et al.*, 2002) which, as demonstrated by nest-guarding behaviours of the smallmouth bass *Micropterus dolomieu* Lacépède 1802, includes fanning the nest using movements of the pectoral and caudal fins to increase oxygenation and actively chasing brood predators from the vicinity of the nest (Ridgway, 1989; Hinch & Collins, 1991; Cooke *et al.*, 2002, Gravel & Cooke, 2009). Despite the increased energetic investment accrued during the care period, paternal *M. salmoides* refrain from actively foraging, instead of relying on endogenous energetic reserves. For *M. dolomieu*, this results in an overall decline in somatic and physiological condition throughout the parental care period (Gillooly & Baylis, 1999; Hanson & Cooke, 2009; Hanson *et al.*, 2009), a factor that could also potentially affect survival and future reproductive capacity of parental *M. salmoides*.

Abandonment of a brood prior to offspring independence has been observed in *M. salmoides* and *M. dolomieu*, being attributed to acute changes in water temperature (Steinhart *et al.*, 2005; Suski & Ridgway, 2007; Landsman *et al.*, 2011), energetic and physiological costs associated with increased vigilance under high densities of brood predators (Gillooly & Baylis, 1999; Steinhart *et al.*, 2005; Gravel & Cooke, 2009) and angling-induced reduction in physiological condition of the male (Suski *et al.*, 2003; Steinhart *et al.*, 2005; Wagner *et al.*, 2006). Brood abandonment in *M. salmoides* and *M. dolomieu* is also more likely to occur due to a decrease in reproductive value following brood depredation, either because that depredation occurred naturally or because the parental male was removed from a nest during capture by an angler (Philipp *et al.*, 1997; Suski *et al.*, 2003; Lunn & Steinhart, 2010). Philipp *et al.* (1997) demonstrated that the occurrence of brood loss by depredation during an angling

event increased the rate of brood abandonment among parental *M. salmoides* and *M. dolomieu*. Additionally, parental *M. salmoides* that experienced a 50% reduction in BS abandoned their brood up to 70% of the time (Suski *et al.*, 2003). Despite the potential for negative fitness and recruitment effects of brood abandonment in *M. salmoides* (Sutter *et al.*, 2012), few studies have tested for the magnitude of decrease in reproductive value that is needed for parental *M. salmoides* to abandon their brood. The goals of the current study were to test whether nest abandonment decisions in *M. salmoides* are influenced by (1) initial BS, (2) magnitude of brood loss and (3) the size of the remaining brood, following depredation.

## MATERIALS AND METHODS

### SNORKEL OBSERVATIONS

This study was conducted on Lake Opinicon, an 890 ha mesotrophic lake in eastern Ontario, Canada (44° 33' N; 76° 19' W). From early May to mid-June 2011, after water temperatures reached 13° C, daily snorkel surveys were performed in the littoral zone to locate nesting *M. salmoides*. Upon discovery of a *M. salmoides* nest containing eggs, male total length ( $L_T$ ) was visually estimated to the nearest 2.5 cm (Suski & Philipp, 2004), depth of the nest in the water column was recorded to the nearest 0.25 m and a uniquely numbered polyvinyl chloride (PVC) tag was placed near each nest for identification. BS, a long-standing categorical ranking of the quantity of eggs within a nest, was visually estimated from 1 (few eggs) to 5 (many eggs) upon discovery of each nest (Suski *et al.*, 2003; Suski & Philipp, 2004). In Lake Opinicon, male *M. salmoides* guarding a BS of 1 produce  $840 \pm 80$  (mean  $\pm$  S.E.) swim up fry, and males with an estimated BS of 5 produce  $25\,500 \pm 1\,500$  swim up fry (Stein & Philipp, 2014). Estimates of expected fry production are included in the current study only as a numerical reference and are not included in any analysis. BS was subsequently verified by at least two additional snorkellers to ensure precision of estimates (Suski *et al.*, 2003; Suski & Philipp, 2004). Estimates of BS from *M. salmoides* nests have been further demonstrated to correlate positively with the number of eggs in a nest, thus an estimation of BS from 1 to 5 provides an accurate ranking of the expected fitness contribution of the current brood based on expected fry production for each parental male (Parkos *et al.*, 2011; Stein & Philipp, 2014).

