



# Post-spawning defence by male brook charr is linked to perceived paternity

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**Abstract** Salmonine fishes are generally thought not to exhibit male parental care, although brief post-spawning mate-guarding by males is known for a number of species, often for populations where eggs are subjected to intense predation (egg cannibalism). Here, detailed in situ data on the spawning behaviour of male brook charr, *Salvelinus fontinalis*, from a naturally reproducing lake population is used to test whether post-spawning mate guarding (i.e. paternal care) is related to perceived paternity. From video records of spawning events ( $n=20$ ), we documented a novel behaviour whereby the dominant male curtails spawning ahead of the female (by ~3 s) and immediately inspects the nest. Afterwards, the dominant male significantly reduces courtship behaviour (quivers) but aggressively defends the female with the same intensity as prior to spawning. The duration of mate guarding (range: 3–48 min), however, declined

with increasing numbers of peripheral males that had rushed into the nest at spawning. Neither the number of active females present on the spawning grounds nor male body size influenced the amount of time dominant males spent mate guarding. Extensive revisitation (80% of visits) by males to spawning sites and to females during focal sampling bouts highlights the importance of a male's ability to predict female readiness to spawn as a significant component of reproductive success. Thus, dominant males appear to guard females at a cost of acquiring other mating opportunities and adjust the time spent guarding depending upon their perceived paternity.

**Keywords** Salmonine · Mating system · Behaviour · Cost · Mate-searching

## Introduction

The mating system of most salmonine fishes (charr, trout and salmon) is characterised by female preparation and defence of a site for spawning and male competition for access to females (Esteve 2005). Male salmonine reproductive success is often determined by mating frequency, which is influenced by the availability of mates, as well as a male's ability to find a mate and to prevent others from gaining access to this mate. Synchronous preparation of spawning sites by females leads to intense male-male competition, especially for the semelparous species in this group

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(*Oncorhynchus* spp.) which display the most pronounced secondary sexual characteristics (e.g. Quinn and Foote 1994). Males compete for access to females with the dominant male aggressively driving away other males at the site (called peripheral males) to be the sole male spawning (Keenleyside and Dupuis 1988). Despite these aggressive efforts by the dominant male, it is common for other males to rush in at the moment of gamete release by the spawning pair to attempt to fertilize eggs (Foote et al. 1997). Genetic evidence, however, supports a first male spawning advantage in terms of the number of eggs fertilized (Mjølnerød et al. 1998; Blanchfield et al. 2003).

It is generally maintained that male parental care does not occur among salmonines because males maximize their reproductive success through spawning frequency (e.g. Fleming and Gross 1994). Early observations of salmonine spawning behaviour documented that male brook charr (*Salvelinus fontinalis*) remain with females after spawning and chase away other males while the female covers the eggs (White 1930). Likewise, Greeley (1932) observed that for brook charr, brown trout (*Salmo trutta*), and rainbow trout (*Oncorhynchus mykiss*), post-spawning defence of the nest site by males occurs only briefly (~5 min) during the early stages of covering by the female. Dominant male pink salmon (*Oncorhynchus gorbuscha*) were also observed to leave females shortly after spawning (<3 min, Keenleyside and Dupuis 1988). While a number of factors can influence the male duration of post-spawning guarding, such as the number of females available to mate (i.e. intensity of competition) and male body size (Morbey 2002), male associations with females after spawning are thought to be brief for this group of fishes (Esteve 2005).

The consumption of newly-deposited eggs by peripheral males, often termed egg cannibalism, has been documented among all genera of the Salmoninae: *Oncorhynchus* (Greeley 1932; Garner et al. 2009); *Salmo* (Greeley 1932; Jones and King 1950; Aymes et al. 2010); *Salvelinus* (White 1930; Maekawa and Hino 1990; Blanchfield and Ridgway 1999; Frye et al. 2021). Egg cannibalism occurs immediately after spawning by peripheral males because females are usually able to initially cover the eggs within a few minutes of spawning (Jones and King 1949; Aymes et al. 2010). Heterospecific egg predation is also a threat to salmonine fishes and is thought to account for the increased digging rates of females immediately after spawning (Sheridan 1960). Dominant males could

potentially defend against all forms of egg predation by remaining in close proximity to females. Post-spawning chasing of peripheral males by dominant male brown trout has been shown to reduce the probability of egg cannibalism, which Tentelier et al. (2011) proposed ought to be considered a form of paternal care. Thus, time spent by the dominant male guarding the female after spawning, even for a brief period, may be beneficial to that male if it reduces the loss of eggs through predation, especially for populations where a high percentage of spawning events are subject to egg cannibalism by peripheral males, such as brown trout (~20%, Tentelier et al. 2011), brook charr (~25%, Blanchfield and Ridgway 1999) and Arctic charr (*Salvelinus alpinus*; ~50%, Frye et al. 2021).

