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Fitness conflicts and the costs of sociality in communal egg layers: a theoretical model and empirical tests

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Abstract

Individuals within complex social groups often experience reduced reproduction owing to coercive or suppressive actions of other group members. However, the nature of social and ecological environments that favour individual acceptance of such costs of sociality is not well understood. Taxa with short periods of direct social interaction, such as some communal egg layers, are interesting models for study of the cost of social interaction because opportunities to control reproduction of others are limited to brief periods of reproduction. To understand the conditions under which communal egg layers are in fitness conflict and thus likely to influence each other's reproduction, we develop an optimality model involving a brood guarding 'host' and a nonguarding disperser, or 'egg dumper'. The model shows that when, where intermediate-sized broods have highest survival, lifetime inclusive fitnesses of hosts and dumpers are often optimized with different numbers of dumped eggs. We hypothesize that resolution of this conflict may involve attempts by one party to manipulate the other's reproduction. To test model predictions we used a lace bug (Heteroptera: Tingidae) that shows both hosts and egg dumpers as well as increased offspring survival in response to communal egg laying. We found that egg-dumping lace bugs oviposit a number of eggs that very closely matches predicted fitness optimum for hosts rather than predicted optimum of dumpers. This result suggests that dumpers pay a social cost for communal egg laying, a cost that may occur through host suppression of dumper reproduction. Although dumper allocation of eggs is thus sub-optimal for dumpers, previous models show that the decision to egg dump is nevertheless evolutionarily stable, possibly because hosts permit just enough dumper oviposition to encourage commitment to the behaviour.

Introduction

Social living is often characterized by compromised self-interest. In many eusocial arthropods and vertebrates, for instance, worker individuals completely forgo their own reproduction in order to care for the offspring of others (Wilson, 1971; Emlen, 1991; O'Riain *et al.*, 2000). When worker individuals do gain reproductive status it is often under constraints enforced by other group members, such as when dominant individuals physically suppress subordinate reproduction (Roseler, 1991; Clutton-Brock & Parker, 1995; Queller *et al.*, 1997). Similarly, membership with good standing in human societies is contingent upon adherence to social norms and rules governing use of shared resources (Fehr & Gachter, 2002). Violation of norms and rules may elicit punishment (Boyd *et al.*, 2003) that curtails individual access to the benefits of sociality. Thus a paradoxical yet widespread feature of sociality is that group membership may entail acceptance of socially imposed constrains on individual fitness, or social costs.

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It is not immediately clear, however, how sociality remains evolutionarily stable despite potential conflicts over payment of social costs. If all else is equal, natural selection within groups favours individuals whose reproduction is least socially compromised. Moreover, competition to avoid social costs may weaken group functionality and thus threaten benefits of living in groups. An important challenge for evolutionary biology is to thus predict the ecological, genetic and morphological conditions under which sociality evolves when some individuals pay social costs.

Here we test the nature and magnitude of social costs in a relatively simple yet seldom-studied form of sociality. Communal egg laying is a taxonomically widespread social behaviour that occurs in birds (Vehrencamp, 2000), salamanders (Harris *et al.*, 1995) and insects (Tallamy, 1985; Zink, 2003). In communal egg layers two or more conspecific females lay eggs within a common space. Although some communal egg layers have complex nests structures and prolonged periods of social interaction (e.g. Vehrencamp *et al.*, 1986; Macedo & Bianchi, 1997; Haydock & Koenig, 2003), 'nests' within a subset of communal taxa are simple and may consist of no more than a scrape on the ground (Bertram, 1992), mosses on water's edge (Harris *et al.*, 1995), or unprepared host-plant foliage (Tallamy, 1985). In these species, eggs and young are usually guarded by fewer 'host' individuals than contributed eggs, suggesting strong asymmetries in parental effort between hosts and nonhosting, dispersing individuals (Zink, 2000,2001). Moreover, communal egg layers that do not inhabit long-lived and defensible nests have a relatively short duration of direct social interaction. Thus it would appear that opportunities for some egg layers to impose social costs on others might be limited.

We hypothesise, however, that in at least one communal egg-laying species, the eggplant lace bug *Gargaphia solani*, individuals incur social costs for at least three reasons. First, communal egg laying increases survival of *G. solani* offspring (Loeb, 2003) but these benefits are limited because very large broods have relatively low survival (Tallamy & Horton, 1990). Thus, total number of eggs per brood affects fitnesses of egg-guarding hosts and nonhosts that oviposit and then disperse from the brood, or 'egg dump' (Tallamy, 1985). Second, dumpers lay smaller clutches than hosts of similar genotypic and phenotypic quality (Loeb, 2003), a pattern that suggests conflicts over clutch size. And finally, reproductive suppression may occur through host aggression towards dumpers (Tallamy & Tallamy, 1993), one mechanism, which could explain persistence of small dumper clutches.

We use both analytical and empirical approaches to explore the nature of social costs and the potential for fitness conflicts over clutch size in *G. solani*. The model makes assumptions regarding key ecological and genetic factors affecting fitnesses of egg-guarding and egg-dump-ing individuals. We then use this model in combination with field-based parameter estimates of *G. solani* reproduction to predict the number of dumped eggs that maximizes inclusive fitnesses of both dumpers and hosts. To estimate the magnitude of social costs paid by egg dumpers and the range of clutch-size optima, we conducted controlled experiments that compared fecundity of females experimentally induced to guard or to egg dump. We then compared experimentally estimated clutch sizes to those predicted by the model to determine if observed values fall on or between predicted host and dumper optima. Observed divergence from one party's optimal dumper clutch size towards optimal clutch size of the other participant is potential evidence for reproductive conflict. The direction of conflict, in favour of either dumpers or hosts, further suggests the nature of social costs and the biological solution to conflict.

