

LETTER

Exclusive male care despite extreme female promiscuity and low paternity in a marine snail

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Abstract

Males exhibit striking variation in the degree to which they invest in offspring, from merely provisioning females with sperm, to providing exclusive post-zygotic care. Paternity assurance is often invoked to explain this variation: the greater a male's confidence of paternity, the more he should be willing to provide care. Here, we report a striking exception to expectations based on paternity assurance: despite high levels of female promiscuity, males of a marine snail provide exclusive, and costly, care of offspring. Remarkably, genetic paternity analyses reveal cuckoldry in all broods, with fewer than 25% of offspring being sired by the caring male, although caring males sired proportionally more offspring in a given clutch than any other fathers did individually. This system presents the most extreme example of the coexistence of high levels of female promiscuity, low paternity, and costly male care, and emphasises the still unresolved roles of natural and sexual selection in the evolution of male parental care.

Keywords

Conflict, gastropod, mating system, parental care, paternity, polyandry.

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INTRODUCTION

One of the cornerstones of the theory of parental care is that, all else being equal, the greater a male's confidence of paternity, the more he should be willing to invest in post-zygotic care of offspring (Clutton-Brock 1991). Consistent with this prediction, several experimental studies have shown that males adjust care according to their perceived paternity (Neff & Gross 2001; Neff 2003; Mehliis *et al.* 2010). Variation in patterns of paternal care across species also reveals the expected positive relationship between average paternity and paternal investment (Moller & Cuervo 2000; Arnold & Owens 2002). In principle, to the extent that male care entails the loss of future mating opportunities, the benefits accrued by a caring male from increased offspring fitness must outweigh the costs to his residual reproductive value (Queller 1997; Alonzo 2010).

Despite being taxonomically widespread, exclusive male care is the rarest form of post-zygotic parental investment (Clutton-Brock 1991), presumably because males in most species maximise their reproductive success by deserting females and acquiring additional matings. In previously described examples of exclusive male care where paternity has been characterised, including fishes (Jones *et al.* 1999, 2001), sea spiders (Barreto & Avise 2008), isopods, amphipods, polychaetes (Reish 1957) and giant water bugs (Smith 1979), males exhibit a variety of pre- and post-mating behaviours, such as mate guarding, that eliminate or severely reduce cuckoldry in their broods. This ensures that males are maximising their immediate genetic benefits of caring by privatising care-giving behaviours towards their own offspring.

In other settings, the social system can introduce uncertainty in a given male's paternity, especially where males guard nesting sites that successive females visit (Birks 1997; Emlen *et al.* 1998). In bluegill sunfish, for example, 'sneaker' males trespass on nest sites during spawning and release viable sperm without providing parental care (Neff 2003). Nevertheless, in all of these cases, average paternity of the caregiver consistently exceeds 70%, and males in these taxa might pay relatively low mating costs, as territoriality

itself can lead to increased mating opportunities (Ah-King *et al.* 2005). Where females prefer males that demonstrate care-taking abilities, either through nest building (Soler *et al.* 1998) or the presence of eggs in their nests (e.g. Marconato & Bisazza 1986; Knapp & Sargent 1989), such preferences can lead to the evolution of male care even in the absence of high paternity (Alonzo 2012).

Gastropod molluscs exhibit a variety of parental care behaviours, from brooding offspring in modified pouches (Hull *et al.* 1999) to the production of egg capsules attached to the benthos (Pechenik 1986); however, males typically provide no post-zygotic investment in offspring. The marine snail *Solenosteira macrospira* presents a remarkably different scenario, in which females apparently oviposit exclusively on conspecific males and are incapable of ovipositing on themselves (Berry 1957; Houston 1978; Fig. 1). Despite extensive sampling at multiple sites throughout the mating season, we have never observed females carrying egg capsules (Table S1; Fig. S1; see also Houston 1978). By the end of the annual reproductive season, the shells of virtually all males are completely covered by egg capsules, which they carry for up to a month. Within the fluid-filled capsules, trophic egg and embryo cannibalism represents a major source of maternally derived nutrition for developing offspring. Explicit genetic analyses of gastropod mating systems are rare, although the limited available evidence suggests that multiple mating is common, and that clutches contain multiple patrilines (Gaffney & McGee 1992; Paterson *et al.* 2001; Panova *et al.* 2010; Brante *et al.* 2011). However, multiple paternity in species with male care represents cuckoldry, which care-giving males should be selected to prevent (Coleman & Jones 2011). This raises the question of whether male care in *S. macrospira* is accompanied by extensive cuckoldry or whether paternity assurance mechanisms prevail.