The number of potential brood predators [bluegill *Lepomis macrochirus* Rafinesque 1819 and pumpkinseed *Lepomis gibbosus* (L. 1758)] within a 2 m radius of each nest was quantified by instantaneous counts both upon the snorkeller's approach to and departure from the nest (Gravel & Cooke, 2009; Zuckerman & Suski, 2013). The mean of these counts provides an estimate of brood predator burden in proximity to a nest and the potential cost of brood defence as perceived by the brood-guarding *M. salmoides* at the time of nest manipulation (Zuckerman & Suski, 2013). The relative spawn date for the nests used in this study was determined by the first date of observed egg deposition and ended with the last date of observed egg deposition.

Following brood predator counts, nests were randomly assigned to a treatment of 0, 25, 50, 75 or 100% brood removal (devaluation), stratified by BS. Devaluations were conducted by a snorkeller removing the designated percentage of eggs from the nest using a 30 ml rubber bulb pipette, with the devalued eggs being placed in a jar and removed from the vicinity of the nest. Control nests (*i.e.* nests that received 0% devaluation) were treated similar to devalued nests in that a snorkeller spent the same time at the nest to quantify BS without removing eggs. To minimize potential influence of offspring age and past investment on parental decisions, only nests containing eggs  $\leq 3$  days old were included in the study.

To quantify abandonment rates, a second snorkel survey was conducted 24 h following brood devaluation. Males that were present on a devalued nest were deemed to have maintained parental care following devaluation; nests with no male present were deemed to have been abandoned (Philipp *et al.*, 1997; Hanson *et al.*, 2007).

## DATA ANALYSIS

A one-way ANOVA was used to compare  $L_T$ , BS, nest depth, relative spawn date and predator burden across devaluation categories. Means were separated using a Tukey's *post hoc* test where appropriate (JMP v. 7.0, SAS Institute Inc.; www.sas.com) (Zar, 1999). A  $\chi^2$  test was used to determine whether brood devaluation resulted in different abandonment rates between treatment levels (JMP v. 7.0, SAS Institute Inc.). To quantify the influence of independent variables and treatment on brood abandonment (a binary response: abandon or continue guarding), data were analysed using fixed-effect generalized linear models (GLMs) *via* the GLIMMIX procedure using the default binary logit link function (Wagner *et al.*, 2006; SAS Institute); initial BS was included as a random effect in a mixed-effect GLM to test for a block effect of initial BS on the abandonment response at each treatment level (SAS v. 9.2, SAS Institute Inc.). The GLIMMIX procedure allows for robust modelling of non-continuous explanatory variables (*e.g.* the ordinal variables BS and proportion of a nest devalued) against non-Gaussian-dependent distributions, in particular, the binary response (SAS Institute Inc.). Biologically significant models that may explain patterns in brood abandonment were developed *a priori* and contained the covariates relative spawn date, nest depth, male  $L_T$ , predator burden, proportion of brood removed (per cent devalued), change in BS (the relative change in BS following devaluation) and remaining BS (the BS remaining following devaluation). Because male  $L_T$  was positively correlated with BS (linear regression,  $P < 0.001$ ,  $r^2 = 0.289$ ), no interaction between BS and  $L_T$  was included in any model.

Model fit was verified by Pearson's  $\chi^2$ :d.f., which, as  $\chi^2$ :d.f. approaches 1.00, signifies a lack of residual overdispersion. Model rank was determined using a Wald-type Z-test when  $\chi^2$ :d.f. signified a lack of overdispersion; a Wald-type *t*-test was used when  $\chi^2$ :d.f. signified overdispersion (*i.e.*  $\chi^2$ :d.f.  $> 1.50$ ; Greenwood, 2008; Bolker *et al.*, 2009). Statistical significance for all tests was concluded at  $\alpha \leq 0.05$  and all means are reported as  $\pm$  s.e. where appropriate. Following model generation, the relationship between nest abandonment and significant models was visualized using logistic regression, where appropriate, by plotting the predicted probability of abandonment against the main effect of each respective model.

