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# Parental care trade-offs and the role of filial cannibalism in the maritime earwig, *Anisolabis maritima*

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Animals that provide parental care are expected to weigh the value of current offspring against the value of future offspring, such that total investment across all offspring is allocated to maximize lifetime fitness. In this study, we characterize the trade-offs associated with maternal care in the maritime earwig, *Anisolabis maritima* (Dermaptera: Anisolabididae). We measured the benefits of care in terms of hatching success through removal experiments and the costs of care by comparing the future fecundity of caring females to that of removals. We show that the benefits of care greatly outweigh the costs, providing a seven-fold increase in hatching success. Artificially removed females had larger subsequent clutches and shorter internest intervals, but very low hatching success. Naturally abandoning females always cannibalize all their eggs. Partial clutch cannibalism was a ubiquitous feature of maternal care, although rates were variable among individuals. In post hoc tests, we first addressed the ultimate explanation that filial cannibalism is a way for females to facultatively adjust their investment per clutch in order to maximize future reproduction. We then tested two proximate explanations for filial cannibalism: (1) females that lay more eggs for their given body size tend to consume more eggs, reflecting a nutritional deficiency; (2) females prefer to cannibalize the youngest eggs to reduce the overall duration of egg care. In addition, we consider the alternative explanation that females eat unviable eggs for hygienic reasons. Our results provide support for both energy limitation and hygienic maintenance. Higher rates of egg cannibalism near the very end of nesting were also suggestive of nymphal cannibalism, a phenomenon that will be examined in future work.

Life-history theory predicts that parental care evolves when the benefits of care outweigh the costs to future reproduction (Williams 1966; Tallamy & Denno 1982; Clutton-Brock 1991). Animals that lay multiple clutches in their lifetime must weigh the survival of their current clutch against the potential value of future clutches (Fritz et al. 1982; Tallamy & Brown 1999), and as a result face a trade-off between current and future reproduction (Trivers 1972). While the principal benefit of parental care is increased offspring survival (Clutton-Brock 1991), the costs of parental care manifest in a variety of ways. In species where the female is the primary caretaker, time and resources required for care tend to be the limiting factors (Trivers 1972). The energetic demands of care, for instance, can reduce the size of future clutches and the quality of future care (Zink 2003; Buzatto et al. 2007; Ward et al. 2009). Mortality risks also increase during parental care, as dangers of starvation and exposure to predation intensify (Stearns 1976). Therefore, parents that provide care are expected to distribute their reproductive investments across bouts such that these costs and risks are minimized.

One approach to balancing limitations on time and energy is to adjust reproductive investment per clutch in a condition-dependent manner (Williams 1966; Trivers 1972). Rather than withholding eggs in anticipation of future costs (Lack 1947), parents may facultatively reduce clutch size through filial cannibalism (i.e. by consuming their own eggs or offspring; Sargent 1992) as a result of intrinsic or extrinsic changes. For example, male assassin bugs, *Rhinocoris tristis*, offset the energetic demands of care through filial cannibalism, eating more eggs later in nesting as energy reserves decline (Thomas & Manica 2003). In addition, the scissortail sergeant, *Abudefduf sexfasciatus*, retroactively adjusts clutch size by eating eggs in the face of unexpectedly reduced resources (Manica 2004). In more extreme cases, a parent may abort its entire nest through whole clutch filial cannibalism (Sargent 1992). Whole clutch filial cannibalism usually occurs when conditions become

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so inhospitable or energetically taxing that caring significantly reduces the probability of a parent surviving to care for the clutch adequately (Klug & Bonsall 2007). While filial cannibalism has been documented in several taxa, especially in fish, few empirical studies have focused on filial cannibalism as a way for parents to titrate their parental investment within a clutch or between clutches (Manica 2002, 2004; Klug & Lindström 2008; Aymes et al. 2010).

In this study, we quantify the costs and benefits of maternal care in the maritime earwig, *Anisolabis maritima*, by measuring current offspring survival and future reproduction. While maternal care is ubiquitous across earwigs (Vancassel 1984; Radl & Linsenmair 1991; Rankin et al. 1996), only one study has experimentally measured the life-history trade-offs of care. In the European earwig, *Forficula auricularia*, Kölliker (2007) found that female presence increases current offspring survival and delays future reproduction. Here we detail similar removal experiments using *A. maritima*. We quantified the fitness costs of maternal care in terms of future fecundity (by comparing the fecundity of females that were allowed and not allowed to provide maternal care) and the fitness benefits of egg care in terms of hatching success in the presence and absence of the mother.

In this study we also characterize, for the first time, filial egg cannibalism as a common feature of maternal care in *A. maritima*, with whole clutch cannibalism being an obligate prerequisite to clutch abandonment. We also characterize partial clutch cannibalism when females remain with eggs. We compare measures of female fitness to patterns of maternal egg consumption in order to generate hypotheses about the adaptive value of filial cannibalism. Cannibalism in the context of parental care has been examined before in earwigs; for example, nymphs of the hump earwig, *Anechura harmandi*, are matriphagous (Kohno 1997; Suzuki et al. 2005), and nymphs of the European earwig cannibalize siblings (Dobler & Kölliker 2010). However, there has been no work to date on filial cannibalism in earwigs. In post hoc analyses, we tested the ultimate hypothesis that females eat eggs as a way to titrate their reproductive investment across clutches by first measuring how filial cannibalism affects future reproduction and then by examining two proximate explanations: (1) females that lay more eggs for their given body size tend to consume more eggs, reflecting a nutritional deficiency; (2) females eat eggs to minimize the overall duration of egg care by preferring to cannibalize the youngest eggs. We address an alternative hypothesis that filial cannibalism instead functions to sanitize the nest, by which unviable eggs are consumed.