In this study, we experimentally manipulated egg-capsule load in *Solenosteira macrospira* to determine whether carrying egg capsules is costly to males, and therefore constitutes parental investment. We then used microsatellite markers to quantify parentage and brood composition and to ask whether the mating system of *S. macrospira* differs substantially from the polyandrous mating system character-



Figure 1 Male (left) and female (right) *Solenosteira macrospira*. The male's shell is completely covered with egg capsules. Photograph courtesy of P.B. Marko.

istic of other gastropods that lack male parental care. We also characterised temporal variation in patterns of paternity by comparing parentage across broods in different stages of development. Our results show that exclusive and costly male parental care occurs despite considerable female promiscuity and very limited paternity within cared-for broods.

MATERIAL AND METHODS

Study system

Solenosteira macrospira is an omnivorous marine whelk in the family Buccinidae (Houston 1978), native to sandy mudflats of the northern Gulf of California. Females and males are polygamous, with a reproductive season that extends from February to June. Females are internally fertilised, and package their offspring in chitinous capsules, each containing ≈ 250 eggs. Mating pairs of *S. macrospira* remain side-by-side, often for several hours or more, with the female repeatedly extending her foot and head to deposit egg capsules on the male's shell. Females typically lay 4–31 (mean = 18.3 ± 13.2) capsules per clutch. Females produce multiple clutches during the reproductive season, and males carry clutches from several different females (mean = 3.2 females, range: 2–5), which can be distinguished by differences in colour, morphology, and developmental stage of the embryos. Male parental care in *S. macrospira* is essential for offspring survival as it reduces thermal and desiccation stress during low tides, keeps egg masses from becoming progressively buried and anoxic (Houston 1978) and reduces tumbling and abrasion of egg capsules (personal observations). About 1 month after oviposition, 3–10 crawl-away hatchlings emerge from each capsule. Given that males carry capsules at different stages of development, the period of care likely extends over several months. We have never observed males attempting to remove capsules, nor have we seen freshly laid capsules superimposed over older ones. Once offspring emerge, however, capsules deteriorate in the time between reproductive seasons.

Measuring costs of parental care

To estimate the costs of egg-carrying by *S. macrospira*, we collected 169 male and 200 female adults in April 2004 from a 500-m-long site 2 km north of San Felipe (Baja California, Mexico). We collected only those males completely covered by egg capsules; none of the females had any egg capsules. We used a non-toxic marine-grade cyanoacrylate adhesive to attach uniquely numbered, colour-coded Floy® (Floy Tag Inc., Seattle, WA, USA) shellfish tags to all individuals, then weighed each snail on a digital balance, after blotting it with dry paper towels. We then removed all egg capsules from the males, and re-weighed each individual. The males and females were then randomly divided into a control and experimental group. The controls were left unmanipulated; in the experimental males and females, we used the same non-toxic glue to attach enough egg capsules on to each snail's shell so that they were completely covered. We then weighed each of the experimentally treated individuals. Both control and experimental snails were tethered in the field with a 2-m length of monofilament fishing line (tested to hold 8 kg) knotted through a small hole drilled near the aperture of the snails' shell, and anchored to the substrate with a U-shaped 40-cm-long stainless steel rod. After 14 days in the field, we recovered 70% of the originally tethered snails and re-weighed them, allowing us to calculate net change in mass over the course of the experiment. Using initial body weight as a covariate, we performed a two-factor ANOVA using sex and capsule presence as fixed factors to assess the treatment effect on the change of body weight. We assumed that any changes in snail mass over the course of the field experiment reflected the effects of the experimental manipulations of egg capsules themselves, and were not due to the effects of glue *per se*. The total mass of adhesive used to attach the capsules to each individual contributed less than 5% of the total weight of the reattached capsules (i.e. on the order of several capsules). Moreover, comparable adhesives have never been reported to affect snail performance, especially in open field systems where any toxic effects would be quickly diluted (E. Carrington and D. Padilla, pers. comm.). Finally, we performed control experiments on another predatory whelk of similar size (*Nucella ostrina*), where we compared growth rates of glue-covered vs. uncovered snails ($n = 20$ snails per treatment). We found no significant effect of the glue on the change in mass between the two groups.