## RESULTS

*Micropterus salmoides* spawning began on 9 May and lasted to 5 June 2011. A total of 123 nests were located and included in this study, of which 45 males (37%) abandoned within 24 h following devaluation treatments. Male  $L_T$ , BS, brood predator number or nest depth varied across treatments (Table I). Despite random assignment of devaluation treatments, there was minor variation in spawn date among treatment groups (ANOVA, d.f. = 4, 118,  $P < 0.01$ ; Table I). Because the distribution of spawn date for nests included for treatment was contained within the first 2 weeks of the spawning period, this variation is unlikely to have affected further results.

Generalized linear mixed-modelling indicated a lack of block effect by initial BS on the abandonment response of parental *M. salmoides*; thus, all 123 nests were pooled for analysis ( $P > 0.05$ ). No model containing relative spawn date, nest depth or predator burden as covariates explained any significant variability in abandonment ( $P > 0.05$ ; Table II). Brood loss did induce nest abandonment in *M. salmoides*, with the rate of brood abandonment increasing with the proportion of brood devalued ( $\chi^2 = 50.389$ , d.f. = 4,  $P < 0.001$ ; Table I and Fig. 1). At the extremes, all controls that experienced 0% devaluation maintained parental care beyond the 24 h follow-up snorkel survey, while all males that experienced 100% devaluation abandoned their broods (Fig. 1). Although a decrease in BS was the mechanism in the current study by which a parent was forced to re-assess the contribution of a brood to its reproductive value, the model

TABLE I. Mean  $\pm$  S.E. values for offspring- and parent-related variables collected from brood-guarding *Micropterus salmoides* nests. Means sharing the same lower case letters are not significantly different from one another ( $P > 0.05$ ; ANOVA; Tukey's *post hoc*). The number of males that abandoned before offspring independence varied significantly across brood devaluation treatments ( $\chi^2$  test), and the per cent of males that abandoned within each treatment is in parentheses

	Treatment (% devalued)					<i>P</i>
	0	25	50	75	100	
<i>n</i>	26	26	26	26	19	NA
Male $L_T$ (mm)	360 $\pm$ 9	347 $\pm$ 9	352 $\pm$ 9	353 $\pm$ 6	345 $\pm$ 10	>0.05
Spawn date	3.8 $\pm$ 0.6 <sup>a</sup>	4.8 $\pm$ 0.8 <sup>ab</sup>	6.7 $\pm$ 1.1 <sup>ab</sup>	7.7 $\pm$ 0.9 <sup>b</sup>	9.9 $\pm$ 1.9 <sup>b</sup>	<0.001
Nest depth (m)	1.2 $\pm$ 0.1	1.1 $\pm$ 0.1	0.8 $\pm$ 0.1	0.8 $\pm$ 0.1	0.9 $\pm$ 0.1	>0.05
Predator burden	3.4 $\pm$ 0.7	4.2 $\pm$ 1.3	3.5 $\pm$ 0.5	2.7 $\pm$ 0.6	3.5 $\pm$ 1.0	>0.05
Initial BS	3.2 $\pm$ 0.2	3.0 $\pm$ 0.2	3.2 $\pm$ 0.3	3.1 $\pm$ 0.2	3.1 $\pm$ 0.3	>0.05
$\Delta$ BS	0 $\pm$ 0	-0.8 $\pm$ 0.1	-1.6 $\pm$ 0.1	-2.3 $\pm$ 0.2	-3.1 $\pm$ 0.3	NA
Remaining BS	3.2 $\pm$ 0.3	2.3 $\pm$ 0.2	1.6 $\pm$ 0.2	0.8 $\pm$ 0.1	0 $\pm$ 0	NA
Abandoned males	0 (0%)	6 (23%)	9 (35%)	11 (42%)	19 (100%)	<0.001

Predator burden, mean number of potential brood predators observed within 2 m of each nest; initial BS, initial brood size, a categorical ranking (1–5) of the number of eggs in a nest prior to devaluation treatment;  $\Delta$ BS, change in BS following brood devaluation; remaining BS, number of brood remaining following brood devaluation treatment;  $L_T$ , total length; NA, not applicable.

based solely on the per cent of brood devaluation failed to significantly predict brood abandonment ( $P > 0.05$ ; Table II).