## METHODS

### *Study Organism:* Anisolabis maritima

The maritime earwig inhabits a narrow strip along the high tide line along ocean coasts and estuaries (Bennet 1904) and builds chambers and galleries under rocks or driftwood where sand or soil is available and sufficiently deep (ca. 10 cm; Bennet 1904; Guppy 1950; Langston 1974; R. S. Howard, unpublished data; Fig. 1). Females excavate their own nest chambers, often against the smooth underside of a rock (J. S. Miller, personal observation). In the nest chamber, the female lays a mean ± SE of 42.1 ± 7.3 eggs (Miller et al. 2011) and stays with offspring until hatching and first moult to the second instar, lasting around 28 days. Some females continue to add eggs to their clutch throughout nesting, but the majority of eggs are laid over the first 3 days. During incubation, the female frequently rolls eggs through her mandibles and rearranges them into different piles around the nest cavity. In northern California we find that both males and females forage in the intertidal zone as predators on arthropods (such as the land crustacean *Megalorchestia*). Juveniles overwinter and reach reproductive maturity in the year following their birth; mating occurs in May–July, and females begin laying clutches in late May. Under laboratory conditions, females undergo senescence at the end of their second year, allowing only a single season for reproduction, in which they may produce two or, rarely, three clutches.

**Figure 1.** Nesting maritime earwig female. An adult female attending to the egg pile in her nest chamber. The ceiling of the chamber has been lifted to reveal the structure of the nest. Photo: Jonathan Wright.

### *Field Experiment*

The field site was located at Richardson Bay Audubon Sanctuary in Tiburon, California. Adult females were collected from the field site, brought to the laboratory, and placed individually in a 900 ml transparent plastic container (19 × 13 × 5 cm, décor Tellfresh®, Decor Corp. Pty Ltd, Scoresby, Victoria, Australia) filled 1.5 cm deep with a soil/clay mixture. We drilled six holes (1.8 cm in diameter) evenly spaced along the bottom of each container to allow drainage when inserted into the field and to allow multiple access points for potential predators that might have otherwise been artificially excluded. While in the laboratory, masking tape was used to cover the holes to prevent earwigs from escaping. Females were fed an unlimited supply of wet cat food and provided water ad libitum while in the laboratory. Within 3 days of nest appearance, the eggs were counted and a transparent square red plastic dish was placed over the nest for structural support before transferring the box to the field. If a female was found with fewer than 15 eggs, she was allowed 3–4 more days to continue laying before her container was introduced to the field, since minimum and maximum clutch sizes were 16 and 66 eggs, respectively, among laboratory females in a pilot study (J. S. Miller, unpublished data).

In the year prior to the experiments (summer of 2008), we placed 240 concrete blocks measuring 10 × 20 × 5 cm along the beach in a continuous row wherever the ground consisted of soil and/or sand. A décor Tellfresh® container was dug into the ground under each block. The container could easily be removed and replaced by an introduced nestbox of the same shape and size, so that the soil surrounding it was not disturbed. In the summer of 2009, such boxes containing a nest (as described above) were brought to the field site, filled with additional soil and placed under a randomly assigned concrete block using a random number generator without replacement.

To examine the effect of maternal care on nest survival experimentally and to identify potential threats to nests under natural conditions (predators and pathogens), we transplanted nests into the field, applying one of four treatments: (1) the mother was removed from the nest and released elsewhere at the field site ('Removed'); (2) the mother remained in the nest ('Control'); (3) the mother remained in the nest, but the nest was covered with a metal mesh having a mesh size of 1.5 × 1.5 mm ('Caged'); (4) the mother was removed and the nest was covered with a metal mesh having a mesh size of 1.5 × 1.5 mm ('Caged + Removed'). Nests were assigned treatments using a randomized block design to distribute treatments equally over the season. All transplanted nests were covered by concrete blocks, but these blocks acted as shelter, not as protection from ground-dwelling predators. Excluding predators with an additional mesh enclosure in the caged treatments was an attempt to eliminate the effects of predation from the effects of pathogens on egg survival.

We checked field nests every 3–4 days for presence of eggs and guarding by the female by lifting boxes from the ground and visually inspecting them for less than 5 min. Nests were ordinarily against the wall or floor of the container or under the red plastic. When nests were not readily visible, we dug into the soil directly above the red plastic, until the nest was visible through the red plastic ceiling. When possible, egg counts were made and visually checked for fungal infection. We also counted the number of arthropods directly above and below each box during each visit to the nest, and we made note of egg predation events when observed in the field. Nymphs were collected prior to dispersal using an aspirator and counted. At the end of the experiment, we excavated the container and recorded any uncounted eggs, other earwigs or arthropods. Data were collected from 30 June through 2 October 2009 on 97 individuals, each under a unique block ($N_{\mathrm{Control}} = 23$, $N_{\mathrm{Removed}} = 25$, $N_{\mathrm{Caged}} = 24$, $N_{\mathrm{Caged\ +\ Removed}} = 25$).