Genetic analysis of paternity and brood composition

We collected 287 adult male and female *S. macrospira* from Bahia de las Chollas, near Puerto Peñasco (Sonora, Mexico), in May 2005 to estimate baseline population allele frequencies, and 15 egg-carrying snails (all males) in April 2005 for paternity analysis. All snails were transported in coolers and returned alive to UC Davis. We genotyped approximately 90 offspring from each of the 15 males ($n = 1326$ total offspring from 43 different clutches) at six microsatellite loci (Table S2). We assumed that each visually distinguishable clutch on a male's shell was produced by a different female, and we sampled clutches from two to four females per male (Table S3). We categorised each clutch as being composed of either early-stage (pre-veliger) or late-stage (veliger) embryos. We also genotyped all of the offspring from a subset of six clutches to determine the full extent of female promiscuity. Each clutch was taken from a different male's shell and corresponded to a unique female. In addition to genotyping, the developing embryos, we were able to genotype hatchlings collected

from 5 of the 15 males. These hatchlings were found crawling around the shell of the care-giving male.

We extracted genomic DNA from ethanol-preserved muscle tissue following the cetyltrimethyl ammonium bromide (CTAB) protocol described in (Grosberg *et al.* 1996). All PCRs were performed in 15 μ L volumes using a GenAmp[®]9600 thermocycler (Applied Biosystems, Carlsbad, CA, USA). PCR mixes consisted of 1.5–30 ng of template DNA, 1x PCR Buffer, 2.5 mM MgCl₂, 0.2 mM dNTP (Promega, Madison, WI, USA), 0.1 mg/mL bovine serum albumin (BSA, NEB), 0.25 μ M forward and reverse primers, 0.6 U of AmpliTaq[®] DNA polymerase (Applied Biosystems). The cycling protocol consisted of an initial denaturation step of 3 min at 94 °C, followed by 35 cycles of 94 °C denaturation for 30 s, annealing at 49 °C for 30 s and extension at 72 °C for 30 s. PCR products were run on an ABI Prism 3100 Capillary Electrophoresis Genetic Analyzer and analysed using the GeneScan software (Applied Biosystems, Carlsbad, CA, USA). Fragment data were visualised and scored using STRand Version 2.3.69 (Toonen & Hughes 2001).

Paternity analyses

With the complete data set of 15 males and 1326 offspring, we used COLONY (Wang 2004) to reconstruct sibships, to infer maternal genotypes for all 43 clutches and to infer the number of sires per clutch. We ran the analyses five times varying the random seed generator and the error rate; results did not vary across replicates. In addition, we ran the analyses assuming no *a priori* information about the number of mothers on a given male's shell, allowing the programme to independently estimate the number of contributing females. This was done to validate our assumption that visually distinguishable clutches corresponded to different females. We also ran the above analyses on the subset of females ($n = 6$), for which all the offspring were genotyped.