Materials and methods

Study system natural history

Gargaphia solani is distributed throughout the middle-Atlantic and middle-western regions of the USA in habitats where its native host plant, the horsenettle *Solanum carolinense*, is abundant. Horsenettle is a weedy herbaceous perennial that is common in disturbed areas such as old-fields, pastures and spoil areas. Adult *G. solani* over-winter in leaf litter in these same habitats and emerge in late spring to forage and oviposit on horsenettle. Eggs are laid on the abaxial surface of host foliage in a loosely arranged cluster that is one layer of eggs deep (i.e. eggs are not stacked on top of each other), and after hatching nymphs forage together in a dense aggregation.

Social behaviour of adult females is explained by density of conspecifics on the host plant and the presence of pheromonal cues. For instance, gravid females that are isolated and deprived of social interaction will eventually oviposit and guard their own eggs and nymphs (Tallamy & Denno, 1981). But if gravid females are instead exposed to a volatile compound secreted by a guard, or 'host', individual then a physiologically induced shift in behaviour occurs that causes egg dumping (Monaco *et al.*, 1998; Tallamy *et al.*, 2002). Moreover, the individual female that initiates the brood generally remains and protects eggs and nymphs from predators such as pirate bugs (Anthocoridae), damsel bugs (Nabidae), lacewing larvae (Chrysopidae) and jumping spiders (Salticidae) (Loeb, MLG personal observation). Individuals can guard one brood and then behave as an egg dumper on subsequent broods, or vice versa (Tallamy & Horton, 1990).

Gargaphia solani lacks stings or biting mouthparts and instead host females use wing fanning and bodily interference to deter predators (Tallamy & Denno, 1981). Although hosts significantly improve offspring survival (Tallamy & Denno, 1981), protecting young is

risky and females are often killed while defending the brood (Tallamy & Horton, 1990; Loeb, 2003).

Host-secreted pheromones may also contain kinship cues used by dumpers to find genetically related hosts (Loeb *et al.*, 2000; Loeb, 2003). Attracted females remain with the egg mass for up to 1.5 days while ovipositing with hosts and then disperse to nearby horsenettle. Dispersal distance for egg dumpers depends on the dispersion of host plants within a habitat, but in one natural stand of horsenettle dumpers began their own clutches about 1 m on average from an initial egg-dumping location (Loeb, 2003). Dumpers in the wild are more likely to survive to initiate a second brood than are guards, but dumpers nevertheless have low success in rearing the second brood to adulthood (Loeb, 2003). Thus both guards and dumpers are faced with ecological challenges that shape the fitness costs and benefits of pursuing each behaviour.

Modelling egg dumper optimal clutch size

In light of an earlier experimental study showing that offspring survival increases with total brood size, it is not immediately obvious why dumpers lay clutches with approximately 59% as many eggs as host clutches (Loeb, 2003). In particular, if offspring survival is positively density-dependent then dumpers should devote all available resources to the first-encountered host clutch rather than partition resources between current and future clutches. But dumpers and hosts each have low probability of initiating a second clutch (0.40 and 0.03, respectively; Loeb, 2003), and thus if all else is equal eggs dumped in a current clutch should have higher reproductive value than eggs laid in future clutches.

One hypothesis to explain reduced size of dumper clutches relative to hosts is that dumpers optimally allocate reproductive resources across first and second clutches. An alternative hypothesis is that dumper clutch size is suppressed by the host. We explore these alternatives by deriving a theoretical framework for understanding clutch-size evolution in communally egg-laying insects. We use the model to derive the optimal number of dumped eggs for both host and dumper and to identify ecological, life historical and genetic conditions under which inclusive fitness interests of hosts and dumpers are divergent (i.e. in conflict) with respect to the number of dumped eggs.

We assume that prior to beginning reproduction all mature individuals have an average total quantity of resources T to allocate across lifetime reproductive events. We also assume that there are costs of egg dumping which hosts do not incur. These costs may be physiological in nature and result from secretion of hormonal factors necessary to induce phenotypic change from egg guarding to egg dumping (Tallamy *et al.*, 2002), or costs may result from the energetic demands of search for host clutches and dispersal from communal broods.

Regardless of the proximate causes of what we define as 'commitment costs' of egg dumping, we assume that commitment costs Q are fixed in that magnitude of Q does not depend on initial resources T. We assume that Q is deducted from T prior to dumper allocation of resources. Thus the quantity of resources available for dumping is $T - Q = S$.

In addition to commitment costs, dumpers may also pay costs of social interaction with hosts. Social costs C depend on both the magnitude of conflict over dumper clutch size and the degree to which hosts cause dumpers to lay a number of eggs that diverges from dumper optimum clutch size. Unlike commitment costs that are paid prior to oviposition, we assume that C is paid during oviposition and manifest as reductions in clutch size of dumpers due to sub-optimal allocation. The model we develop below allows us to predict optimal allocation of S resources from the perspective of dumpers and hosts and in turn estimate the degree to which observed allocation of S deviates from predicted dumper optimum and toward host optimum. It is the magnitude of deviation from optimum clutch size, which yields our estimate of social costs of egg dumping C.

Survival rate of eggs and nymphs in our model depends on total number of eggs laid in a brood, where the quantitative relationship between survival and total eggs may be either linear or nonlinear. In both linear and nonlinear cases we assume that first and second clutches conform to the exact same survival functions.