The generation of competing models identified four variables that explained significant variation in brood abandonment, with remaining BS following devaluation being the best predicting model ( $P < 0.001$ ; Table II). *Micropterus salmoides* with a remaining BS of 3 (expected fry production of 7900  $\pm$  310) or greater had <1.0% probability of abandoning their brood within 24 h of brood devaluation [ $r^2 = 0.411$ ; Fig. 2(a)]. The likelihood of abandoning a brood increased markedly when BS was reduced below 2, and a threshold for 50% probability of premature abandonment is estimated at a remaining BS of *c.* 1 [ $r^2 = 0.411$ ; Fig. 2(a)]. Male *M. salmoides* showed an increasing likelihood of brood abandonment as the magnitude of devaluation of a brood increased ( $P < 0.001$ ; Table II). Initial BS, prior to devaluation, influenced nest abandonment decisions in male *M. salmoides*, with the likelihood of brood abandonment declining with increasing initial BS [ $P < 0.05$ ,  $r^2 = 0.9419$ ; Table II and Fig. 2(b)]. Modelling further indicated that parental males were less likely to abandon a brood with increasing  $L_T$  ( $r^2 = 0.9963$ ,  $P < 0.05$ ; Table II and Fig. 3)

## DISCUSSION

Care-providing organisms adjust investment into their offspring based on the perceived fitness contribution of a brood. Parents may also choose to abandon their brood in favour of investing towards potential future reproductive efforts (Carlisle, 1982; Beauchamp & Kacelnik, 1990; Gross, 2005; Bourgeon *et al.*, 2006). In the current

TABLE II. Generalized linear fixed models explaining variation in premature brood abandonment in *Micropterus salmoides* following experimental brood devaluation. Model selection of independent variables and interactions are based on Wald-type hypothesis tests, and all models were developed *a priori* to model testing

Model	$\chi^2$ :d.f.	F	P*
Remaining BS	0.86	28.06	<0.001
$\Delta$ BS	0.99	13.00	<0.001
Initial BS	1.04	3.04	<0.05
$L_T$	1.01	5.31	<0.05
Nest depth	1.01	2.85	>0.05
Remaining BS $\times$ relative spawn date	1.71	2.61	>0.05
Relative spawn date	1.02	1.95	>0.05
Remaining BS $\times$ nest depth	0.88	1.95	>0.05
Predator burden $\times$ initial BS	1.01	1.84	>0.05
Predator burden $\times L_T$	1.01	1.65	>0.05
Initial BS $\times$ relative spawn date	1.10	1.39	>0.05
Remaining BS $\times$ predator burden	0.94	1.28	>0.05
Remaining BS $\times$ predator burden $\times$ nest depth	0.98	1.17	>0.05
Remaining BS $\times$ per cent devalued	0.60	1.08	>0.05
Remaining BS $\times L_T$	0.87	0.32	>0.05
Remaining BS $\times \Delta$ BS $\times$ initial BS	0.80	0.80	>0.05
Per cent devalued	0.66	0.54	>0.05
Predator burden	1.02	0.46	>0.05
Predator burden $\times$ nest depth $\times$ initial BS	1.10	0.39	>0.05

Predator burden, mean number of potential brood predators observed within 2 m of each nest; initial BS, initial brood size, a categorical ranking of the number of eggs in a nest prior to devaluation treatment;  $\Delta$ BS, change in BS following brood devaluation; remaining BS, BS remaining following brood devaluation treatment;  $L_T$ , parental male total length.

\*Significant predictor of brood abandonment based on Wald-type *t*- or Z-test.

study, abandonment decisions were based on both the initial level of mating success (BS and expected subsequent fry production) and the level of devaluation of the brood. That is, although brood devaluation did induce abandonment in parental *M. salmoides*, this treatment alone did not predict the likelihood that a male will abandon his brood. Rather, brood abandonment by parental *M. salmoides* was best explained by the number of offspring remaining in the nest following devaluation. When remaining BS was at least 2 (an expected reproductive value of  $2400 \pm 160$  fry), paternal males were unlikely to forfeit parental care activities. The likelihood for brood abandonment, however, increased quickly to 50% abandonment when remaining BS approached 1 (an expected reproductive value of  $840 \pm 80$  fry). This marked increase in the rate of abandonment represents a threshold at which further investment into the remaining brood outweighs potential fitness benefits, thus evoking the decision by parental male *M. salmoides* to abandon what remains of the devalued brood.