### *Laboratory Experiment*

Earwigs were collected between 21 May and 14 August 2009 on the shoreline of Richardson Bay in Marin County, California, and brought to the laboratory on the same day as collected. We did not know the reproductive history of each individual, but treatments were assigned at random within each time block, in order to distribute (unknown) reproductive histories evenly across treatments. Each earwig was assigned a unique number and placed in a cylindrical glass jar (9 cm height, 8 cm diameter, Environmental Sampling Supply®, Oakland, CA, U.S.A.), with a layer of clay and soil approximately 1 cm deep. We placed a transparent red tinted plastic dish (5 × 5 × 1 cm) face down on the soil, under which females nested, allowing us to monitor females with minimal disturbance. All earwigs were provided unlimited wet cat food and water ad libitum, and kept in controlled temperature chamber set at 25 °C, with a 14:10 h light:dark cycle.

Once a female began laying eggs, we assigned her to a treatment using a randomized blocked design that spread treatments evenly over time: (1) mother removed or (2) mother in nest. In nests with a mother, we counted eggs every 3–4 days by lifting the red plastic and spreading out the eggs with a moist paintbrush with minimal disturbance to the female. Females clump eggs together in a pile, so spreading out the eggs with a paintbrush enabled the observer to see all eggs for an accurate count. For removal nests, eggs were counted once and the female was allowed up to 1 h to restack her eggs so that any effects of egg stacking could be remedied before the female was removed. In these mother-removal nests, eggs were not disturbed again for counting until hatching in order to prevent introducing other contaminants. Just as in the field experiment, if a female was found with fewer than 15 eggs, she was allowed 3–4 more days to lay her full clutch before applying a treatment. For all nests, we noted the presence of fungus, discoloration or infection on eggs at the time of data collection. Eggs that died from infection or that fell out of the nest were easily observed and accounted for, and these eggs were not included in any of the calculations of filial cannibalism. To calculate hatching success, total nymph counts were made after all of the remaining eggs had hatched, but before nymphs dispersed from the nest. Nymphs were removed from the nest using an aspirator, and then counted. Data were collected from 20 May through 16 September 2009 on 72 individual nests ($N_{\mathrm{Control}} = 37$, $N_{\mathrm{Removed}} = 35$). Sixteen nests were videotaped continuously for 24 h in the laboratory using a Sony DCR-HC52 MiniDV Camcorder under infrared light for a more comprehensive repertoire of parental care behaviours.

To determine the effects of maternal care on subsequent reproduction (i.e. the costs of providing care), we maintained both the removal and the control laboratory females after completion of nesting. We placed removal females in a new jar similar to the first immediately after removal from eggs, while the other females stayed in their original containers. Removal females therefore spent only 3–7 days with their eggs whereas control females stayed with eggs for 18–24 days until complete hatching. We checked containers every 3–4 days for a subsequent nest. If a nest was found, we counted eggs twice a week using the same technique described above. For the removal treatment we supplemented data using 37 additional individuals that were removed from care (in the exact same manner using a randomized block design) for another experiment in the same room during the same time period. This resulted in a total of 72 removal individuals, in addition to 37 control females, for a total of 109 individuals.

To control for the effects of female body size on fecundity, hatching success and filial cannibalism, we measured pronotum width of each individual as a proxy for body size (Simmons & Tomkins 1996) using a National 430-430 PHF Binocular Stereo Microscope and 10 mm Micrometer Eyepiece.

### *Analysis*

All analyses were performed using JMP statistical software v8.0.2 (SAS Institute, Cary, NC, U.S.A.). All means are presented with ±1 SE.

#### *Benefits of care*

We analysed laboratory and field data together in a generalized linear model with binomial distribution because of the high number nests with zero hatching success (76 of 97 nests in the field, 78.4%; 38 of 72 nests in the laboratory, 52.7%). We used nymphs and total eggs as response variables with a logit link function and correcting for overdispersion ($N_{\mathrm{Total}} = 169$; field: $N_{\mathrm{Control}} = 23$, $N_{\mathrm{Removed}} = 25$, $N_{\mathrm{Caged}} = 24$, $N_{\mathrm{Caged\ +\ Removed}} = 25$; laboratory: $N_{\mathrm{Control}} = 37$, $N_{\mathrm{Removed}} = 35$). We entered mother's presence, location (laboratory or field) and cage (nested within location) into the GLM as test factors, and included mom by location and mom by cage interaction effects. To exclude the possibility that hatching success (number of nymphs/total eggs laid) is dependent on clutch size, we plotted hatching success against (1) total eggs and (2) clutch size just prior to hatching using a linear regression. We also calculated mean hatching success for each treatment in the laboratory and field (see Results, Fig. 2).

To test the importance of predator defence in maternal care, we looked at the effect of predator-excluding cages on nests using independent contrasts. We predicted that hatching success would be lowest in uncaged nests without a mother, greatest in caged nests with a female, and intermediate in uncaged nests with a mother. In addition, if predator defence is important, we predicted that eggs in uncaged nests without a mother would disappear more suddenly than eggs in caged nests without a mother, which should instead become infected and disappear more gradually. We compared the time to disappearance of eggs between caged and uncaged nests without a mother with a survival analysis, with time to disappearance as the number of days from introduction to the field until no more than one egg remained. We also compared infection rates with a logistic regression.