The next step of the analysis involved using the reconstructed maternal genotype obtained from COLONY and the egg-carrying male's known genotype to estimate his share of the paternity. We used the population allele frequencies and equation (9) in Neff *et al.* (2000). We also estimated paternity using a more conservative model, which only uses the egg-carrying male's genotype [see the two-sex paternity model in Neff *et al.* (2000)]. For the hatchlings, we estimated the caring male's paternity using the two-sex paternity model, because we could not be sure that all individuals came from the same mother. The exclusion probability (the power of a locus to genetically exclude candidate individuals as parents) for all six microsatellite markers combined was 0.9931. We used linear regression analyses to test for a relationship between male body size and total paternity. We used a single-factor ANOVA to test for differences in paternity across developmental stages and Student's *t*-test to test for differences in paternity between the care-giving male and the next most successful male.

Estimating relatedness

We determined the relatedness (r) among siblings within a capsule using the program STORM (Frasier 2008). This method was chosen out of the many available approaches for calculating relatedness because it is unbiased, it is never undefined and it consistently performs well in a variety of situations, and often outperforms all other estimators (see Frasier (2008) and references therein). In the absence of inbreeding, the expected value of r for (1) unrelated individuals, (2)

parent-offspring or full-sibs and (3) half-sibs is 0, 0.5 and 0.25, respectively. We used linear regression analysis to test for a relationship between within-clutch relatedness and the number of sires. Where applicable, results are presented as means \pm standard deviations.

RESULTS

Costs of parental care

The capsules of a fully covered male represent approximately 40% of a male's wet mass (mean weight before capsule removal: 11.29 \pm 1.32 g; weight after capsule removal: 7.02 \pm 0.85 g, $n = 139$). Controlling for initial body size, we found a significant negative effect of capsule presence on the change in snail weight ($F = 12.36$, $P < 0.001$), which corresponded to a loss of approximately 8% of body mass. We also found a significant effect of sex on change in weight ($F = 58.46$, $P < 0.001$), with manipulated males losing more weight than manipulated females (Fig. 2). There was also a significant interaction between capsule presence and initial weight ($F = 5.00$, $P < 0.03$), because snails with capsules were all heavier than snails without.

Distribution of paternity

The results of the paternity analysis were striking: on average, males sired only 24% of the offspring they were carrying. Paternity estimates varied widely among clutches, but never exceeded 61% (range: 1–61%, which was found in 1 of 43 clutches; Table S3). There was no significant relationship between male body size and his proportion of clutch paternity ($R^2 = 0.09$, $P = 0.29$). In fact, a given male could be simultaneously caring for the offspring of over 20 different males (Fig. 3). Paternity of the care-giving males was significantly higher than the paternity of the next most successful males (*t*-test: $t = 4.06$, $P < 0.05$).

The whole-clutch analyses of paternity revealed that female *S. macrospira* are highly promiscuous, mating with 13.2 \pm 2.1 males in a

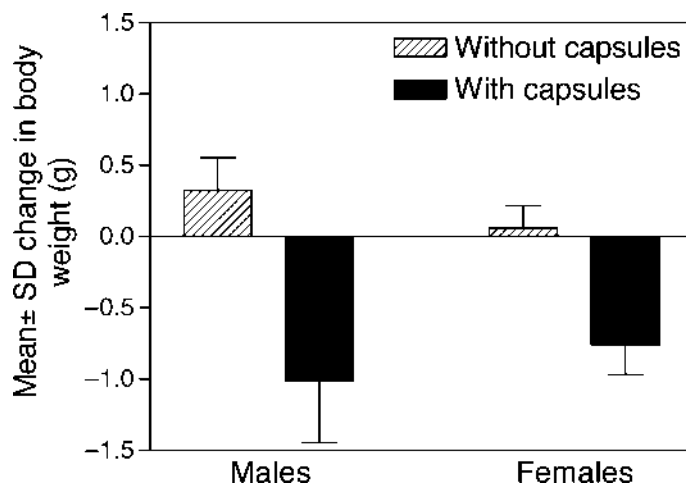


Figure 2 Mean \pm SD of the change in body weight, with and without experimentally attached egg capsules on males' and females' shell in the snail *Solenostrea macrospira*. Hatched bars represent individuals without egg capsules on their shells, and black bars represent individuals with experimentally attached egg capsules.