To explore different egg-allocation optima, we define egg dumper lifetime inclusive fitness as:

$$W_d = f_{(H+pS)}(rH + pS) + g(f_{(S(1-p))})(S(1-p)). \quad (1)$$

The first term in eqn 1 describes overall success of the first communal clutch formed through egg dumping. Here H is the number of eggs laid by the host and p is the fraction of S eggs (or resources) dumped among the host clutch. The sum of dumped eggs pS and host eggs H is multiplied by a density-dependent survival function $f_{(H+pS)}$, with host eggs devalued by genetic relatedness between hosts and dumpers. The second term in eqn 1 describes survival of eggs and nymphs in the second clutch of former dumpers, a clutch initiated with probability $g < 1$. We define g as a parameter that embodies a combination of constraints on finding a second oviposition site and fecundity costs associated with laying a second clutch. Size of a former dumper's second clutch is the remaining number of eggs, $S(1-p)$, multiplied by expected offspring survival for a given clutch size, $f_{(S(1-p))}$.

To examine potential conflict over dumper clutch size we define the lifetime inclusive fitness of hosts as

$$W_h = f_{(H+pS)}(H + rpS) + rg(f_{(S(1-p))})(S(1-p)). \quad (2)$$

Note that eqn 2 differs from eqn 1 in that both first and second terms in eqn 2 now have dumper eggs devalued by genetic relatedness between females. In line

with field experimental observations (Loeb, 2003), we assume that number of dumped eggs does not affect probability of hosts establishing a second clutch, an assumption, which allows us to exclude second clutches of hosts from our model. In addition, published data shows that host probability of successfully starting a second clutch is extremely low ($g = 0.03$; Loeb, 2003) and can therefore be ignored in our analysis. Table 1 summarizes parameters of the model.

Conflict over number of dumped eggs

General solutions for offspring survival rates may be complex, nonlinear functions of total egg number. However, it is instructive to begin by analysing the simple case of a linear survival function. It should be noted that when $g < 1$ and survival is not dependent on egg density (i.e. f equals some constant a), fitness of hosts and dumpers alike is maximized when $p = 1.0$ and dumpers lay all of their S eggs in host broods. In addition, when offspring survival is a linear function $f_{(H+pS)} = a + b(H + pS)$, both host and dumper fitness is maximized when $p = 1.0$ provided $b > 0$. The variable b describes change in offspring survival for each additional egg laid in a communal clutch. In both linear cases there is no conflict because both hosts and dumpers optimize fitness when $p = 1.0$.

We now introduce a general quadratic form of offspring survival. Under a quadratic form the proportion of a brood surviving to adulthood increases as total brood size grows from small to an intermediate range of brood size values, but then begins to decrease as total brood size becomes ever larger. We characterize quadratic survival as:

$$f_{(N)} = a + b(N) + c(N)^2, \quad (3)$$

where N is the total number of eggs within a brood and a, b and c are defined constants. In this case optimal values of inclusive fitness derived by eqns 1 and 2 do not have a

general and simple form. Therefore we used results of field experiments described in the methods section to derive a general form of quadratic survival for *G. solani* broods of varying sizes. Although initially reported without a quadratic term, we reanalysed untransformed offspring survival data published in Loeb (2003) and found a significant quadratic relationship between percentage of offspring within a brood surviving to adulthood and total number of eggs, where $a = -0.4822$ ($P = 0.083$), $b = 0.01441$ ($P = 0.014$) and $c = -0.00005$ ($P = 0.051$; Test for overall model: $r^2 = 0.264$; $F_{2,51} = 8.791$; $P = 0.0005$). We then used these field data for the values of a, b and c described in eqn 3. We also used published mark-recapture data to estimate dumper probability of initiating a second clutch g and published host-dumper relatedness r estimated with genetic markers. These published results showed that for a population located in Northern Virginia, USA, $g = 0.4$ (SE = 0.062) and $r = 0.362$ (jack-knifed 95% confidence intervals (CI) = ±0.304; Loeb, 2003).

Experimental estimates of model parameters

We estimated each of the parameters H, S, p, and social costs of egg dumping C from experimental results that follow. Let $N_{j(i)}$ represent mean number of eggs from the jth clutch type (solitary, host, dumper or communal) of the ith clutch number (first or second). We assume that total resources available for reproduction by nonhosting, solitary guards equals ($N_{sol(1)} + N_{sol(2)}$), where $N_{sol(1)}$ is mean number of eggs laid solitarily by guards in the first clutch and $N_{sol(2)}$ is the mean number of eggs laid solitarily in the second clutch. Hosts and solitary guards in *G. solani* lay the same number of eggs, i.e. $H = N_{sol(1)}$ (Tallamy & Horton, 1990); thus for broods created by one host and one dumper, mean number of dumped eggs $N_{d(1)}$ is the difference between mean number of eggs in communal broods and mean number in first solitary broods, or $N_{d(1)} = (N_{com(1)} - N_{sol(1)})$. Lifetime total

Table 1 Model and experimental variables and their definitions.

Model parameter or experimental variable	Definition
$f(N)$	Per egg survival rate in broods with N total eggs
H	Number of eggs laid by hosts
S	Lifetime total number of eggs available to females that eggs dump their first clutch and solitarily guard their own second clutch
p	Fraction of S dumper eggs laid with hosts where $0 < p < 1$ and p_d^* and p_h^* are theoretically derived optimal fractions for dumpers and hosts, respectively
r	Genetic relatedness between hosts and egg dumpers
g	Probability of a former egg dumper establishing a second clutch
$N_{j(i)}$	Observed mean number of eggs from the jth clutch type (solitary, host, dumper or communal) of the ith clutch number (first or second)
$N_{sol(1)} + N_{sol(2)}$	Observed total number of eggs available for oviposition by solitary guards
$N_{d(1)}$	Observed number of eggs dumped in the first clutch of single-dumper broods
$N_{d(1)} + N_{sol(2)}$	Observed S, total lifetime number of eggs laid by individuals that dumped the first clutch and solitarily guarded the second clutch
p_{obs}	Observed proportion of total available eggs that are dumped, or $p_{obs} = N_{d(1)}/(N_{d(1)} + N_{sol(2)}) = N_{d(1)}/S$
C	Cost of egg dumping expressed as a deviation from p_d^* or $C = (|p_{obs} - p_d^*|)(S)$

number of eggs laid by dumpers S is the sum of the mean number of dumped eggs laid communally in the first clutch and the mean number of eggs laid solitarily in a second clutch by a former dumper, or $S = (N_{d(1)} + N_{sol(2)})$. Note once again that we assume S is the quantity of resources available after Q commitment costs have been paid and allocated across clutches. The observed proportion of eggs dumped $p_{obs} = N_{d(1)}/(N_{d(1)} + N_{sol(2)}) = N_d/S$. Social costs C is thus the absolute difference between p_{obs} and theoretically derived optimal dumper clutch size p_d^* multiplied by total dumper resources, or $C = (|p_{obs} - p_d^*|)(S)$. These experimental variables are summarized in Table 1.