To address the role of sanitation in maternal care, we tested whether maternal presence influenced infection rates. For field nests, we predicted that the rate of infection would be higher in caged nests without mother than in nests containing a female (i.e. with or without a cage). We did not include uncaged nests without a mother in this analysis because fungal measurements on this treatment would be obscured by predation. We also predicted that the rate of infection would be higher in laboratory nests without a mother than in control nests. Nests were categorized as 'infected' if any fungal growth or decomposition was visible; otherwise, nests were labelled 'healthy' and compared using a logistic regression.

### *Costs of care*

By comparing control and removal females from the laboratory, we measured the costs of care on future fecundity in terms of mortality rate, the probability of renesting, subsequent clutch size, the latency between nests and total number of eggs laid. We compared the frequency of renesting between control and removal females using a logistic regression, predicting that liberated females would be more likely to renest. In addition, we repeated the above analysis considering only early season individuals, collected on or before 25 June 2009, to control for any effect of late season nesting. We calculated the difference between first and second clutch size for each female in the laboratory. Then, to see whether care reduced subsequent clutch size, we compared the mean difference in clutch size between control and removal treatments using an *F* test. We compared the internest interval, or the time between oviposition events (nest initiation) between control and removal females using survival analysis (Kaplan–Meier method) and report the mean internest interval for the two treatment groups. We also compared mortality rate (number of days from first oviposition to death) between the control and removal females using survival analysis. We compared the mean number of eggs between treatments using a two-tailed *t* test.

### *Filial cannibalism*

We documented whole and partial clutch filial cannibalism by counting eggs throughout nesting. We are confident that eggs that went missing were cannibalized. We have directly observed females eating their own eggs and so have colleagues (I. De La Torre, personal communication). For each egg count, we thoroughly searched the nest chamber and visually inspected the rest of the container's soil for any eggs and/or their remains. When eggs became infected, they did not disappear within the 3–4 day time frame between observations, as was observed in the 35 removal treatment nests. When infected eggs were found (rarely), they were not included in counts of cannibalism. Furthermore, eggs go missing even for females nesting in clean glass jars without soil (I. De La Torre, personal communication).

In our analysis, we separated prenymph cannibalism from postnymph cannibalism to distinguish filial cannibalism (eating of eggs by mother alone) from possible nymphal cannibalism (eating of eggs by first-hatched nymphs). Any eggs lost after the appearance of at least one nymph were included in postnymph cannibalism. We calculated the fraction of clutch cannibalized as the number of eggs lost divided by the total eggs laid in that clutch. We compared the fraction of clutch cannibalized pre- and postnymph using a two-tailed *t* test.

To test whether consumed eggs translate into future reproduction, we compared the number of eggs cannibalized (pre- and postnymph and in total, but not including aborted nests) to the probability of renesting and mortality rates with a logistic regression ($N = 25$). Sample sizes were too small for a meaningful analysis of secondary clutch size and internest interval, as only 5 out of 25 females laid a secondary nest.

To test the hypothesis that the function of filial cannibalism is to titre reproductive investment across clutches, we examined two possible mechanisms. First, to see whether filial cannibalism is a facultative response to energy limitation during care, we looked at whether females that laid more eggs in proportion to their body size had higher cannibalism rates. We first obtained the residuals from a linear regression between body size (pronotum width) and total clutch size ($N = 68$). We then tested for a positive relationship between the residuals and the level of filial cannibalism, analysing pre-, post- and total cannibalism for the number of eggs cannibalized (excluding aborted nests). Inspection of the box plot for residuals revealed two outliers, which when standardized were $-2.72$ and $-2.60$ standard deviations from the mean. We chose to exclude these data points given our sample size ($N = 25$), using $+/-$ 2.5 SD as the cutoff. Additionally, to see whether cannibalism rates (mean number of eggs eaten per day) increased later in the nesting period, as females depleted their energy reserves, we compared prenymph cannibalism rates with time using a linear regression.

We also tested whether females eat eggs to shorten the duration of nesting. With what appears to be a set development time for eggs, eggs added later should extend the period of care by hatching later. Therefore, we expected females with greater laying asynchrony to consume more (younger) eggs. Duration of nesting was calculated as the time from the first appearance of eggs until total hatching. We derived a laying asynchrony index as follows:

$$\frac{\sum_{i=1}^{n} i(\text{number of eggs added on day } n) \times n}{\text{maximum number of eggs}}$$

Eggs added per observation day are summed until the maximum number of eggs is reached. A higher value indicates greater laying asynchrony. For instance, if a female had 34 eggs on the first observation, 63 eggs on the second observation and 65 eggs on the third observation, but her clutch size never exceeded 65 eggs, her laying asynchrony index would be $(34 \times 1 + (63 - 34) \times 2 + (65 - 63) \times 3)/65 = 1.5$. In contrast, a female that had 47 eggs on the first observation and 51 eggs on the second observation, but her nest never exceeded 51 eggs, would have a laying asynchrony index of $(47 \times 1 + (51 - 47) \times 2)/51 = 1.07$.

First, to test whether laying asynchrony is related to higher filial cannibalism rate, we compared laying asynchrony to the number of eggs cannibalized (prenymph, postnymph and total) with a linear regression. In addition, we analysed the effects of laying asynchrony and filial cannibalism on the duration of care using a multiple regression. If filial cannibalism acts to dampen the effect of laying asynchrony on nesting duration, then we would expect a significant interaction effect between laying asynchrony and filial cannibalism. For instance if laying asynchrony were high, then a high filial cannibalism rate would lessen the duration of care, whereas a low filial cannibalism rate would lengthen the duration of care. Alternatively, we hypothesized that females eat unviable eggs, which should not depend on the energetic state of the mother or influence the duration of care. We would, however, still expect to see an energetic benefit to filial cannibalism.