If post-spawning guarding or protective behaviour by the dominant male can be considered a form of paternal care, then one expectation is that dominant males should reduce their paternal effort in relation to perceived lower paternity (Trivers 1972). Substrate-spawning fish are ideal organisms in which to examine the relationship between paternal effort and paternity because fertilization is external and instantaneous, thereby providing visual cues to the primary male to assess whether other males have participated in a spawning event and gauge the likelihood of reduced paternity. Evidence from nesting fish with sole male parental care has demonstrated that males can adjust parental care in response to perceived paternity (Neff 2003). For brown trout, post-spawning aggression (chases) by the dominant male was not lower for multiple-male matings, suggesting that paternity certainty did not influence paternal effort (Tentelier et al. 2011). However, the post-spawning effort was examined for only a short period in that study (5 min), with dominant male brown trout presumed to depart females shortly after spawning (within ~10 min, Tentelier et al. 2011), which may not have encompassed all aspects of the paternal effort.

Theoretical and empirical studies of fishes with male care have shown that a reduction in breeding frequency is one cost of paternal effort (Gross and Sargent 1985; Balshine-Earn 1995; Smith and Wootton 1995). For example, male Galilee St Peter's fish (*Sarotherodon galilaeus*) that cared for egg broods experienced significantly greater weight loss and took more than twice as long before spawning with a new female compared to males who had no parental care duties (Balshine-Earn 1995). Mate guarding is thought to be an energetically demanding endeavour

that has been shown to reduce the breeding lifespan of male kokanee (*Oncorhynchus nerka*, Morbey 2003). Consequently, the duration of guarding may also be an important, but overlooked, aspect of the paternal effort. The ability to predict female readiness to spawn and gain access to females are strong determinants of male mating success for salmonine fishes. Dominant males that choose to guard females, therefore, do so at the cost of searching for other spawning opportunities. Defining this cost has been challenging for salmonine mating systems because it is often difficult to assess the searching behaviour of males and the opportunities this searching affords under natural conditions, such as in small rivers and streams where many salmonines spawn. Thus, post-spawning mate guarding by males is a costly activity competing temporally with acquiring other mating opportunities and requires further investigation.

The mating system of an intensively studied population of lake-spawning brook charr provides the opportunity to examine post-spawning mate guarding behaviour by dominant males and to assess the associated costs of this guarding for males. For this population, peak spawning occurs over a 2-week period in early October during which females select sites of groundwater upwelling to dig a pit and spawn, taking up to 10 days between the first and last spawning (Blanchfield and Ridgway 1997, 2005). Males actively search the spawning grounds and compete for access to females (Blanchfield 1998; Blanchfield and Ridgway 1999). Dominant males guard females but peripheral males frequently do participate in spawning events, often with limited success (mean  $\pm$  SE =  $21 \pm 14\%$  parentage; range = 0–100%) as the first male to release gametes fertilizes most of the eggs in a given spawning event (Blanchfield et al. 2003). Egg predation by peripheral males is common and occurs following almost one-quarter of spawning events (Blanchfield and Ridgway 1999). Here, we provide further detailed analysis of the spawning behaviour of dominant male brook charr using previously recorded spawning events (Blanchfield and Ridgway 1999) to test whether males which have had the potential to lose paternity by peripheral males show a corresponding reduction in paternal effort. ‘Perceived paternity’ in this case is quantified as the number of peripheral males rushing into the nest at the time of spawning, which dominant males can visually assess for a given spawning event and therefore gauge the

potential for loss of paternity (Neff 2003). Because male reproductive success is related to spawning frequency in this group of fishes, we use the intensity and amount of time spent in post-spawning defence as measures of paternal effort (Kawase and Nakazono 1995). In addition, we examine whether other factors that may increase mating opportunities for dominant males (body size and number of active females) influence the post-spawning defence of females. Lastly, we assess the potential costs to males by remaining with females after spawning through an examination of mate-searching behaviour by mobile males across the spawning area. Here, the number of sites and females visited during these focal male observations represent a loss of information on female spawning readiness or mating opportunities.

## Methods

### Field observations

We individually marked and followed the reproductive behaviour of most individuals in a lake-spawning population of brook charr (Scott Lake, Ontario; 45°29′N, 78°43′W) on a daily basis over two spawning seasons (1994 and 1995). Fish were captured prior to spawning using trapnets, and thereafter with dip nets by swimmers. Individual fish were anaesthetized with tricaine methanesulfonate (MS 222), measured for fork length (FL, to the nearest mm), weighed (nearest 10 g, Pesola™ 2.5 kg scale) and a T-tag (Hallprint Co., Australia) was inserted just below the dorsal fin of the fish, to which we applied a uniquely coded disc to allow for individual identification (for complete details of the study site, fish tagging, and field methods see Blanchfield and Ridgway 1997). Eighty-two and 127 brook charr were tagged in 1994 (47 females, 35 males) and in 1995 (47 females, 80 males), respectively.