Individuals that dump both first and second broods or those that guard first and then dump may each have different values of S and p. However, our focus here is on the simpler and more biologically widespread case where, if given the opportunity, individuals dump the first clutch and guard the second one (Tallamy & Horton, 1990).

Insect culture methods and experimental design

In the experiments that follow we placed special emphasis on control of phenotypic and ecological factors affecting *G. solani* fecundity. To control such factors we implemented two experimental procedures. First, we standardized social and developmental conditions of pre-experimental individuals by rearing eggs, nymphs and teneral adults on potted horsenettle grown within a glasshouse located in Northern Virginia, USA. Experimental individuals were at least one generation removed from the field. To prevent uncontrolled mating, we reared teneral adults in same-sex groups of 10–15 virgin individuals per potted host plant. We maintained same-sex groups until females began to show enlarged abdomens indicating onset of oogenesis and sexual maturity. Thus, within each experimental cohort individuals experienced relatively similar ecological, social and developmental conditions.

Second, we precluded potentially confounding correlation between individual behavioural preference and individual fecundity. For instance, fecundity may affect propensity to egg dump. To control correlation between fecundity and behaviour, we experimentally induced individuals to behave as egg guards or egg dumpers. In particular we took advantage of the fact that gravid, mated females that are isolated on a healthy plant will eventually initiate and guard a clutch (Tallamy & Denno, 1981). By contrast, gravid, mated females that are released directly onto a guard's freshly laid egg mass will egg dump with high predictability (Tallamy & Horton, 1990; Loeb, 2003). Thus by exploiting the strongly environmentally determined nature of reproductive behaviour in *G. solani*, we created hosts and dumpers in such a way that overrides possible correlation between behaviour and fecundity.

Previous studies have shown considerable within-population variation in fecundity between years (Loeb, 2003). To account for such variation in our parameter estimates we estimated H, S, p, and social costs of egg dumping C by taking the mean of each parameter across three independently replicated experiments. One experiment was conducted in a glasshouse in Northern Virginia and the second and third experiments were conducted in natural field habitats.

Each experiment differed in an important respect from the three others. In the glasshouse experiment we removed all host guards, solitary guards and dumpers before hatching of the first brood and then transferred each adult to a fresh horsenettle plant with no history of insect herbivory or oviposition. Each female, including former dumpers, was thus forced to behave as a solitary guard on the second clutch. After removal of adults we clipped away the egg-bearing portion of the host leaf and counted eggs under a dissection scope.

Field experiments were previously reported in detail by Loeb (2003). Briefly, field sites were located approximately 0.5 km from each other within the same *G. solani* population in the Shenandoah Valley of Northern Virginia, USA. One field site is an old-field habitat studied in the year 1999 and the other is a dry lakebed studied in 2000. Both study sites had naturally dense stands of horsenettle. In each field experiment Loeb (2003) induced guarding and egg dumping within pairs of glasshouse reared females released onto natural ramets of horsenettle. During oviposition horsenettle ramets were enclosed within fine mesh bags.

In the old-field experiment dumpers were transferred after oviposition to a nearby horsenettle ramet. Once transferred, former dumpers were enclosed again in mesh on the host plant and thus forced to oviposit as a solitary guard. Eggs of the first clutch and second clutches were subsequently counted under a dissection scope.

In the lakebed experiment by contrast, mesh bags were removed after oviposition and paint-marked dumpers were then able to disperse to nearby horsenettle ramets. Opportunities for egg dumping the second clutch were limited by systematic removal of free-ranging lace bugs from the lakebed habitat, and intensive recapture efforts subsequently yielded approximately 40% recapture of former dumpers, each of which was guarding its own clutch (Loeb, 2003). Given short mean dispersal distance of egg dumpers (148.0 ± 37.30 cm) and nonsignificant effects of dumper initial distance from the habitat margin on the probability of recapture, Loeb (2003) concluded that unrecaptured former egg dumpers had died before laying a second clutch. Total number of eggs in both initial and second broods was then counted after individuals completed oviposition and hatchlings had moved away from the empty eggs.

Gargaphia solani samples for each of the two field experiments and the glasshouse experiment were originally collected from the same Virginia source population.

Thus our results yield three independent samples of variation in dumper clutch size for a single *G. solani* population. We estimated average S across samples as the unweighted arithmetic mean of $(N_{d(1)} + N_{sol(2)})$ observed in each experimental sample. We also averaged $N_{sol(1)}$ across samples to yield a mean value of H. To obtain a mean value of the proportion of dumped eggs p_{obs}, we divided the mean number of dumped eggs across the three independent samples by our estimate of average S.