## RESULTS

### Benefits of Care

Mother presence had a highly significant effect on hatching success (GLM: $\chi^2_1 = 38.65$, $P < 0.0001$). In the field, the mean hatching success of nests with a mother was 23.5 ± 0.1% while nests without a mother had a mean hatching success of 3.2 ± 0.0% (Fig. 2). Fifteen out of 23 field nests with a mother completely failed (0% hatching success), but the remaining nests had a 67.7 ± 0.1% hatching success. In the laboratory, mean hatching success was 55.3 ± 0.1% for all control nests and 7.9 ± 0.0% for removal nests. Twelve out of 37 control laboratory nests completely failed, leaving the remaining nests with a mean hatching success of 81.9 ± 0.0%. Clutch size (both maximum and prehatching) was not significantly related to hatching success (linear regression: maximum: $R^2 = 0.002$, $N = 25$, $P = 0.8269$; prehatching: $R^2 = 0.014$, $N = 25$, $P = 0.5776$).

Location also had a significant effect on hatching success (GLM: $\chi^2_1 = 13.11$, $P = 0.0003$), with laboratory nests doing better than field nests. There was no effect of a cage on hatching success ($\chi^2_1 = 1.02$, $P = 0.3120$) and no interaction effect with maternal presence ($\chi^2_1 = 0.03$, $P = 0.8565$).

Arthropods found on or above the nestboxes included earthworms, intertidal isopods spiders, cockroaches, soil mites, centipedes, hemiptera, flies and ants. The only arthropods we observed depredating nests were ants, which were seen recruiting to 17 nests, including inside caged nests. Predictions about the relative success of caged and uncaged treatments were not entirely satisfied. While uncaged nests with a mother did better than uncaged nests without a mother (GLM, independent contrasts: $\chi^2_1 = 8.74$, $P = 0.0031$), erecting a protective cage around nests with a mother did not improve hatching success ($\chi^2_1 = 2.36$, $P = 0.1241$).

Our prediction that unguarded eggs in nests with a cage would disappear more gradually than unguarded eggs in nests without a cage was also unsatisfied, as we found no significant difference in their respective times to disappearance (survival analysis, Mantel–Cox: $\chi^2_1 = 2.89$, $N = 50$, $P = 0.0889$), but caged nests without a mother were infected more, although not significantly (logistic regression: $\chi^2_1 = 3.55$, $N = 50$, $P = 0.0594$).

Egg infection was apparent in two forms: fungal hyphae, which grew filaments on the egg's surface, and decomposition, which caused eggs to deflate and change colour. Contrary to predictions, nests with a mother present (control and caged treatments, $N = 47$) in the field did not have significantly lower infection rates than caged nests without a mother ($N = 25$) (logistic regression: $\chi^2_1 = 1.32$, $P = 0.2498$). Caged nests without a mother were infected 8.7% of the time, removal nests were infected 30.4% of the time, while nests with a mother had a 2.1% infection rate. In the laboratory, maternal presence had a significant effect on infection rate ($\chi^2_1 = 40.76$, $N_{\text{Control}} = 37$, $N_{\text{Removed}} = 35$, $P = 0.0001$), with 74.3% of removal nests but only 5.4% of control nests becoming infected.

### Cost of Care

In laboratory experiments, removal from care had no significant effect on female mortality rate (survival analysis, Mantel–Cox: $\chi^2_1 = 1.26$, $N = 109$, $P = 0.2613$), internest interval (survival analysis, Mantel–Cox: $\chi^2_1 = 2.11$, $N = 109$, $P = 0.1461$), or the probability of renesting (logistic regression: $\chi^2_1 = 1.26$, $N_{\text{Total}} = 109$, $P = 0.2614$) as compared to females that stayed at nests to care. Even when controlling for an early versus late season effect, we found no significant effect of care on the probability of renesting (logistic regression: $\chi^2_1 = 0.77$, $N_{\text{Total}} = 91$, $N_{\text{Control}} = 30$, $N_{\text{Removed}} = 61$, $P = 0.3797$). However, control females had significantly reduced clutch sizes in their second nests (F test: $F_{1,32} = 6.482$, $N_{\text{Total}} = 34$: $N_{\text{Control}} = 9$, $N_{\text{Removed}} = 25$, $P = 0.0159$) relative to liberated (removed) females (see Table 1 for mean values). Both control and removal females laid the same number of eggs across their lifetimes (two-sided t test: $t_{107} = -0.896$, $N = 109$, $P = 0.8130$).