The main brook charr spawning area of Scott Lake is ~350 m in length, which we monitored by swim surveys four times daily (weather permitting) using drysuits, mask and snorkel. We mapped the location of spawning sites used by female brook charr using a combination of permanent shoreline markers and markers placed at the spawning site (Ridgway and Blanchfield 1998). During each census swim, we recorded the location of individual males and females

on the spawning grounds (Blanchfield and Ridgway 1997). For females, we also determined their reproductive activity (i.e. nest construction, spawning behaviours or covering of eggs, Jones and Ball 1954; Tautz and Groot 1975). Census swim data were used to assess the number of active females on the spawning grounds at the time closest to when spawning events were captured on video, as well as to determine the extent to which male charr surveyed the entire spawning grounds during focal male follows (see below). We determined the latency between consecutive spawnings for marked females using both video recordings and observations of female behaviour during the census swims to determine the timing of spawning (Blanchfield and Ridgway 1997).

#### Video observations

We videotaped the spawning behaviour of brook charr during autumn 1994 and 1995 (Blanchfield and Ridgway 1999). The video camera (Sony® Hi-8 with Amphibico® under-water housing) was placed on the bottom and within 1 m of the spawning fish and left there until the batteries or videotape expired. We were selective in the video records we used for analysis. It was essential that we could clearly observe the actual spawning (i.e. behaviours associated with spawning, including simultaneous gaping and quivering of the male and female during the release of gametes, Tautz and Groot 1975), as well as the behaviour of all competitors prior to, during and after the spawning. Twenty spawnings met these criteria, 16 of which we were able to determine the timing of gamete release (based on observations of gaping) of both the female and dominant male.

We analysed video records of spawning events for the frequency and duration of interactions by the dominant male 5 min immediately prior to and after spawning using The Observer® (v. 3.0) software (Blanchfield and Ridgway 1999; Blanchfield et al. 2003). We focused our analysis on the following dominant male behaviours associated with female defence and courtship: (1) cross-over—male remains in close proximity to the female (<30 cm) and prevents access to the female by other males, (2) chase—male aggressively charges another male (including bites), (3) threat—male lateral displays at or attempts to charge other males and (4) quiver—male quivers laterally against female. We quantified the proportion of time spent in

cross-over and chasing, and the frequency of threats and quivers by the dominant male. Previous studies have examined the frequency of chases; however, to account for variation in male chasing behaviour (i.e. few long chases versus many short chases) that can be influenced by the number of peripheral males surrounding the nest, we chose to present the proportion of time spent chasing other males. We compared the intensity of pre- versus post-spawning behaviours by the dominant male using paired *t*-tests. Proportion data (cross-over and chase) were arcsine transformed and frequency data (threat and quiver per 5 min) were log<sub>e</sub> transformed prior to statistical analyses. We examined whether any change in the behaviour of the dominant male before and after spawning (change in behaviour = pre-spawning behaviour – post-spawning behaviour) was related to the number of peripheral males rushing into the nest at the moment of spawning using correlation analyses.

The total time males spent post-spawning mate guarding was recorded from the moment of spawning until the dominant male left the female for a period of greater than 2 min. For five spawning events, the videotape recording ended while the dominant male continued to mate guard. Four of these five spawnings did not involve peripheral males rushing into the nest at the moment of spawning and thus our estimate of time spent mate guarding for this group may be an underestimate. One spawning included a male rushing into the nest at the moment of spawning. The time spent mate guarding for this spawning (12 min) was within one standard deviation of the mean for other spawnings which had one male rush into the nest during spawning (19 ± 10 min). We have included these data in our analysis, using the duration of time dominant males were present with females when the video ended as a minimum estimate of mate guarding by these males.

We tested for differences in the time spent guarding by dominant males spawning solely versus with multiple males (*t*-test). The relationship between parental care (time spent mate guarding) and certainty of paternity, which we define as the number of males rushing into the nest during a spawning event, was tested with forward stepwise multiple regression. We included two other variables that can influence time spent mate guarding by dominant males; dominant male body size and number of active females present on the spawning grounds at the time closest to when the spawning occurred

(determined from the daily transect swims, see above). Lastly, we compared the time spent guarding by dominant males with increasing numbers of peripheral male participation (0, 1,  $\geq 2$ , ANOVA). All data were natural log-transformed. For dominant males in which body size was unknown, we estimated fork length (to the nearest 50 mm) based on the size of marked individuals present on the video records.

### Male mate-searching behaviour

To understand the potential costs associated with post-spawning protective behaviour by dominant males, we conducted focal observational swims to determine the number of sites and females visited by mobile males during a 30-min period. Observations of male movements were conducted over the period of peak spawning activity (26 Oct.–10 Nov., 1995). We selected focal males that were initially observed moving between spawning sites. One assumption implicit to this work is that all male movement is a result of searching for mates. The prediction that small males move as a result of takeovers still assumes a choice to move rather than to remain at a given spawning site as a peripheral male. During each 30-min observation period, the sites visited by the focal male and the presence and activity (see above) of spawning females at those sites were recorded on underwater slates. In total, 59 focal male observations were conducted; however, males that we were not able to observe for periods of about 30 min (i.e. usually lost) or showed no movement between sites were excluded from the analysis. Also, we included only one observation period per male. Twenty observations of individual males met the above criteria. We standardized the total number of sites and females visited by males to account for variation in the 30-min observation period for individual data but used the raw data for frequency distribution plots.