We obtained theoretical optimal clutch sizes p_h^* and p_d^* by setting the first derivatives of eqns 1 and 2 equal to zero, solving for p, and then substituting in field-based parameter estimates for H, S, r and g. We confirmed that p_h^* and p_d^* were each local maximum values (i.e. the second derivatives of W_d and W_h were negative) rather than local minimum values, suggesting that natural selection would favour a population settling on this maximum value. We then tested predicted optima against p_{obs}. We tested theoretical predictions for p against p_{obs} averaged across our three samples because the highly variable nature of *G. solani* clutch size makes it unlikely that any single estimate of p_{obs} approaches what could be considered an evolutionarily relevant value. Average p_{obs}, however, is more likely to approximate such a value.

Finally, we conducted a fourth experiment in a Virginia glasshouse where we estimated number of egg follicles remaining within ovaries of guards and dumpers that had recently completed oviposition. Ovary dissections allow us to test if relative size of dumper clutches is explained by retention of eggs (or follicles) from one clutch to the next. For example, if the difference between dumper and guard clutch size is explained by egg retention then the sum of mean dumper clutch size and mean number of follicles should be equivalent to mean clutch size of solitary guards. Individuals in the ovary dissection experiment were cultured according to our protocols described above and guarding and egg dumping was induced in the standardized manner. We collected guards and dumpers 4 and 2 days, respectively, after egg laying began and then preserved each individual at −80 °C. We later dissected egg follicles from ovaries of each previously frozen female and categorized follicles according to degree of cuticular tanning. We used an additional sample of gravid *G. solani* to standardize follicle developmental. The most highly tanned and thus most developed follicles received a rank of 3; follicles of intermediate tanning and development received a rank

of 2; and the least-developed follicles that had no sign of tanning were ranked as 1. We counted eggs under a dissection scope as described above. Since we killed guards and dumpers after the first clutch we could not obtain estimates of H and S from the ovary dissection experiment.

Results

Effects of egg dumping on fecundity

We observed in each of our four experiments that mean number of eggs in communal broods N_{com} was significantly greater on average than number of eggs in noncommunal broods $N_{sol(1)}$ (old-field: $t_{49} = 6.55$, $P < 0.0001$; lakebed: $t_{72} = 6.85$, $P < 0.0001$; glasshouse: $t_{53} = 14.21$, $P < 0.0001$; ovary dissection experiment: $t_{42} = 9.47$, $P < 0.0001$). Frequency distributions of the number of eggs per brood appeared normally distributed within each treatment and sample. Subtraction of $N_{sol(1)}$ from N_{com} within each experiment showed that mean dumper clutch size N_d was significantly smaller than $N_{sol(1)}$ (Table 2).

We used ovary dissections to determine the fate of unlaid dumper eggs. In this experiment dumpers laid on average 48.9 eggs (SE = 5.16, $n = 24$) in their first clutch whereas solitary guards laid 82.0 (3.81, 20), for an average clutch size difference between guards and dumpers (i.e. $N_{sol} - N_d$) of approximately 33.1 eggs (bootstrapped 95% CI: 16.1 − 48.3). Although egg-dumper ovaries contained significantly more stages 1 and 2 follicles and more follicles total than did ovaries of each egg dumper's host individual (paired *t*-tests: $P < 0.05$ for each test after Bonferroni correction; d.f. = 12; Fig. 1), dumpers did not, however, have enough follicles to account for the average difference in clutch sizes between dumpers and guards. Average total number of follicles in dumpers was 8.3 (1.0), or approximately 24.8 fewer follicles than the difference in clutch size between dumpers and solitary guards.

Interestingly, we did not observe developmentally advanced stage 3 follicles from either dumpers or guards. Absence of nearly mature follicles suggests that our sampling scheme did not prematurely interrupt oviposition. Moreover, the fact that dumpers lacked any mature follicles indicates that dumpers were more likely producing eggs for a future clutch rather than for the clutch, which they had just laid communally (Fig. 1).

Table 2 Estimates of host and egg dumper clutch size and total dumper resources in three experimental settings.

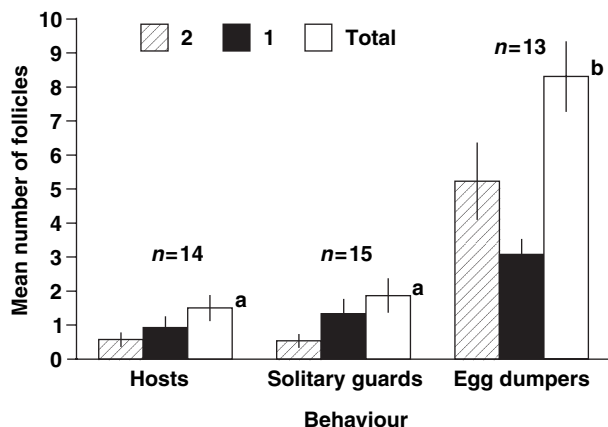| Parameter	Estimator	Observed mean (SE)			
		Old-field	Lakebed	Glasshouse	Grand mean
Host clutch size, H	$N_{sol(1)}$	68.6(5.2)	98.1(5.96)	114.9(3.93)	93.9(13.52)
Dumper clutch size, N_d	$N_{d(1)}$	42.3(6.46)	51.7(7.54)	79.7(5.6)	57.91(11.25)
Total dumper resources, S	$N_{d(1)} + N_{sol(2)}$	86.8(13)	136.5(16.5)	171.7(12.5)	131.68(42.0)

Fig. 1 Number of follicles dissected from ovaries of lace bug females that were experimentally induced to behave as egg hosts, hosts without dumper eggs (i.e. solitary guards) or egg dumpers. Ovaries were dissected after completion of the first clutch. Legend describes developmental stage of follicles where stage 2 is more advanced than stage 1. Note that the most developed stage 3 follicle was not observed in our sample. Means with different superscripts are significantly different ($P < 0.05$); see text for results of other statistical tests. Error bars = ±1 SE.

Thus, ovary dissections indicate that small size of dumper clutches cannot be explained proximately by retention of immature follicles from first clutches to later clutches.