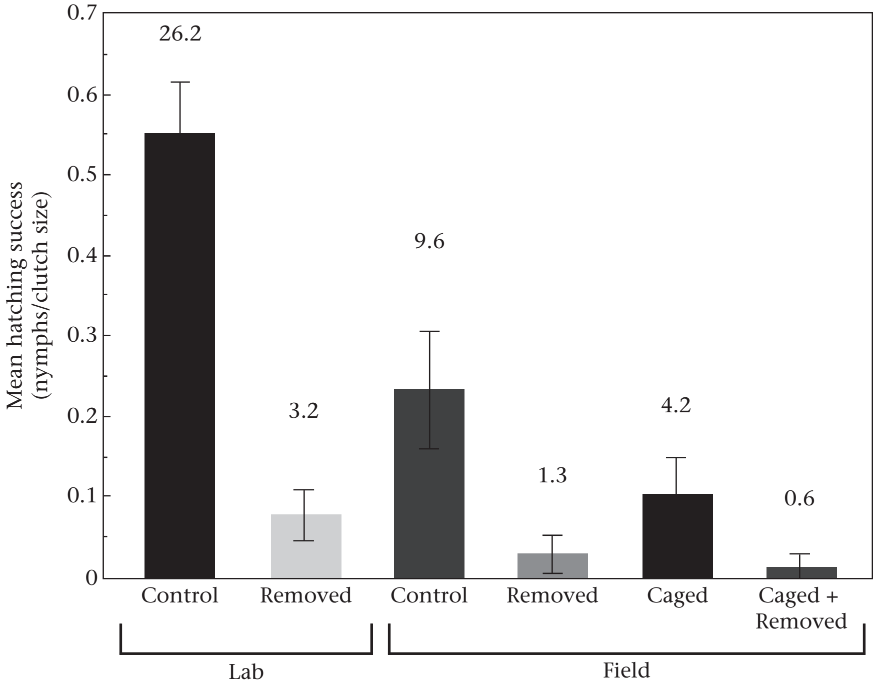

**Figure 2.** Mean ± SE hatching success of maritime earwig clutches (number of nymphs/total eggs laid per clutch) in the laboratory and in the field. Control: females remained in the nest; Removed: females were removed from the nest; Caged: females remained in the nest, but nests were covered with a wire mesh cage. Caged + Removed: females were removed and nests were covered with a wire mesh cage. Numbers above bars indicate the mean number of nymphs per treatment.

**Table 1**
Mean ± SE clutch sizes and internest intervals for female maritime earwigs that were allowed to remain in the nest and care for their clutches (control) and that were removed from the nest (removals)

| | First clutch size (no. of eggs) | Second clutch size (no. of eggs) | Δ Clutch size (2nd clutch − 1st clutch; no. of eggs) | Internest interval (days) |
|---|---|---|---|---|
| Controls | 46.2±12.9<br>*N*=37 | 27.6±17.3<br>*N*=9 | −20.0<br>*N*=9 | 34.1±9.8<br>*N*=9 |
| Removals | 38.1±11.2<br>*N*=72 | 32.0±11.1<br>*N*=25 | −4.9<br>*N*=25 | 19.2±11.3<br>*N*=25 |

### *Filial Cannibalism*

Considering only laboratory nests, all control nests ($N = 37$) lost some eggs to cannibalism, either by the mother or by the nymphs. In total, 32.4% of control nests ($N = 12$) were completely aborted through whole clutch filial cannibalism. In nonaborted nests ($N = 25$), a mean of 17.4 ± 0.0% of eggs were cannibalized, resulting in 81.9 ± 0.0% hatching success. Among these nonaborted nests, the mean fraction of prenymph egg cannibalism was 6.3 ± 0.0% (3.2 ± 0.8 eggs), but mean postnymph cannibalism was significantly higher, at 11.1 ± 0.0% (5.1 ± 0.9 eggs; two-sided $t$ test: $t_{46.3} = -2.147$, $N = 25$, $P = 0.0370$).

Females that had higher prenymph cannibalism rates were significantly less likely to have a subsequent clutch (logistic regression: $R^2 = 0.222$, $N = 25$, $P = 0.0186$), but results were nonsignificant for postnymph ($R^2 = 0.091$, $N = 25$, $P = 0.1313$) and total cannibalism ($R^2 = 0.019$, $N = 25$, $P = 0.4899$). There was no effect of filial cannibalism on female mortality rate (logistic regression: prenymph: $R^2 = 0.000$, $P = 0.9955$; postnymph: $R^2 = 0.064$, $P = 0.3253$; total: $R^2 = 0.035$, $P = 0.4222$).

Body size (pronotum width) and clutch size (first nest) followed a positive trend, with larger females laying significantly more eggs (linear regression: $R^2 = 0.063$, $N = 68$, $P = 0.0386$; Fig. 3). Females that laid more eggs in proportion to the population mean for their body size did not, however, cannibalize significantly more eggs (linear regression: prenymph cannibalism: $R^2 = 0.028$, $N = 23$, $P = 0.4486$; postnymph cannibalism: $R^2 = 0.129$, $N = 23$, $P = 0.0922$; total cannibalism: $R^2 = 0.165$, $N = 23$, $P = 0.0547$). The rate of prenymph egg cannibalism increased over time ($R^2 = 0.077$, $N = 94$, $P = 0.0069$), with higher rates occurring later in the nesting period.

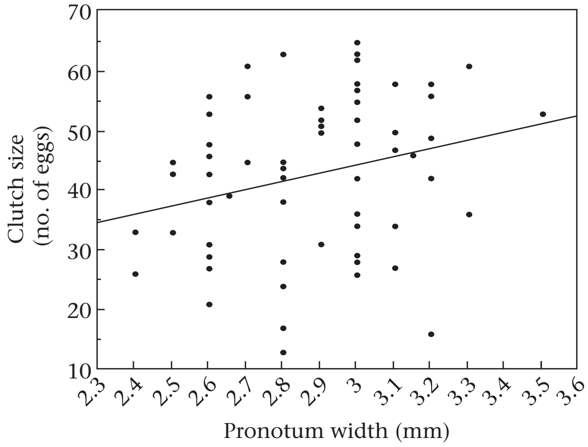

**Figure 3.** Relation between clutch size (total number of eggs/clutch) and female body size (pronotum width) in maritime earwigs. Residuals from this regression were used in the analysis of filial cannibalism rates.