## Results

Peripheral males were present around the spawning pair for all but three of the twenty spawning events captured on video. When present, up to eight peripheral

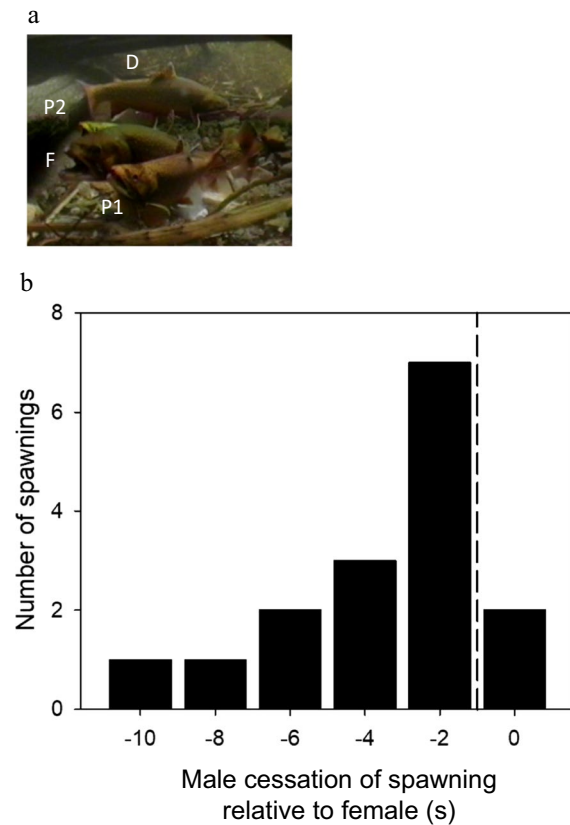
males were in close proximity to the spawning pair. More than half (55%) of all observed spawning events involved peripheral males diving into the nest at the moment of gamete release by the spawning pair (see also Blanchfield and Ridgway 1999).

Our estimate of perceived paternity is based on whether dominant male brook charr are able to determine if peripheral males have rushed into the nest at the moment of spawning. The behaviour of dominant males, observed from video records, suggests that they can assess whether other males have been present in the nest during gamete release. In all spawning events, the dominant male immediately turned and looked into the nest after releasing milt (Fig. 1a). For spawnings where we were able to assess the timing of gamete release by the spawning pair, the dominant male ceased gamete release prior to the female in almost all of these (14 of 16; Fig. 1b). On average, dominant males ceased spawning 3 s (range: 0.4–8.1 s;  $n=14$ ) before females. For two of the recorded spawnings, dominant males continued milt release for  $\sim 0.5$  s after the female had ceased gamete release (Fig. 1b). The curtailing of spawning and immediate turning would allow the dominant male to ward off any later arriving males attempting to rush into the nest and to determine the number of males present in the nest at the time of spawning.

Dominant male brook charr exhibited aggressive behaviours towards peripheral males after spawning and with a similar intensity as prior to spawning (Table 1). The proportion of time that dominant males spent in close proximity to a female increased after spawning ( $P=0.035$ ; Table 1), whereas the proportion of time spent chasing other males, as well as the frequency of threat displays towards conspecifics, did not differ between pre- and post-spawning 5-min observation periods ( $P>0.05$ ; Table 1). Dominant males significantly reduced courtship behaviour, frequency of quivering, directed at females after spawning had occurred ( $P=0.012$ ; Table 1). Only three (15%) of the males exhibited quivering behaviour in the post-spawning period compared to thirteen (65%) in the pre-spawning period. Changes in the intensity of guarding behaviours (differences between pre- and post-spawning values) were not related to the number of peripheral males rushing in at the time of spawning (correlation:  $P>0.05$ ).

Dominant male brook charr remained with females for extended periods (mean: 17 min; range: 3–48 min) after spawning. Males which had other males rush into the nest at the moment of spawning guarded their mates





**Fig. 1** **a** A typical sequence of a spawning event by lacustrine brook charr, *Salvelinus fontinalis*, where multiple males are present. The dominant male guards and courts the female in an attempt to be the sole male spawning; peripheral males also compete with each other for location around the spawning pair. At the moment of spawning, the dominant male (D) and female (F) release gametes while varying numbers of peripheral males (P) present rush into the nest. The dominant male turns around immediately after he finishes spawning, often before the female has completed gamete release, and in doing so is able to witness the number and the extent to which peripheral males (P1 and P2) participate in the spawning event. **b** Dominant males ceased gamete release prior to females for most spawning events (14 of 16, left of the dashed line)

for shorter periods (mean  $\pm$  SE:  $11 \pm 2$  min,  $n=11$ ) than males which spawned solely with a female ( $25 \pm 5$  min,  $n=9$ ;  $t=2.5$ ,  $P=0.020$ ). We further elucidated the role of perceived paternity loss to dominant males versus other factors which might contribute to a decrease in the amount of time mate guarding using multiple regression ( $F_{3,16}=3.5$ ,  $P=0.040$ ,  $R^2=0.40$ ). Only the number of males rushing into the nest during spawning was significantly and negatively correlated to the amount of time spent on mate guarding after spawning (partial