Conflicts over dumper clutch size

Our model predicts that across most biologically realistic values of host clutch size H dumpers and guards have divergent optimal proportions of dumped eggs. Indeed the model shows that dumpers are favoured by natural selection to lay a larger proportions of their eggs than is optimal from the perspective of host inclusive fitness (Fig. 2). In other words, dumpers and guards are likely to be in conflict over the number of dumped eggs. However, given the survival curve estimated in the old-field experiment, fitness interests of host and dumper are convergent when H is less than approximately 45 eggs where $p_h^* = p_d^* = 1.0$ (Fig. 2). Small values of H favour the largest possible dumper clutch size ($p = 1$) because when host broods are small even a large dumper clutch will not push overall offspring survival beyond the maximum possible. Fitness conflicts are most acute, by contrast, when H is relatively large because each additional egg dumped pushes survival of host offspring ever lower. But since dumper inclusive fitness in our model devalues future clutches relative to present clutches (i.e. $g \ll 1$), dumpers are favoured to continue laying more eggs than is favoured by hosts. Hence conflict emerges over optimal p at large values of H. Interestingly, change in genetic relatedness between host and dumper has a
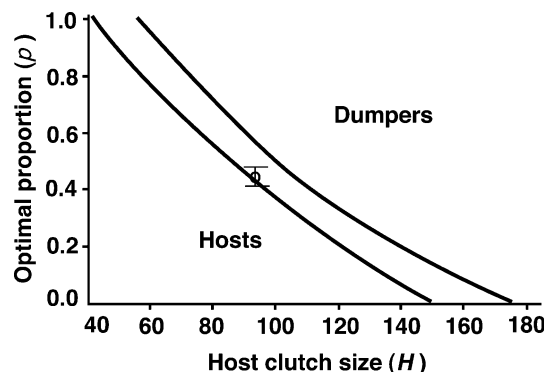

Fig. 2 Optimal proportion of dumped eggs from the perspective of hosts (lower line) and dumpers (upper line) when $S = 131.7$. Plotted point is p_{obs}, the mean observed proportion of dumped eggs across three experiments given an observed estimate of host clutch size H. Error bar spans bootstrapped 95% CI.

relatively small effect on the magnitude of conflict over p for a given value of H, a result discussed in more detail below.

The model also shows that dumpers maximize inclusive fitness across most values of H by laying smaller clutches than possible given S available resources. We observed in each experiment that $N_d < N_{sol(1)}$ and that $N_{sol(1)} < S$ (Table 1); thus our results are qualitatively consistent with the model prediction.

We quantitatively tested model predictions by estimating p_{obs} and other parameters from our three experiments. We used mean of three observed estimates of S and mean of observed estimates of N_d to obtain a population estimate of mean $p_{obs} = 0.4398$. To generate CI we resampled with replacement 1000 times from untransformed clutch size values within each experiment and recalculated p_{obs} after each iteration, a procedure that yielded a bootstrapped 95% CI for p_{obs} of 0.4067–0.47193. Observed mean p falls very close to p_h^* (=0.4345) but is significantly lower than the predicted optimum for dumpers ($p_d^* = 0.5612$ for the observed H of 93.9; Fig. 2). This result suggest that to the extent that conflicts over clutch size in *G. solani* can be resolved evolutionarily, dumper clutch size is closer to satisfying inclusive fitness interests of hosts than it is to satisfying fitness interests of dumpers.

Although we do not yet understand the nature of proximate controls over dumper oviposition, we interpret the close fit between prediction and observation as strong evidence for (i) the utility of our theoretical model and (ii) the possibility that hosts exert some measure of proximate control over dumper clutch size.

Social costs of egg dumping are revealed through divergence between observed and predicted dumper clutch size. Specifically, p_{obs} was lower than p_d^*; thus social costs $C = (|p_{obs} - p_d^*|)(S) = (0.1267)(131.7) = 16.69$ eggs. Resampling with replacement 1000 times from the

untransformed values of dumper clutch size and recalculating social costs after each iteration yielded a bootstrapped 95% CI for C of 11.891–20.131 eggs. Thus dumpers appear to be 'forced' to divert on average 16.69 eggs from their first dumped clutch to future clutches where eggs have lower reproductive value. Relative to the size of first dumper clutches, fecundity costs are approximately 28.8% of mean N_d (i.e. 16.69/57.9 = 0.288; see Table 2 for estimates of S and N_d). Note that even if dumpers laid an additional 8.3 eggs that we observed as immature follicles in dumper ovaries, p_{obs} would still be too low by approximately one-half to optimize dumper inclusive fitness. Thus hosts may be suppressing dumper egg maturation in addition to suppressing oviposition behaviour itself.

One surprising outcome of the model was sensitivity of the direction of conflict to values of g, the probability of establishing a second clutch. For instance, when g for dumpers is very low, dumpers maximize inclusive fitness by laying a majority of their eggs in the host brood, eggs that would otherwise have little reproductive value if saved for a second brood (Fig. 3a). Under this same condition of g, hosts, by contrast, are favoured to limit the number of dumped eggs in order to maintain

relatively high survival for their own offspring. But when g is high the model predicts that dumpers should save more of their eggs for a second clutch, which results in a relatively small p_d^* (Fig. 3b). Moreover, under high g dumpers are expected to reduce their own clutch size by such a large quantity that survival of host young will be sub-optimal (i.e. dumpers lay fewer eggs than is favoured by hosts). Thus when g is high hosts might be expected to encourage larger dumper clutches than is optimal for dumpers.

When we fit our field-estimated values to the model we see that the switch point for the direction of conflict falls at $g = 0.64$ (Fig. 3a). However, our field estimate of $g = 0.4$ is well below 0.64, which suggests that for our population of *G. solani* the direction of conflict is positive and dumpers are favoured to lay more eggs than is optimal for the host.