Females are constrained to oviposit one egg at a time, over a period of days, resulting in slight laying asynchrony, with larger clutches taking longer to complete. Asynchrony in development is also observable, as eggs change size and transparency throughout development. The mean time to hatching was 18.9 ± 0.3 days. Laying asynchrony had a significant effect on the duration of care (multiple regression: $F_{1,21} = 6.014$, $N = 25$, $P = 0.0230$), with greater asynchrony leading to longer care periods. Filial cannibalism did not have a significant effect on the duration of care (multiple regression: $F_{1,21} = 3.347$, $N = 25$, $P = 0.0816$), and the interaction effect was also nonsignificant ($F_{1,21} = 2.014$, $N = 25$, $P = 0.1706$). Laying asynchrony was not significantly related to the number of eggs cannibalized in total (linear regression: $R^2 = 0.009$, $N = 25$, $P = 0.6595$), nor before (linear regression: $R^2 = 0.001$, $N = 25$, $P = 0.8642$) or after hatching ($R^2 = 0.022$, $N = 25$, $P = 0.4795$).

## DISCUSSION

### *Benefits and Costs of Maternal Care*

Our results show that maternal care in the maritime earwig provides a substantial survival advantage to offspring. Clutches with a guarding female had approximately seven times the hatching success of nests in which the female had been removed under both laboratory (55.3% versus 7.9%) and field (23.5% versus 3.2%) conditions. This is an especially strong effect in comparison to similar studies. Maternal care increases survival by about 20% in a subsocial spider, *Coelotes terrestris* (Gundermann et al. 1997), and by 50% in the treehopper, *Publilia concava* (Zink 2003). While relative field survival rates corroborate the laboratory experiment, hatching success in field nests was significantly lower overall. Under the control treatment, a higher fraction of nests had complete mortality in the field than in the laboratory, reflecting additional pressures in the field on both the mother and her eggs, such as pathogens, predation, variation in food abundance or submersion under high tide.

Despite the potential threat of predators, our field data provide mixed support for predator defence in maternal care. Erecting a protective mesh cage around guarding females did not increase hatching success, and depredation rates were similar for caged and uncaged nests without a guarding female. However, ants and other earwigs (conspecifics) were directly observed consuming or taking eggs (for more detailed discussion of conspecific egg cannibalism, see Miller et al. 2011), and in some cases, were found inside the mesh cage. These observations may render the caged treatments obsolete, since caged treatments were most likely exposed to the same small predators as uncaged nests. This would explain why our results showed no effect of predator exclusion cages on hatching success; therefore, we are not ready to dismiss predation as an important factor in maternal care, especially given the relatively frequent observations of nest predation in the field.

Our results suggest that egg cleaning is an important function of maternal care. Both field and laboratory nests developed fungal or microbial growth, but always at higher rates in unguarded nests. High levels of fungal infection in the laboratory (74%) may none the less exaggerate the importance of egg sanitation; consistent effects of maternal care on field infection rates confirm that mothers are important for preventing and removing infection. Studies on different earwig species have shown that females also clean fungus off their eggs, either manually or with a fungicide (Klostermeyer 1942; Bhatnagar 1963; Knabke & Grigarick 1971), although we did not investigate the mechanism of egg cleaning.

We measured the costs of care in terms of future fecundity by comparing female mortality rate, probability of renesting, subsequent clutch size, internest interval and total eggs laid. We could not measure lifetime fitness or total number of hatched nymphs per female because secondary nests were reared under separate experimental conditions. We detected only minor costs to maternal care when weighed against the benefits. The only cost we detected was that caring females tended to have smaller subsequent clutch sizes. An extended internest interval is not a clear cost to care, since females that were liberated from care still had to wait, on average, 19 days before they could initiate a subsequent clutch. The large standard error for internest interval, however, suggests that some females are able to reinitiate a nest immediately, while others wait, perhaps due to physiological constraints on hormone levels (Vancassel 1984). In contrast to our results, similar studies on a burrower bug *Sehirus cinctus* (Agrawal et al. 2005) and a subsocial spider (Gundermann et al. 1997) found that the major cost to egg guarding is an extended internest interval. We also found that providing care did not impair the chances of renesting, increase mortality or affect the total eggs laid. However, our findings are probably an underestimate since all measurements were taken on laboratory-nesting females. Agrawal et al. (2005) found no reduction in lifetime fecundity for caring in burrower bug females, but their work was also conducted under laboratory conditions. In contrast, a field study on treehoppers (Zink 2003) and a laboratory study on lace bugs, *Gargaphia solani* (Tallamy & Denno 1982) both showed that maternal care lowers lifetime fecundity. Costs to lifetime fecundity may be greater in species with facultative care, like in treehoppers (Zink 2003). Consistent with a relatively low cost of care, nest abandonment, in which the eggs are left behind, was never observed either in our laboratory nests or in our field nests. Natural abandonment, or more accurately, abortion, always coincided with whole clutch filial cannibalism, making it unlikely that females ever leave their clutch intact for the purpose of starting a new one.