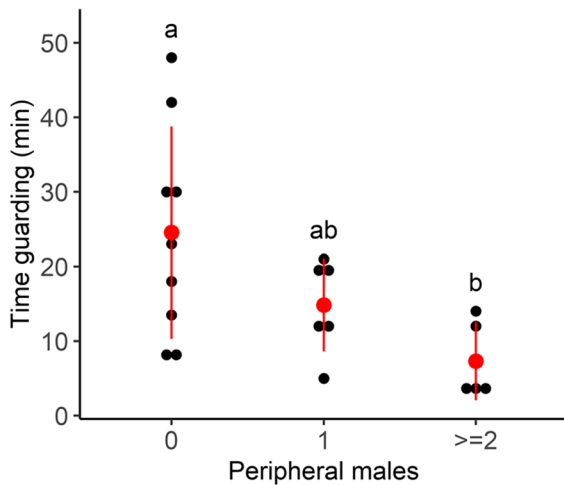
**Table 1** Behaviour of the dominant male during the 5-min periods immediately preceding (pre) and after (post) spawning determined from video records ( $n=20$ ) of a lake spawning population of brook charr, *Salvelinus fontinalis*. Data are means ( $\pm$  SE) compared with a paired  $t$ -test

Behaviour	Pre-spawning	Post-spawning	$t$	$P$
Proportion of time:				
Cross-over	0.66 (0.058)	0.80 (0.029)	-2.27	0.035
Chasing	0.099 (0.021)	0.12 (0.026)	-0.84	0.41
Frequency:				
Threats	8.2 (2.0)	6.2 (1.41)	1.35	0.19
Quivers	4.4 (0.95)	1.9 (0.80)	2.78	0.012

correlation:  $t=-3.0$ ,  $P=0.0091$ ). Neither the number of active females present on the spawning grounds at the time the spawning occurred (mean: 5; range: 1–18 females, partial correlation:  $t=-1.2$ ,  $P=0.26$ ) nor male body size (mean: 43 cm; range: 32–53 cm, partial correlation:  $t=-0.64$ ,  $P=0.53$ ) influenced the amount of time dominant males spent mate guarding after spawning. Peripheral male participation in spawning events reduced the amount of time dominant males guarded females (ANOVA:  $F_{2,17}=6.1$ ,  $P=0.010$ ; Fig. 2). Dominant males guarded females for significantly longer periods when no other males participated in gamete release than when two or more peripheral males had rushed into the nest during spawning (Tukey HSD unequal  $n$ :  $P=0.018$ ; Fig. 2).

Egg predation by peripheral males was observed in about one-third (30%) of the recorded spawning events. Duration of mate guarding by the dominant male was similar for spawning events with egg cannibalism ( $17 \pm 4$  min,  $n=6$ ) versus those spawnings where peripheral males did not consume deposited eggs ( $17 \pm 4$  min,  $n=14$ ;  $t=0.65$ ,  $P=0.53$ ). We estimated that females spent, on average, roughly one and a half days between consecutive spawnings (1994:  $1.3 \pm 0.1$  days,  $n=34$ ; 1995:  $1.4 \pm 0.1$  days,  $n=23$ ).

Focal animal observations quantified the extent to which males sampled among all available sites and females on the spawning grounds, which provided an estimate of missed opportunities by dominant males (i.e. cost) when they chose to remain and defend females. Male brook charr showed considerable movement among spawning sites as well as a frequent revisitation of sites. An example of one male's visits to spawning sites during a 30-min observation is shown in Fig. 3. On average, males visited 25 spawning sites (range: 12–43 sites) and encountered 12 females (range: 1–28 females) during



**Fig. 2** The duration of post-spawning mate guarding by dominant male brook charr with varying numbers of peripheral males rushing into the nest at the moment of spawning. Individual guarding times are shown for each spawning event (black dot) with means and standard deviation (red dot and line) shown for each group. Significant differences in time spent guarding by the dominant male among groups is indicated by different letters (Tukey’s post hoc test for unequal *n*)

the 30-min focal swims. Because these estimates include revisitation to sites, the numbers of different spawning sites visited (mean: 11; range: 5–19 sites) and individual females encountered (mean: 5; range: 1–11 females) were lower. Revisitation to sites and females by male brook charr was a common feature of male searching behaviour (Fig. 3). Twenty percent of all sites and females were visited only once by males, with repeated visits accounting for the majority (80%) of male-searching behaviour to spawning sites as well to females (Figs. 3, 4).