Variation in relatedness between host and dumper has a relatively small effect on the magnitude of conflict over optimal dumper clutch size (Fig. 3a,b). This is true for values of g that fall above and below the switch point for the direction of conflict. However, for values of g that fall above 0.64 the solutions for the magnitude of conflict are undefined for values of r below 0.3 (Fig. 3b). This is because where $g > 0.64$ and $r < 0.3$ the optimal value of p for dumpers includes an imaginary number (i.e. the square root of a negative value). But solutions for both host and dumper were available for all values of relatedness $0 < r < 0.5$ when the values of g fall below the switch point (Fig. 3a).

Magnitude of conflict is also sensitive to changes in dumper resources S. When we compare the magnitude of conflict across values of S greater than H, we see that higher S reduces conflict and that conflict is constant above $S > 150$ (Fig. 4). When S is low, however, dumpers will have relatively few eggs remaining after they have increased communal brood survival to its maximum possible. Indeed it is better for dumpers to lay these few additional eggs in the host clutch and to reduce
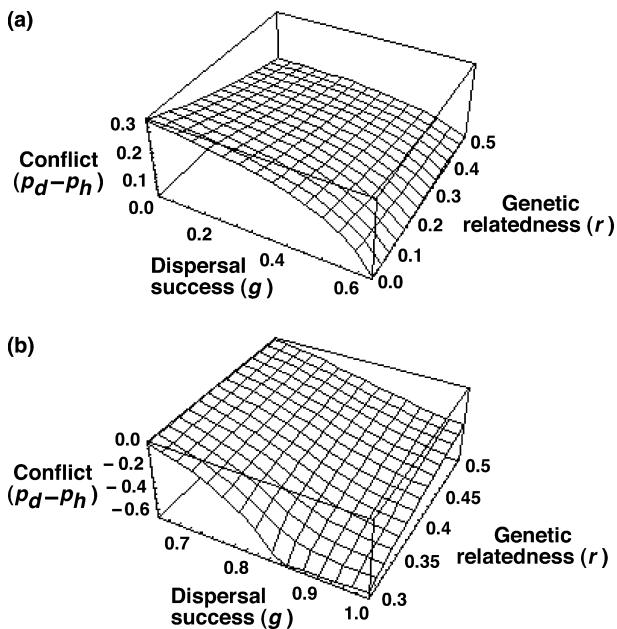
(a)

(b)

Fig. 3 The degree of conflict over the optimal proportion of dumped eggs from the perspective of the dumper (p_d^*) and the host (p_h^*). In (a) where dispersal success is low (below $g = 0.64$), dumper fitness is maximized at a higher value of p relative to hosts (i.e. $p_d^* - p_h^*$ values are positive). In (b) where dispersal success is high (above $g = 0.64$), host fitness is maximized at a higher value of p relative to dumpers (i.e. $p_d^* - p_h^*$ values are negative). For all values of dispersal success increasing genetic relatedness r decreases conflict but does not change direction of conflict. Note that in (b) conflict values are undefined when $r < 0.3$.
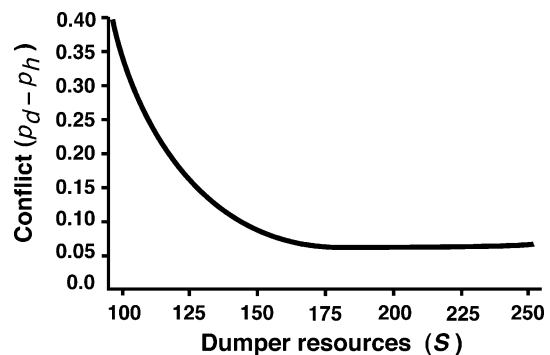

Fig. 4 A graph of conflict vs. dumper resources (S) where from previously published results $r = 0.362$ and $g = 0.4$. Note that the magnitude (but not the direction) of conflict is sensitive to the overall dumper resources (S). Here we assume $S > H$.

overall survival than it is to lay them in a second, solitary clutch with survival compromised by low numbers of eggs. This increases conflict between host and dumper because hosts want dumpers to lay no more eggs than that which yields the optimal survival rate. With higher values of S, however, dumping fewer eggs in accord with host fitness interests does not necessarily result in a lower reproductive value for these diverted dumper eggs. This is so because when S is high dumpers can lay a second clutch solitarily that is large enough for offspring survival to be close to or equal to that of a communal brood. Therefore conflict over number of dumped eggs is reduced with increases in resources available for egg dumping.

Discussion

One of the goals of evolutionary theory is to understand how sociality evolves given personal costs of social interaction. Costs may arise because of life-history trade-offs or because fitness interests of some individuals are compromised by actions of other group members. In the lace bug *G. solani* there are fitness conflicts over the number of eggs that dumpers oviposit within communally formed broods. Conflict may emerge in this social system because even though communal egg laying increases offspring survival, inclusive fitnesses of host and dumper are maximized under different ecological, genetic, and life historical conditions. Our model showed that under biologically realistic assumptions regarding genetic relatedness, total number of clutches laid in a lifetime, and size of host clutches, dumpers are favoured to lay more eggs than is desirable from the perspective of host fitness. However, we found in a natural *G. solani* population that host inclusive fitness, rather than dumper inclusive fitness is more likely to be maximized by dumper clutch size. Thus it appears that fitness conflicts in *G. solani* are resolved in favour of hosts, a counter-intuitive result that raises the important question of how such a resolution of conflict is reached given obvious asymmetries in control of dumper reproduction.

