

Kin-selected siblicide and cannibalism in the European earwig

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Aggression levels among individuals can severely increase under high density or shortage of crucial resources, sometimes resulting in individuals killing conspecifics. This is not uncommon in family groups of diverse taxa, where the dependent offspring compete for the limited resources provided by their parents. Killing a nest mate can relax the level of competition, and cannibalism provides a direct nutritional benefit. However, nest-mate killing bears the risk of reducing indirect fitness if the victim is related (i.e., siblicide), imposing selection on kin-recognition abilities. Based on this hypothesis, we predicted that first instar juveniles (nymphs) of the European earwig (*Forficula auricularia*) kill and cannibalize unrelated nest mates earlier and more often than related nest mates and that cannibalism has a direct nutritional benefit in terms of survival. We tested these predictions experimentally by establishing related and unrelated pairs of nymphs and recorded survival, aggregation behavior, and cannibalistic outcomes in the absence of alternative food sources. In order to obtain expected survival probabilities of victims and survivors in the absence of any interaction, we simulated virtual nymph pairs based on survival data of singly held control individuals. As predicted, victims lived for less time and survivor for longer than expected from the simulated survival distributions, demonstrating nest-mate killing and cannibalism. Furthermore, unrelated individuals were killed significantly earlier and were more often cannibalized than related individuals. The survival patterns of victims and survivors were quantitatively consistent with the expectations of Hamilton's rule. Our study shows that earwig nymphs recognize kin and adjust their nest-mate killing and cannibalistic behavior as predicted under the hypothesis of kin-selected siblicide and cannibalism. *Key words:* *Forficula auricularia*, Hamilton's rule, intraspecific predation, kin recognition, sibling rivalry. [*Behav Ecol* 21:257–263 (2010)]

In social animals where caregivers (e.g., workers or parents) invest continuously essential resources for juvenile development, competition among the juveniles can be very intense, in particular in large broods/litters or under resource limitation by the caregivers (Fox 1975; Mock and Parker 1997). Under intense competition, selection may favor aggressive interactions among juveniles (i.e., siblings), which may go as far as siblicide (O'Connor 1978; Mock and Parker 1997). There are many anecdotal reports, suggesting that siblicide (and/or cannibalism) is a common phenomenon in diverse taxa, including insects (Grbic et al. 1992; Van Buskirk 1992; Fincke 1994; Osawa 2002; Ohba et al. 2006), spiders (Bilde and Lubin 2001), snails (Baur 1992), amphibians (Pfennig et al. 1993, 1994), fish (FitzGerald and Whoriskey 1992), and mammals (Fox 1975). Importantly, this occurs not only under harsh environmental conditions (Fox 1975) and is not limited to competing juveniles. Individuals of different live stages may kill and cannibalize conspecifics when in competition for critical resources (e.g., mates or food; e.g., Baur 1992; Sargent 1992; Stevens 1992), which can have important consequences for the population dynamics of some species (Fox 1975; Polis 1981; Wise 2006). The evolutionary function is of similar nature in most cases: Killing a conspecific can reduce the competition level for the access to the limited resources, whereas cannibalism provides additional nutrition.

For offspring of group living or social species, chances are high to kill a closely related individual (Pfennig 1997). If the killed individual is a full or a half sibling, the term siblicide is used to describe the behavior (Mock 1984). The potential costs due to

reduced indirect fitness are expected to generate selection on mechanisms that enables individuals to avoid killing siblings. One mechanism is to avoid encounters with relatives by spreading over space and time via dispersal (Perrin and Goudet 2001; Ohba et al. 2006), which is of limited scope in cases when siblings compete in a brood for parental resources. Alternatively, individuals can recognize kin directly (genetically) or indirectly through phenotypic or environmental correlations with kinship (Pfennig 1997; Tang-Martinez 2001). Siblicide should not disappear with the ability of kin recognition, but its incidence should become rarer (Gardner and West 2007), and it should only occur when the direct fitness benefits outweigh the costs due to indirect fitness losses (Hamilton 1964a, 1964b; Mock and Parker 1997; Pfennig 1997).

A variety of experiments were carried out with different study organisms to gain insight into the evolution of siblicide or cannibalism (e.g., Van Buskirk 1989; Fincke 1994; Pfennig et al. 1999; Hvam et al. 2005; Schneider and Bilde 2008). As expected, it was generally found that siblicide reduced density and competition and that cannibalism increased the survival of the aggressor (Van Buskirk 1989; Fincke 1994). It has also been shown that body size or weight can influence the siblicidal and cannibalistic behavior (e.g., O'Connor 1978; Van Buskirk 1992; Fincke 1994; Hvam et al. 2005). However, our quantitative understanding of fitness components due to siblicide and cannibalism in the evolution of sibling interactions is still limited.