We compared the number of different females visited by males during the observation period to the number of available females. Available females were those that were present at spawning sites during the census swim nearest in time to the male observation period. Males visited almost one-third of the available females ( $29 \pm 4\%$ ) during a 30-min observation period, which was fewer females ( $5.1 \pm 0.6$ ) than were available ( $18.5 \pm 1.1$ ; paired *t*-test:  $t = -11.2$ ,  $P < 0.001$ ).

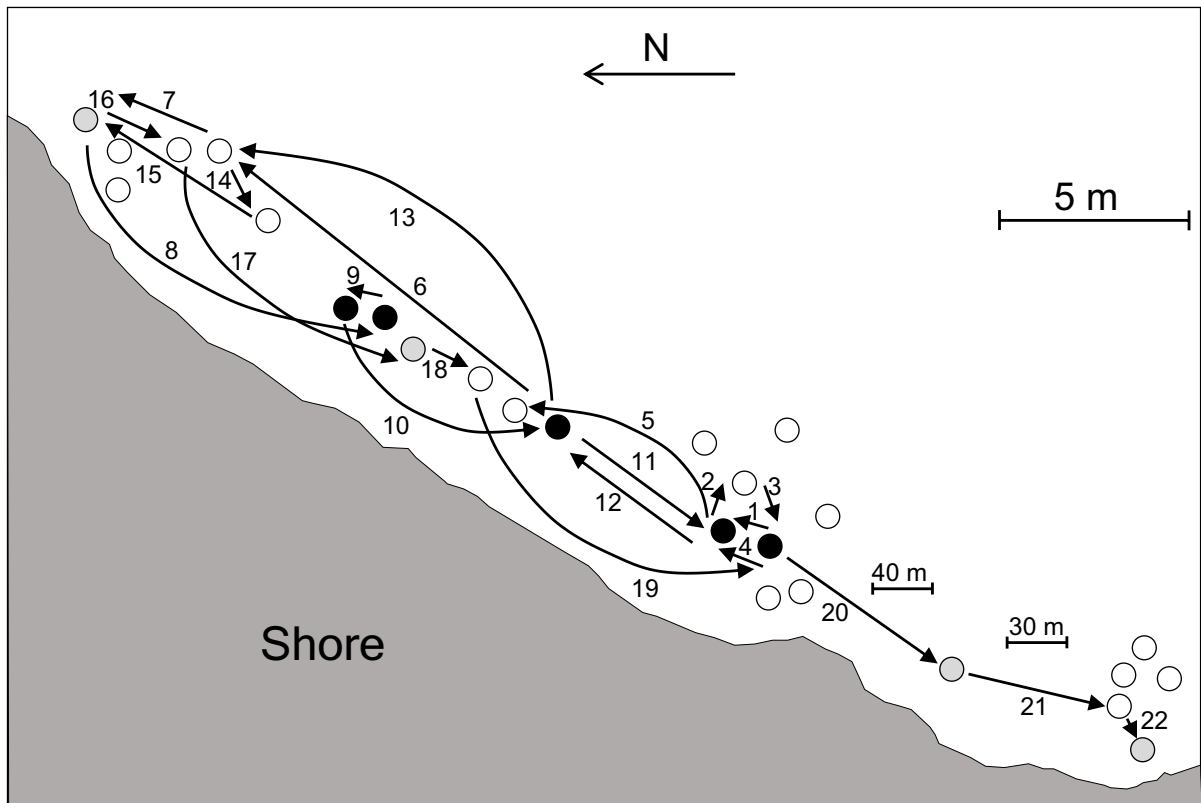
**Discussion**

Aggressive contests to acquire dominance with a spawning female, and sneaker tactics to acquire matings, have long been the focus of studies on male

salmonine reproductive behaviour (e.g. Jones and King 1949). The post-spawning behaviour of males, in contrast, has received very little attention beyond the general description that males leave spawning partners shortly after gamete release in search of other mating opportunities (Esteve 2005). Yet, studies have demonstrated that even brief paternal effort in the form of continued mate guarding by the dominant male after spawning may expedite the covering of the newly deposited eggs by females and thereby lessen the risk of egg cannibalism by peripheral males (Tentelier et al. 2011; Frye et al. 2021). Multiple-male spawning is common in this group of fishes (reviewed in Blanchfield et al. 2003), and here, we tested whether the paternal effort is related to perceived paternity by examining the intensity and duration of post-spawning mate guarding by dominant male brook charr. Based on predictions across a variety of taxa that cuckolded males should reduce paternal effort (Zimmermann et al. 2019), we find that duration of mate guarding is shorter for males with a lower certainty of paternity for this lake spawning population.