Significantly reduced hatching success in the field (by almost half) reflects substantial challenges of nesting in the natural environment. These challenges (i.e. from predators, pathogens, unpredictable resources, etc.) probably have long-lasting effects on future reproduction as well. By feeding females ad libitum, energetic exhaustion and the risk of predation, either on the nest or on the female, while foraging cannot be accounted for in our laboratory study. Although females in the laboratory rarely left the nest to feed, our field results showed lower hatching success when the female was caged, suggesting that foraging during care may be important (see Suzuki 2010). However, in a recent study in the European earwig (*F. auricularia*), intrinsic differences in female quality led to variation in maternal care investments even when females were fed ad libitum (Meunier et al. 2011). Even though we were unable to measure energetic components directly related to the cost of care, we did detect indirect costs of care.

### *Filial Cannibalism*

A parental care strategy including filial cannibalism can evolve when the energy gained from eating eggs improves the quality of care for the current clutch, or improves future reproductive success (Klug & Bonsall 2007). As the female's energy reserves diminish during care, it would be advantageous to replenish reserves without compromising the survival of the rest of the clutch. Leaving the nest to forage could be fatal to the clutch, making it vulnerable to predation, so females may instead sacrifice a portion of the clutch to avoid starvation. The number of eggs eaten should therefore reflect the energetic demands of the female.

Our results show that females lay clutch sizes roughly in proportion to their body size, but there is substantial variation around this trend. Using this variation, we asked whether females that overshoot clutch size in proportion to their body size eat more eggs, since they will have exhausted more energy and nutrients than their more conservative counterparts. A strategy of laying a surplus of eggs probably has its benefits, since those extra eggs would survive to hatching under favourable environmental and energetic conditions. Maintaining extra eggs is of little cost to the female, since hatching success was not dependent on clutch size. Despite the plausibility of this strategy, we found no evidence for it in our data, as females that laid proportionally more eggs did not cannibalize more. However, energy limitation may still be a factor in filial cannibalism rates, as egg cannibalism rates (prenymph) increased later in the nesting period, when energy reserves were hypothetically at their lowest. Ad libitum feeding before and during nesting may have reduced the energetic incentive for filial cannibalism, although females were not observed to leave the nest to feed during care (based on videotaped records of nests). We also found that female body size was not related to the quality of care, as body size was not predictive of hatching success. Therefore, the variation in cannibalism across female body sizes was not explained by variation in the quality of care.

We found evidence that laying asynchrony staggers development and increases the length of care in the maritime earwig. Females are expected to devote a certain amount of time to care until reaching a point of diminishing returns, at which point it is in their interest to terminate care and initiate another nest (Clutton-Brock 1991). Filial cannibalism has the potential to ameliorate the effects of asynchrony and reduce the duration of nesting by eliminating less mature eggs. Male sand gobies, *Pomatoschistus minutus*, that provide care to eggs regulate the duration of care by selectively cannibalizing slower-developing eggs or by consuming the remaining eggs after asynchronous hatching (Klug & Lindström 2008). Our results were inconsistent with this hypothesis, as we found that the degree of laying asynchrony was not predictive of filial cannibalism rates and that filial cannibalism rates did not covary with the duration of care. Therefore, we found no evidence that filial cannibalism regulates the duration of care.

As an additional test of egg cannibalism as a way for females to titrate energetic investments across clutches, we examined whether eggs eaten in the current clutch translate into future reproduction. We predicted that females that ate more eggs would be more likely to have a subsequent nest, but our results showed the opposite trend: females with higher prenymph cannibalism rates were less likely to have a subsequent clutch. These results suggest that filial cannibalism is a last resort strategy to sustain the female through to the end of nesting, and would therefore support the energy limitation hypothesis.

We consider an alternative hypothesis for the function of filial cannibalism in which females consume unviable eggs that become infected or that fail to develop properly, encompassing the hygienic services already discussed. We could not directly address this hypothesis because we were unable to mark individual eggs or observe early-stage egg infection. If more eggs become infected over time, unviable eggs may be consumed disproportionately later in the nesting period, as it may take time for infection to become apparent. Our finding that prenymph filial cannibalism rates increased over time is consistent with this hypothesis, but is also consistent with the energy limitation hypothesis.

Interestingly, the highest rates of egg cannibalism occurred after the appearance of nymphs, implicating nymphs as egg cannibals as well. Nestmate cannibalism occurs in the European earwig, but only at the nymphal stage after all eggs have hatched (Dobler & Kölliker 2010). Asynchronous hatching could facilitate nymphal cannibalism while both nymphs and eggs overlap in the nest. It is also plausible that eggs laid later on serve as food for nymphs; however, they do not appear to be true trophic eggs (Perry &

Roitberg 2006), since all eggs undergo development. Alternatively, females could eat the eggs before the nymphs do to mitigate sibling conflict or because the energetic demands of care increase as nymphs begin hatching.

We show that the benefits of maternal care in the maritime earwig are substantial and greatly outweigh the costs, which are minor by comparison, even if our measures underestimated these costs. The function of filial cannibalism in the maritime earwig remains inconclusive, but we found indirect support for both nest sanitation and energy limitation. Filial cannibalism is expected when there are relatively high costs of care (Manica 2002; Klug & Bonsall 2007); yet, we found that the costs of care are relatively low. This discordance suggests that filial cannibalism does not function primarily to offset the costs of care in this system. Future work should manipulate female condition and egg development to disentangle the roles of filial cannibalism in the maritime earwig.

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