A substantial body of theoretical work on the evolution and stability of siblicide and cannibalism was developed (e.g., O'Connor 1978; Mock and Parker 1998; Pexton and Mayhew 2002; Nishimura and Isoda 2004; Perry and Roitberg 2005). In these models, kin recognition is predicted to be a key factor (Mock and Parker 1997, but see also Crozier 1986; Fletcher and Doebeli 2009). Although genetic kin recognition is observed at much lower frequencies than expected (Gardner and West 2007), probably because this form of kin recognition

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is often evolutionarily not stable (Rousset and Roze 2007), indirect phenotypic mechanisms are widespread. An added component of selection for kin recognition specific to the evolution of cannibalism may be due to the differential risk of transmission of pathogens within a species (Polis 1981). Pathogens may be adapted to a specific host genotype, in which case cannibals can minimize the infection probability with such pathogens by avoiding scavenging on bodies of related individuals (Pfennig 1997).

A lot of empirical and theoretical work has been done on siblicide and cannibalism, but to our knowledge, no empirical work experimentally disentangled siblicide and cannibalism and partitioned the corresponding fitness consequences. We carried out experiments to discriminate between benefits and costs of nest-mate killing and cannibalism among juveniles (first instar nymphs) of European earwigs (*Forficula auricularia*, Dermaptera). In this species, nymphs of a brood (nest mates) stay together during the first juvenile instar (about 10 days) before they disperse. Diversity in kinship among family members of 1 brood can be high because offspring in 1 brood are typically sired by multiple males (Guillet 2000) and nymphs may join other family groups (Kölliker and Vancassel 2007). We therefore expect in this system selection on kin-recognition abilities that modulate siblicide and/or cannibalism.

Based on the hypothesis of kin-selected siblicide and cannibalism, we predicted that 1) victims of nest-mate killing live for less time than expected in the absence of interactions, 2) the individuals that kill nest mates and cannibalize the victim live longer than expected, and 3) relatedness reduces the likelihood of nest-mate killing and cannibalism. The distribution of survival times expected for victims and survivors in the absence of interactions was generated by using survival data from control nymphs held singly under identical conditions and pairing them virtually in computer simulations.

MATERIALS AND METHODS

Study organism

We caught adult European earwigs (*F. auricularia*) on an organic pear orchard near Opfershofen (Thurgau, Switzerland) in September 2008 and brought them to the laboratory. *Forficula auricularia* is a subsocial insect species with a 1-year generation cycle. Females care for eggs overwinter and provide newly hatched offspring with food during the first juvenile instar (Kölliker 2007).

The earwigs were set up in Petri dishes (10-cm diameter) on humid sand as substrate in male–female pairs or female alone. After setup, the animals were kept under standard rearing conditions (for details, see Kölliker 2007; Staerkle and Kölliker 2008; Mas et al. 2009) until the females laid their eggs and the eggs subsequently hatched. It is presumable that the females already mated with several males in the field. The offspring of one female (family) are therefore assumed to be a mixture of half sibs and full sibs. Number of eggs and hatchlings per family were recorded. The mean number of eggs per clutch was 45.530 ± 0.852 ($N = 213$, data for one clutch missing), and on average, there were 29.233 ± 0.822 ($N = 213$) hatchlings per clutch.

Experimental design

The purpose of our experiment was to test whether siblicide, cannibalism, or both occur in *F. auricularia* and how relatedness affects such behavior. We used newly hatched nymphs for our experiment and set them up in the experimental treatments within 24 h after the first hatching in a family was observed. We paired 2 families hatching on the same day for 1 replicate, and

each family was only used for 1 replicate. Each replicate included 5 different treatments based on nymphs combined from the 2 families in different ways: a control treatment (C), a sib treatment (S), a nonsib treatment (N), a sib treatment with marked individuals (SM), and a nonsib treatment with marked individuals (NM) (see below for detailed description of treatments; Bilde and Lubin [2001] for a similar design). Marking the individuals allowed us to assign the initial weight to the individual nymphs (see below) and include weight asymmetries in the analyses. The nymphs were set up in transparent polystyrene boxes ($22 \times 22 \times 14$ mm, Art. 2964, Semadeni, Ostermundigen, Switzerland) with 1.5 ml of moist sand as substrate according to their treatment. Prior to setup, they were weighed on a Mettler-Toledo microbalance (Mettler AT5, Greifensee, Switzerland) with an accuracy of $1 \mu\text{g}$. The average weight of a hatchling was 1.512 ± 0.007 mg ($N = 1428$) and did not differ significantly between the treatments (Kruskal–Wallis rank sums: $\chi^2 = 1.336$, degrees of freedom [df] = 4, $P = 0.855$; means \pm standard error [SE]: C, 1.525 ± 0.019 mg; S, 1.512 ± 0.013 mg; N, 1.514 ± 0.026 mg; SM, 1.498 ± 0.013 mg; NM, 1.522 ± 0.021 mg). There was a significant family effect on weight (Kruskal–Wallis rank sums: $\chi^2 = 1076.325$, df = 213, $P < 0.001$; intraclass correlation coefficient = 0.49), indicating that weight at hatching may at least partially be inherited.