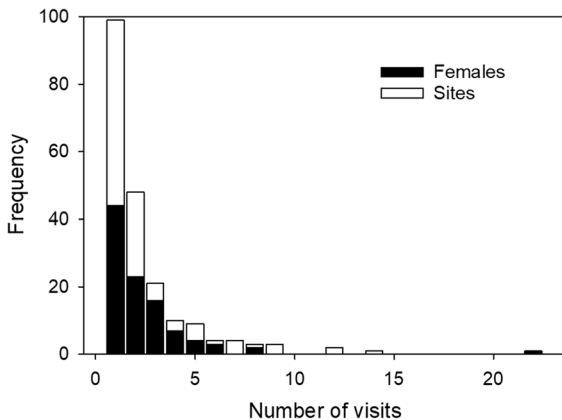
We observed a novel post-spawning behaviour exhibited by all dominant male brook charr, which involved turning around after spawning and immediately inspecting the nest—a behaviour that was preceded, in most instances, with the cessation of gamete release (gaping) prior to the female. To our knowledge, curtailing of gamete release and inspection behaviour by dominant males have not been documented in this group of fishes before. In experimental trials with bluegill sunfish (*Lepomis macrochirus*), nesting parental males used visual cues of sneaker males present in the nest during spawning to assess paternity (Neff 2003). We propose that the immediate post-spawning behaviours of the dominant male brook charr documented in this study would allow for direct visual assessment of the presence (and number) of peripheral males in the nest during gamete release and therefore represent a way for males to gauge the degree of cuckoldry, and perceived paternity, for a given spawning event.

Male brook charr that were dominant at the time of spawning continued to intensely guard females after spawning while reducing courtship behaviour. Post-spawning protective behaviour of the female by the dominant male was with equal or greater intensity compared to the minutes (5 min) leading up to spawning, when guarding against peripheral males



**Fig. 3** An example of the searching behaviour by an individual male brook charr during a 30-min observation period. This male visited 5 active females (solid circles), 4 non-active

females (shaded circles), 6 empty spawning sites (open circles) and covered a distance of ~ 160 m. Arrows indicate direction of movement (numbered sequentially)



**Fig. 4** The frequency by which searching male brook charr ( $n=20$ ) visited and revisited spawning sites (open bars) and females (solid bars) during 30-min focal swims (see Fig. 3)

is often most intense. Post-spawning female defence was examined for brown trout, where guarding by the dominant male was similar to pre-spawning, although

the number of chases showed a steady decline over the 5-min observation period (Tentelier et al. 2011). Although we chose to present our data as the proportion of time spent chasing by the dominant male, when presented as a rate, the average chase frequency of dominant male brook charr before (1.3 chases/30 s) and after (1.5 chases/30 s) spawning was similar to, although slightly greater than, that reported for brown trout (Tentelier et al. 2011). In our study, we found a marked reduction in the frequency of quivers directed at the female, a courtship behaviour, which underscores that post-spawning guarding of females by dominant male charr was not with the intention of seeking additional mating opportunities. In fact, multiple spawning on the same day by an individual female was uncommon for this population (9%), where the average time interval between spawning was longer than a day.

Previous studies of post-spawning mate guarding have been undertaken in salmonine populations



where egg cannibalism by peripheral males is widespread (> 20%, Tentelier et al. 2011; Frye et al. 2021). We had previously noted that egg cannibalism, which is common in our study population as well, occurred when small male brook charr were paired with relatively larger females and was not related to the number of peripheral males present during spawning (Blanchfield and Ridgway 1999). For brown trout, the greater number of chases by the dominant male immediately (2 min) after spawning decreased the probability of egg predation by peripheral males, although this effort was not influenced by the occurrence of multiple mating (Tentelier et al. 2011). Frye et al. (2021), who observed that most (75%) dominant male Arctic charr show post-spawning protective behaviour (i.e. aggression) in a population with a high incidence of egg cannibalism (~50%), suggested that the high investment by dominant males in courtship and fertilization may explain why males do not adjust the intensity of protective behaviour when multiple males have participated in spawning. Thus, the immediate post-spawning protection of the female and site, which has been long observed among salmonine fishes (e.g. White 1930), can be beneficial to dominant males in terms of reducing predation on eggs that they likely have fertilized based on a first male spawning advantage (Blanchfield et al. 2003). Given the brevity of this post-spawning effort (a few minutes), short-term guarding by males represents an insignificant cost in terms of lost mating opportunities with a potentially large benefit for the current brood (i.e. not consumed). Perhaps not surprisingly, then, there is little evidence of an adjustment in the intensity of immediate guarding behaviour by dominant males even with direct visual cues of paternity uncertainty.

Our work shows that male brook charr that were dominant at the time of spawning remained with females for extended periods after spawning. Dominant males guarded spawning partners for an average of 17 min, which is much longer than the few minutes males have typically been observed to remain with females before desertion (e.g. 1–2 min, Keenleyside and Dupuis 1988). We found that the duration of guarding was variable (3–48 min) and appeared to be related to a dominant males' perceived paternity, such that males spent less time guarding females when greater numbers of peripheral males had rushed into the nest at the moment of spawning. Other variables that are known to increase mating opportunities for salmonine fishes, such as larger

male body size (Fleming and Gross 1994; Quinn and Foote 1994) or greater numbers of active females on the spawning grounds (Quinn et al. 1996), did not influence the duration of guarding by dominant male brook charr. Together, these observations indicate that the decision by dominant males to remain with a female after spawning was not due to an absence of other mating opportunities. Past studies of post-spawning mate guarding have not examined the duration of guarding by the dominant male (e.g. Tentelier et al. 2011; Frye et al. 2021), which, as we discuss further, may be a more reliable indicator of paternal effort given the trade-off to seek other mating opportunities; a critical choice when male reproductive success is measured through spawning frequency (Fleming and Gross 1994).