The influence of remaining BS on abandonment confirms that parental *M. salmoides* re-assess the reproductive value of their brood following depredation and adjust parental investment according to the expected fitness contribution of their remaining offspring. This finding is in accordance with results from brood manipulation

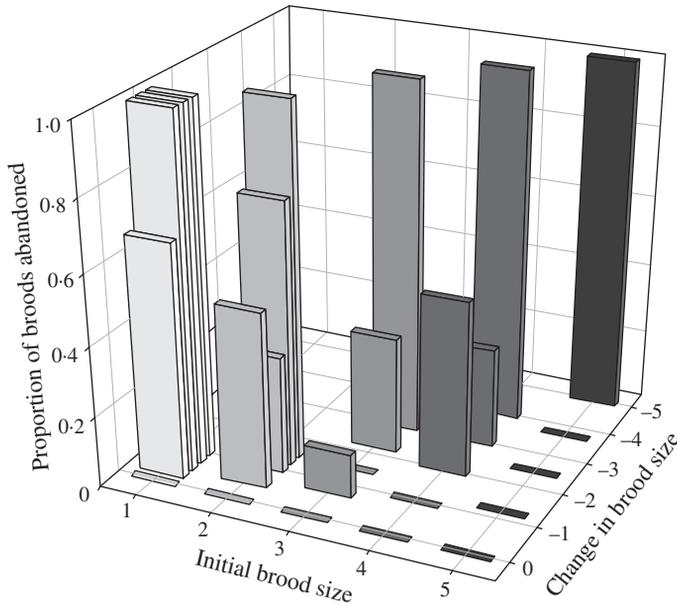


FIG. 1. Proportion of paternal *Micropterus salmoides* that abandoned their brood following experimental brood devaluation. Shading represents initial brood size (BS, a categorical ranking of the number of offspring in a nest) prior to brood devaluation. Change in BS indicates the decrease in BS following experimental devaluation. Starting at a change in BS of 0, bars within each initial BS grouping indicate treatment levels of 0, 25, 50, 75 and 100% brood devaluation, respectively.

experiments that induced premature nest abandonment in *M. dolomieu* (Lunn & Steinhart, 2010) and in the great tit *Parus major* (Verboven & Tinbergen, 2002); both species based abandonment decisions primarily on the number of offspring remaining following brood removal. Ackerman & Eadie (2003) also demonstrated an abandonment threshold in mallards *Anas platyrhynchos*, which experienced an exponential increase in the likelihood of abandonment when clutch size was devalued to 60 or 40% of initial size, depending on the time within breeding season at which the devaluations occurred. The current study, however, only included nests that contained offspring aged  $\leq 3$  days, thereby minimizing the potential influence of offspring age and past investment on parental decisions (Cooke *et al.*, 2002). Together, these results demonstrate that care-providing individuals are capable of re-assessing the reproductive value of their brood following disturbance to a nest, thereby basing the decision to abandon a brood on the expected fitness contribution of the remaining offspring.

Parental *M. salmoides* demonstrated some resilience against brood abandonment following devaluation; the predicted probability of abandonment was low when remaining BS decreased to 2 (an expected reproductive value  $< 2400 \pm 160$  fry), despite this value representing a reduction in BS of  $\geq 50\%$  for some males (*i.e.* males with an initial BS of 4 or greater). Resiliency against premature abandonment in *M. salmoides* may be attributed to the inherently high cost of reproduction for the species, particularly at northern latitudes where males are unlikely to attempt more than a single breeding event within a given reproductive season (Suski *et al.*, 2003;