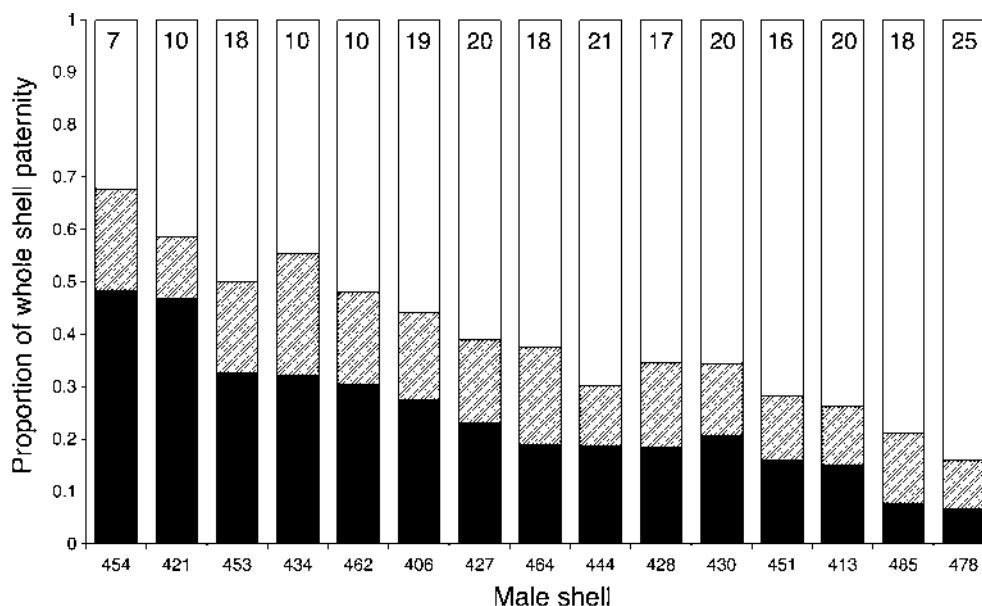


Figure 3 Paternity breakdown for individual male *Solenosteira macrospira*. Black bars represent the caring male's own proportion of total paternity, grey bars represent the proportion of paternity for the next most successful male and white bars represent the proportion of paternity for all other males that sired offspring on that shell. The number of sires included in the final group is indicated.

single breeding season (Table 1). Because of the high degree of multiple mating in *S. macrospira*, the number of males that sired offspring in a given egg capsule ranged between one and six (mean = 2.9 ± 1.1), and this number was negatively correlated with the relatedness of offspring within a capsule ($R^2 = 0.23$, $P < 0.001$).

Mean paternity for clutches with the early-stage veligers was 22% (95% CI: 13–32%), 29% (95% CI: 19–43%) for late-stage embryos and 44% (95% CI: 28–71%) for hatchlings. There was no significant difference in paternity between clutches containing early- and late-stage embryos, but paternity of the genotyped hatchlings was significantly higher than paternity in the early-stage clutches (ANOVA: $F_{2,45} = 4.79$, $P = 0.01$; Tukey *post hoc* test: $P < 0.05$).

DISCUSSION

This study confirms previous assertions (Houston 1978) that males alone provide post-zygotic parental care in *Solenosteira macrospira*. As demonstrated by the significant decrease in male body mass over the course of 2 weeks of caring for capsules, egg-carrying exacts substantial energetic costs. However, females in this species have

some of the highest documented levels of polyandry in an internally fertilised organism (Gaffney & McGee 1992; Paterson *et al.* 2001; Panova *et al.* 2010; Brante *et al.* 2011), with the number of sires per clutch ranging between 6 and 15. Consequently, more than 70% of the developing embryos that males care for are not their genetic offspring. Furthermore, male body size, which often correlates positively with copulation duration and sperm transfer in other species, did not predict paternity in our study (Simmons & Parker 1992). This coexistence of extensive female promiscuity and costly male parental care thus challenges general theoretical predictions of the expected relationships between mating system, parental care and relatedness.