Focal observations of male brook charr provide an estimate of the costs to males by remaining with females as opposed to searching for other mating opportunities. Males visited roughly one-third of the females on the spawning grounds in a span of half an hour, with an extensive revisitation of sites and females (80% visited more than once) being a key tactic to determine female readiness to spawn. We note that our data on mate searching includes only males that were mobile for the entire 30-min observation period; males that took residence at a specific nest site during the observation period were not included. The fact that some fish found a site to remain at in such a short time period is further support that post-spawning guarding is a cost to those males. Wide-ranging movements across the spawning grounds, including repeated visits to spawning sites and females, appear to be key elements that inform male spawning decisions for this population of brook charr. The decision to engage in extended post-spawning female defence by dominant males, therefore, comes at a cost of acquiring spatio-temporal information on female readiness to spawn that could result in lost mating opportunities, especially during periods of peak activity (~2 weeks) when > 80% of annual spawning can occur (4–17 spawnings by the population per day, Blanchfield and Ridgway 1997).

Reasons for extended male defence by brook charr are not entirely clear at this point. Among salmonines, female charr, *Salvelinus*, are known to have a unique undulating behaviour associated with the initial covering of newly deposited eggs (described as a “postnuptial dance” by Power 1980) that differs from the regular “cutting” or digging behaviours used in the creation

of an egg pocket and the later stages of egg covering (Power 1980; Esteve 2005). This telltale egg-covering behaviour may make charr more susceptible to egg predation by peripheral males, as well as to other egg predators that happen to be in the vicinity, and could warrant extended protection by the dominant male. Although we did not specifically examine the duration of undulating behaviour by females in our study, it has been reported to last for 5–20 min for brook charr (Power 1980), but only a few minutes in other charr species (see Esteve et al. 2011). Thus, one possible explanation for the prolonged post-spawning guarding by dominant males may be related to the extended undulation behaviour of female charr. However, given that egg cannibalism has generally been observed to occur almost immediately after egg deposition (Aymes et al. 2010; Frye et al. 2021), extended guarding by the dominant male may not be beneficial.

Post-copulatory mate guarding is prevalent among many internally fertilized organisms, where this reproductive tactic primarily serves to prevent other males from mating with the guarded female as well as to protect the female from predators (e.g. Jivoff 1997). Relating paternity to the paternal effort has been a challenge, especially in taxa where males have less reliable cues to gauge their confidence of paternity (e.g. Hunt and Simmons 2002; Moura et al. 2021). In addition, the paternal effort may not be related to the immediate reproductive event under observation, but instead, accrue future benefits for males. For example, Zimmermann et al. (2019) found that in a socially monogamous, cichlid fish (*Variabilichromis moori*), whose young are cared for by both parents, males were less responsive to threats against offspring than their territories, the latter being more important for future reproductive success. For iteroparous species within the salmonine group of fishes, individual males can spawn repeatedly with a given female within and among spawning seasons. Females impart some control over which male they will spawn with, by delaying spawning when paired with relatively smaller males and thereby allowing larger males to assume dominant positions (Schroder 1981; Blanchfield and Ridgway 1999). The willingness by the dominant male to engage in extended guarding of the female may be indicative of male quality which could influence future mating opportunities.

Noakes (2008) described charrs as “enigmatic fishes” that “are highly variable in almost every aspect of their behaviour”. And while the salmonines are one of the most well-studied groups of fishes, especially when considering their reproductive behaviour, there is still much to learn (Muir et al. 2012). Here, a detailed analysis of spawning by brook charr revealed several distinct and previously unreported behaviours by the dominant male. First, males curtailed spawning ahead of the female and immediately inspected the nest, often while the female was still spawning. Second, males stayed with females for extended periods of time. Third, males were highly mobile and showed extensive site revisitation in their search for mating opportunities. Here, we propose that the behaviour of males during spawning allowed dominant males to assess the degree of cuckoldry by peripheral males, and they adjusted their time spent guarding according to their perceived paternity. We also highlight that mate guarding by males may be an important but overlooked aspect of salmonine mating systems that is perhaps most pronounced among iteroparous species in populations with high incidence of egg cannibalism and deserves further investigation.

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**Declarations**

**Ethics approval** The research presented here was described in Animal Utilization Proposal No. 95–08 approved on 11 Octo-

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**Consent to participate and publication** All authors participated in this study and consent to its publication.

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