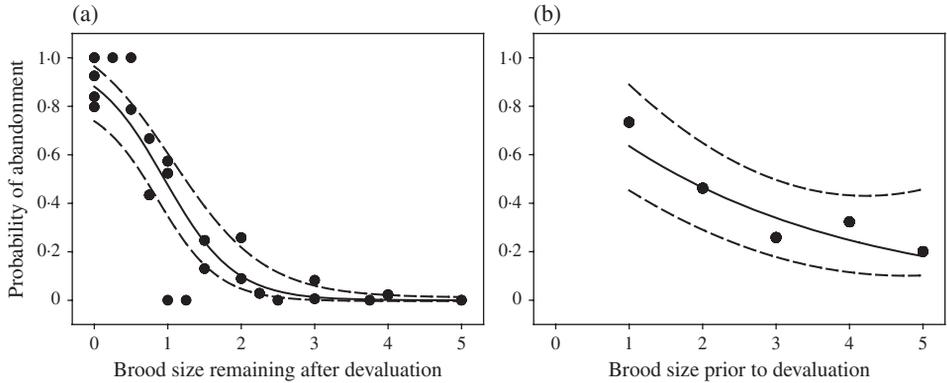


FIG. 2. Probability of premature brood abandonment by parental *Micropterus salmoides* as predicted by generalized linear models, regressed against respective model parameters (a) remaining brood size (BS) following devaluation treatment ( $P < 0.001$ ,  $r^2 = 0.4111$ ), where each point represents the predicted likelihood that a male will abandon given the BS remaining following removal of 0, 25, 50, 75 or 100% from initial BSs 1–5 and (b) initial BS prior to brood devaluation treatment ( $P < 0.05$ ,  $r^2 = 0.9419$ ). — —, 95% upper and lower c.l. as determined by each respective model. Model significance was determined by Wald-type Z-test at  $\alpha = 0.05$ .

Magee & Neff, 2006; Steinhart *et al.*, 2008). Because partial brood loss occurs naturally for centrarchids due to natural nest depredation, storm events, egg fungal infection and potentially poor egg quality (Knotek & Orth, 1998; Steinhart *et al.*, 2005; Steinhart *et al.*, 2008; Gingerich & Suski, 2011), the capacity for brood loss before a male abandons a brood is limited in *M. salmoides*.

The magnitude of change in *M. salmoides* BS following experimental brood devaluation was also a significant predictor of brood abandonment in *M. salmoides*. The probability of abandoning a brood increased from male controls that experienced no loss in BS, to males that experienced a complete loss of brood [100%

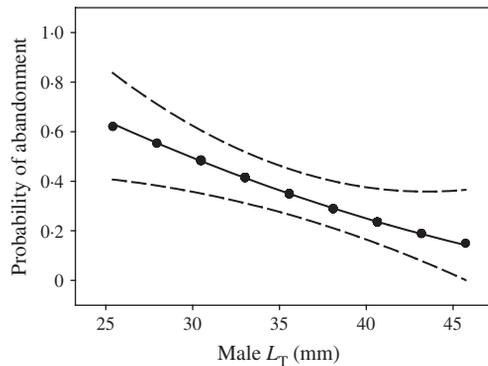


FIG. 3. Probability of premature brood abandonment by parental *Micropterus salmoides* following experimental nest devaluation, regressed against male total length,  $L_T$  ( $P < 0.05$ ,  $r^2 = 0.9963$ ). — —, 95% upper and lower c.l. as determined by each respective model. Model significance was determined by Wald-type Z-test at  $\alpha = 0.05$ . The curve was fitted by  $y = 1.629 - 0.123x + 0.002x^2$ .

devaluation; Fig. 2(a)]. Among centrarchids, Coleman *et al.* (1985) observed a decreased willingness in *L. macrochirus* to defend a brood following a 50% reduction in BS, and male *M. salmoides* and *M. dolomieu* abandon a brood prematurely after the occurrence of natural or experimental brood depredation (Suski *et al.*, 2003; Gross, 2005; Steinhart *et al.*, 2005; Hanson *et al.*, 2007; Lunn & Steinhart, 2010). Although the loss in value of the brood is the mechanism by which an individual is forced to re-assess the fitness benefit of continued care into that brood, it is concluded here that the remaining reproductive value is the primary deciding factor underlying the care-provider abandoning its brood or not.

The likelihood for brood abandonment by *M. salmoides* in the current study decreased significantly with increasing parental male size. Although the non-invasive experimental approach of the current study precluded collection of age data from brood-guarding males, it is generally considered that *Micropterus* spp. size correlates positively with both age and BS (Philipp *et al.*, 1997; Suski & Philipp, 2004; Steinhart *et al.*, 2008; Parkos *et al.*, 2011). Thus, larger nesting male *M. salmoides* in the current study were probably older than their smaller con-specifics with smaller broods and also less likely to abandon their brood before offspring developed to independence. From an energetic standpoint, larger individual centrarchids show increased over-winter survivorship and have greater somatic reserves with which to sustain parental care activities, potentially minimizing costs on future broods (Erikstad *et al.*, 1997; Fullerton *et al.*, 2000; Cooke *et al.*, 2006; DeVries *et al.*, 2009). The finding here that parental *M. salmoides* are less likely to abandon a brood with increasing age provides empirical support for current parental care theory, because potential future reproductive success in iteroparous species is variable due to increased likelihood of mortality with age, it may prove prudent for older males to maintain parental care following a high level of brood devaluation to still accrue fitness when future reproductive opportunities are uncertain (Williams, 1966; Gross, 2005; Steinhart *et al.*, 2008). The findings here demonstrate that the expected fitness contribution of a current brood is weighed together with an individual's potential for future reproductive success when making parental care decisions to maximize the individual's lifetime reproductive success.