Patterns of male care when paternity is high

In species where males carry eggs on or in their bodies, paternity is usually certain. One of the best known examples of this is male pregnancy in sygnathid fishes, where males are consistently the genetic fathers of their offspring (Jones *et al.* 1999). Male care has also evolved independently in at least 16 invertebrate taxa (Nazareth & Machado 2010; reviewed in Tallamy 2000, 2001). Notable among these are the pycnogonid sea spiders, in which uniparental care by males is widespread. In all species studied to date, the male grasps the female, with her gonopores held close to her partner. The eggs are fertilised either while the female still holds them or immediately after they have been deposited onto a male's ovigers. In genetic analyses of mating system in pycnogonids, there were no detectable instances of cuckoldry (Barreto & Avise 2008). In contrast, egg-carrying in the golden egg-bug *Phyllomorpha laciniata* appears to be a form of intraspecific parasitism. Females deposit eggs fertilised by another male on the current male's back prior to mating, which seems to be the price he pays to acquire a copulation (Kaitala & Kaitala 2001).

Table 1 Number of sires per clutch and average paternity of the caring male from six clutches with all offspring sampled

Female clutch ID	N offspring sampled	Proportion of offspring sired by caring male	No. of sires
b427_1	63	0.25	14
b427_3	71	0.27	15
b444_3	79	0.23	14
b406_3	76	0.16	11
b454_3	80	0.26	10
b413_1	81	0.15	15

In other systems, however, males adopt a strategy that involves guarding nests or territories (Coleman & Jones 2011). This strategy is common in many cichlids and sticklebacks, as well as arthropods, in which males build nests and tend developing broods (Clutton-Brock 1991; Tallamy 2001). In these cases, the rate of multiple paternity is often skewed, with most species having low rates of cuckoldry. That is, nest-defending males are usually the true sires of most of the offspring in their nests.

Patterns of male care when paternity is low

The above examples of paternal care assume that investment in current offspring decreases an individual's ability to invest in future offspring (Westneat & Sherman 1993), and that paternal care has evolved because the benefits accrued by a caring male from increased offspring fitness outweigh the costs to his residual reproductive value. While many empirical studies support such a trade-off between parental and mating effort, there are several instances where such a trade-off appears not to exist; that is, investments in parental care and mating effort do not conflict (Stiver & Alonzo 2009). For example, females of some species prefer males whose nests already contain eggs (Marconato & Bisazza 1986; Porter *et al.* 2002), as it apparently indicates a willingness and ability to care for young (Kvarnemo 2006). This preference is often so strong that nest-guarding males may practice nest takeovers or egg thievery and care for offspring that are not their own (Tallamy 2000; Nazareth & Machado 2010; Coleman & Jones 2011). Indeed, recent theory predicts that if females are able to bias mating towards caring males, male care will evolve even when the probability of males caring for their own offspring is low (Alonzo 2012). Despite the theoretical plausibility of the coexistence of male care, low paternity and female promiscuity, *S. macrospira* provides one of the few, and perhaps only, empirical example.