One proximate explanation for observed dumper clutch size is that hosts physically coerce dumpers to lay a number of eggs that maximizes host fitness rather than dumper fitness. In *G. solani* hosts may aggressively use wing fans, body rams and mounting to thwart conspecifics, but such behaviour is not especially frequent, occurring in perhaps 11% of host-dumper pairs (Tallamy & Tallamy, 1993). Thus additional mechanisms, such as pheromone cues secreted by hosts onto eggs (Monaco *et al.*, 1998), might be used by *G. solani* hosts to suppress dumper reproduction.

However, not all forms of host-dumper conflict over dumper clutch size may be controlled by host suppression. For instance, our model revealed that under some parameter values conflict might also exist when dumpers lay fewer eggs than optimum for hosts. In this case hosts

might be expected to entice or to force dumpers to remain at the brood and lay more eggs than is optimal for dumpers, but it is not immediately obvious how such control might be exerted by hosts. Dumpers can easily escape host aggression by simply walking to a nearby plant leaf, away from the host-protected brood (Loeb, MLG personal observation). And moreover, aggression would seem to be more a hindrance than a promoter of increased dumper oviposition. Phermonal cues, by contrast, may be used to manipulate dumpers to oviposit longer. For example, hosts may encourage larger dumper clutches by secreting extra quantities of compounds that are already attractive to gravid conspecifics (Monaco *et al.*, 1998). Indeed such an effect might be functionally easier for hosts to achieve than chemically suppressing dumper oviposition as suggested above. Future studies with *G. solani* will test if hosts exert proximate control over dumper reproduction, and also ascertain if population-level variation in the direction of conflict affects the evolution of mechanisms of social control.

Given that dumper clutch size is suboptimal for dumper fitness, the question remains as to why an individual would choose to egg dump even though all females are phenotypically capable of solitary reproduction. In a previous analysis, Loeb (2003) used the same *G. solani* population reported here to ascertain if the decision to egg dump was evolutionarily stable. Specifically, Loeb used the logic of Hamilton's rule (Hamilton, 1963) to determine if egg dumping is favoured over solitary reproduction. Hamilton's rule specified for *G. solani* posits that if the beneficial effects of egg dumping on reproduction of genetically related hosts, weighted by relatedness, are greater in magnitude than the direct reproductive costs of egg dumping, then natural selection favours egg dumping over solitary reproduction (Loeb, 2003). Loeb's study showed that Hamilton's rule was satisfied for the same Virginia population of *G. solani* studied here, but in terms of direct reproduction dumpers performed just as well as, but no better than, solitary (nonhost) guards. However, positive effects of egg dumping on reproduction of genetically related hosts, i.e. a positive kin component of inclusive fitness, tipped the selective balance in favour of egg dumping over guarding. Thus, for the Virginia *G. solani* population egg dumping may be an evolutionarily stable option, but as we show here this behavioural decision is not necessarily an optimal one from the perspective of dumper clutch size.

Our modelling of social costs of communal egg laying has important conceptual parallels with reproductive skew theory. In so-called classical skew theory one seeks to ascertain the evolutionarily stable proportion of total group reproduction that dominant breeders concede to subordinates in exchange for subordinate cooperation (Vehrencamp, 1983; Reeve & Ratnieks, 1993). In the classical skew framework one also determines the proportion of group reproduction that subordinates must

be permitted in order to encourage subordinates to remain in the group. Thus individuals are in conflict when the ESS proportion of total group reproduction that subordinates are favoured to use is different from the proportion that dominants are willing to yield.

Taking a similar approach to skew theory, we asked what proportion of egg dumper lifetime allotment of eggs should be laid in the host clutch when considering inclusive fitness perspectives of hosts and egg dumpers. Moreover, both classical skew models and our optimality model share some ecological and genetic parameters such as probability of successfully establishing an independent reproduction site (our g in the model) and genetic relatedness between interactants (Vehrencamp, 1983; Reeve & Ratnieks, 1993; Reeve & Keller, 2001). One key difference, however, is that in our model we made no assumptions about the nature and extent of host control over dumper reproduction as in concessions models of reproductive skew (Reeve & Ratnieks, 1993) or host control over group membership as in both concessions and restraint models (Johnstone & Cant, 1999; Johnstone, 2000; Zink & Reeve, 2005). Instead the hypothesis of host control of dumper reproduction emerged from our optimality model as a testable prediction rather than a central assumption.

A second comparison with assumptions of classical reproductive skew theory illuminates the paradox over dumper reproduction and helps reconcile apparently conflicting results of ESS and optimality models. In particular, classical skew theory posits that dominant individuals yield just enough personal reproduction to ensure that subordinate helpers remain with the group (Vehrencamp, 1983; Reeve & Ratnieks, 1993; Reeve & Keller, 2001). In other words, subordinates remain and help if Hamilton's rule specified for such a decision is satisfied, a key prediction of skew theory that has met with equivocal empirical support (Reeve & Keller, 2001). Our results and those of Loeb (2003) suggest the hypothesis that dumpers may be laying just enough eggs to make egg dumping an evolutionarily stable course of action, but not necessarily an optimal one with respect to numbers of dumped eggs. Indeed, if hosts have some control over dumper clutch size, then hosts may be allowing dumpers to lay no more eggs than the quantity that satisfies Hamilton's rule for the decision to egg dump. Thus the previous result showing that egg dumping in *G. solani* is evolutionarily stable is complementary with the result reported here showing that some elements of dumper communal reproduction are suboptimal.

The scope of social conflict and cooperation is relatively poorly understood for communal egg layers. Our theoretical approach to understanding conflict and social costs can be modified to include a wider range of communal life histories, including those where nonhost females show extended parental care and prolonged social contact with other reproductives. In the case of extended care, models could be modified to include effects of a second caregiver on offspring survival and the effects of care on the second individual's own future reproductive value. Such theoretical modifications will help to ascertain if the duration of social contact among communal egg layers affects not only the magnitude social costs, but also the nature of biological solutions to conflict.

Acknowledgments

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