Interestingly, predator burden, spawn date and nest depth, factors previously demonstrated to influence parental investment in centrarchids, were not significant predictors of premature nest abandonment in this study (Magee & Neff, 2006; Wagner *et al.*, 2006; Gravel & Cooke, 2009; Zuckerman & Suski, 2013). Centrarchids increase investment accordingly with the threat of brood depredation, as demonstrated by an increase in brood defence behaviours by *M. dolomieu* in lakes with high brood predator densities (Gravel & Cooke, 2009). Despite variation in nest-specific predator counts in the current study, and the high energetic cost of guarding offspring from depredation by *L. macrochirus* and *L. gibbosus* (Gillooly & Baylis, 1999; Cooke *et al.*, 2002, 2006), paternal *M. salmoides* nesting in areas of relatively higher predator densities were no more likely to abandon their brood than were males nesting in areas of lower predator burden. Also, unlike many avian species or the colonially spawning *L. macrochirus* (Magee & Neff, 2006), *M. salmoides* generally complete only a single spawning bout per season at the northern-most latitudes of its range (Kubacki *et al.*, 2002). With a limited window for reproduction, the relative date at which each brood was fertilized may have little influence on the parental decisions to abandon a brood (Wingfield & Sapolsky, 2003). As a result, these abiotic and biotic variables not related to BS are

unlikely mediators of brood abandonment decisions in *M. salmoides* when considered in conjunction with reproductive value.

Results from this study have several implications for recruitment and fitness in *M. salmoides*. Because *M. salmoides* offspring in the egg and fry stages are not capable of survival without parental care, premature brood abandonment almost certainly results in a complete loss of the brood (Philipp *et al.*, 1997; Parkos *et al.*, 2011). Furthermore, because water temperatures in the portion of *M. salmoides* range where this study was conducted generally preclude a second nesting attempt within a given year, negative effects on fitness or recruitment because of brood abandonment are not likely to be remediated within the same season. Although recruitment of *M. salmoides* can be influenced by density-dependent or environmental variables (Ludsin & DeVries, 1997; DeVries *et al.*, 2009; Gwinn & Allen, 2010), evidence exists that premature brood abandonment may limit the number of offspring produced in a population, potentially at a cost to recruitment (Gross & Kapuscinski, 1997; Parkos & Wahl, 2010; Parkos *et al.*, 2011). Brood-guarding *M. salmoides* are sometimes preferentially targeted by recreational anglers across North America, thereby inducing premature brood abandonment in response to offspring depredation while the male is away from the nest (Philipp *et al.*, 1997; Wagner *et al.*, 2006; Hanson *et al.*, 2007; Siepker *et al.*, 2007; Sutter *et al.*, 2012). In water bodies with high predator burden, removing a brood-guarding male may result in accelerated brood depredation to the point where remaining BS is reduced below the threshold for abandonment. Angling-induced effects on population level reproductive success may be further exacerbated by the fact that larger males are more likely to successfully recruit offspring beyond the parental care period, yet can be more susceptible to capture by angling due to their heightened nest vigilance than are smaller brood-guarding conspecifics, particularly in populations naïve to angling pressure (Suski & Philipp, 2004; Parkos *et al.*, 2011, Sutter *et al.*, 2012). The current study demonstrates the importance of brood loss on parental decisions in care-providing organisms and provides further evidence that parental individuals re-assess their reproductive value following brood loss, using this information together with expected future reproductive output as the basis for making fitness-related abandonment decisions. To minimize potential fitness and population costs of premature brood abandonment in care-providing organisms, disturbances that might allow for nest depredation should be minimized, particularly with regard to the removal of brood-guarding *M. salmoides* from their nest *via* selective angling practices.

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