Causes of female promiscuity

It remains unclear why female *S. macrospira* are so polyandrous. Previous studies have documented that lower relatedness among siblings can increase embryo survival, presumably because genetic variation among siblings reduces competition for resources (McLeod & Marshall 2009; Sagebakken *et al.* 2011). However, the high levels of documented promiscuity could be due to convenience polyandry, where females assume the costs of additional matings instead of expending time and energy attempting to reject harassing males (Panova *et al.* 2010). Given that the genotyped embryos in our study were all in the pre-hatching stages of development, we could not evaluate the effects of genetic diversity on embryonic traits or survival. However, sibling cannibalism and brood reduction are severe in *S. macrospira*, with sibling cannibalism increasing with increasing numbers of patriline present among embryos within a capsule (Kamel *et al.* 2010a). Females may mate with many males to maximise phenotypic and genetic variance among siblings, thereby increasing the scope for cannibalistic selection among offspring within capsules to yield the fittest survivors (Elgar & Crespi 1992). The fact that most surviving hatchlings were sired by a single male is consistent with a particular paternal genotype winning out over others. However, we also found evidence of last male sperm precedence, because caring males sired proportionally more offspring in a given clutch than any other fathers did individually. This simple

numerical advantage could have also lead to the increased representation of the caring male's genotype in the hatchlings.

Temporal increases in female promiscuity might also explain this pattern of high paternity among hatchlings. Given that the hatchlings represent the most advanced stage of development, the capsules we sampled were laid early in the season when females had potentially mated with fewer males. Paternity could then be higher simply by virtue of decreased sperm competition. However, paternity of the caring male was low among late-stage embryos as well; the increase occurred after offspring became cannibalistic. For now, we can only speculate as to why more of the caring male's offspring emerge as the survivors. It might be that fathers can skew hatching success in favour of their own young or that females choose a high-quality male to mate with last. Alternatively, this pattern could be generated by an age effect: older sperm could result in poorer offspring survival, so the offspring of the last male to mate would have higher survival, by virtue of being fertilised by younger sperm (Blount *et al.* 2001). What is clear is that understanding the causes of such promiscuity will be an important direction for future work.

Parental care as a constraint

The relationship between paternity and parental care also reflects the evolutionary history of a species. The simplest explanation here might be that, unlike in many other organisms (Kaitala & Kaitala 2001; Neff & Gross 2001), males cannot avoid caring for offspring. Throughout most of the reproductive season, virtually all males are covered with capsules; there does not appear to be a subset of cheater males that acquires copulations without providing the requisite caring behaviour. Interestingly, with the exception of *S. macrospira* and its congeners, all other cantharid gastropods attach their eggs to hard substrates in the intertidal (Houston 1978). The habit of attaching eggs to conspecifics may have evolved due to the limited availability of rocky substrate in intertidal areas of the northern Gulf of California, or as a way for adults to mitigate risks of predation or thermal stress on developing offspring in these warm, shallow, subtropical and tropical habitats. Males would be the primary targets for oviposition, given their proximity during copulation, and because conspecific females and heterospecifics would have no incentive to allow attachment of egg capsules. An inability for males to perceive or improve their paternity could underlie the persistence of this trait (Maynard Smith 1977; Westneat & Sherman 1993). However, it should not be forgotten that each caring male is likely to sire young in the subsequent mixed-paternity clutches a female produces, which should presumably improve the cost:benefit ratio of care. Indeed, it is possible that having offspring on other males' shells might be an effective form of bet-hedging from the focal male's perspective.

CONCLUSIONS

A clear view of the true winners and losers in this conflict over which parent assumes the burden of parental care requires a comprehensive understanding of the nature of sexual conflict over offspring care, including knowledge of the variance in lifetime reproductive success, an enormous challenge in many species, including *S. macrospira*, where a male's offspring may be distributed widely in space and time. Despite decades of extensive research on parental care, our work provides the most extreme example of the coexistence of high levels of female promiscuity, low paternity and

costly male care. The behaviours exhibited by *S. macrospira* serve as a reminder that observed patterns of parental care reflect not only parentage, but also the interdependent outcomes of ongoing conflicts of interest within and between the sexes, and between parents and offspring (Parker *et al.* 2002; Kamel *et al.* 2010b), along with phenotypic and genetic constraints on the expression and evolution of parental investment (Alonzo 2010, 2012).

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AUTHORSHIP

RKG designed the experiment and collected data. SJK collected and analysed data. SJK wrote the first draft of the manuscript, and both authors contributed substantially to revisions.

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