For the control treatment (C), 1 randomly chosen nymph of each family was set up alone in 1 box. For the sib treatment (S), 2 randomly chosen nymphs of the same family were set up in 1 box, and for the nonsib treatment (N), 2 randomly chosen nymphs from different families were set up together. The marked replicates (SM and NM, respectively) were set up the same way as S and N. Nymphs were marked after weighing for individual recognition with a red or blue CD marker pen (Potaco A.quip, Elgg, Switzerland) on their legs and/or thorax while gently immobilized with a mosquito net on a foam stopper.

Overall, marking had a significant negative effect on survival of individuals ($F_{1,1220} = 16.757$, $P < 0.001$, $r^2 = 0.015$). But this effect was similar for victims (the first individual in a pair to die) and survivors (the second individual in a pair to die; 2-way analysis of variance, interaction effect: $F_{1,1220} = 0.0073$, $P = 0.929$). The marking effect did not confound our statistical analyses as we never compared marked with unmarked individuals.

Each replicate hence consisted of 8 boxes (2 C singlets, 2 S pairs, 2 SM pairs, 1 N pair, and 1 NM pair). The 8 boxes of one replicate were placed on the bottom side of a 10-cm Petri dish lid and position of the treatments was randomized over replicates to avoid position effects. In total, 107 replicates were set up with 214 families.

After setup, each box was checked daily and water was added when necessary to prevent drying out of the sand. Nymphs never got food to avoid any skew in survival (e.g., through differences in food quality) and to precipitate siblicide/cannibalism. Note that siblicide/cannibalism also occurs when food is provided ad libitum but at lower frequencies (Dobler R, Kölliker M, unpublished data). Death of animals was reported daily. When both died on the same day, the roles of victim and survivor were assigned randomly. Bodies were left in the boxes to give the survivor the opportunity to cannibalize the victim. Cannibalism was scored as such when the victim was sucked out or body parts or the whole body were missing. In cases where the body started to grow mold, it was removed to prevent an infection of the survivor. The likelihood of cannibalism was not affected by the marking (sib: loglikelihood = -0.957 , Pearson $\chi^2 = 1.907$, $P = 0.167$; nonsib: loglikelihood = -0.041 , Pearson $\chi^2 = 0.082$, $P = 0.774$). To further assess a potential role of kin recognition on a behavioral level, we scored the aggregation of the individuals in pairs daily. They received a “1” if they were in body contact and a “0” if not. An aggregation index was obtained by averaging this score over the number of days when

both individuals were alive was used as an estimate for aggregation behavior.

Statistical analyses

It is a priori not possible to state a null hypothesis for the survival probability of interacting pairs of individuals. We used the individuals from the control treatment (C) to simulate the null hypothesis for survival patterns in the absence of interactions between nymphs. These simulated pairs provided us with a distribution of survival times for victims and survivors under the null hypothesis of no siblicide and no cannibalism. In a permutation test, we paired individuals from the control treatment virtually and assigned the one that died first to be the victim and the one who lived longer to be the survivor. Like in the real interaction treatments, we assigned victim and survivor randomly when both individuals lived for the same time. Using the “survival” package in R (version 2.8.1; 2009-10-26; R Development Core Team 2009), we calculated the daily survival probabilities for victims and survivors across 1000 permutations to estimate the mean daily survival probability and 95% confidence interval (CI) expected under the null hypothesis of no siblicide and no cannibalism. The 25th and 975th value for the daily survival probabilities, respectively, was used to generate the 95% CI around the expected daily mean survival probabilities.

If siblicide occurs, we predicted that real victims should die earlier than the “victims” in the simulated pairs because they get actively killed by the survivor. Furthermore, we predicted that real survivors should live longer than “survivors” in the simulated pairs because the survivor gains energy when eating the victim. Such an effect was considered to be statistically significant when the observed survival was outside the 95% confidence limits of the simulated null hypothesis.

We used JMP 7.0.2 (JMP Version 702 1989–2007) and R version 2.8.1 (2009-10-26; R Development Core Team 2009) for statistical analyses. We excluded treatment replicates where one individual died within 24 h after set up as we cannot exclude the possibility that they died as a consequence of handling at setup. This resulted in the following numbers of replicates in each treatment (number of setup replicates in brackets): C = 204 (214), S = 208 (214), N = 100 (107), SM = 204 (214), NM = 100 (107).

RESULTS

Siblicide and cannibalism

The observed survival curves deviated from the simulated curves in the case of siblings (Figure 1a) as well as in the case of unrelated pairs (Figure 1b). As expected, if siblicide occurred and reduced the survival of the victims, the survival curve of the victims was significantly below the simulated null expectation curve over parts of the total range of survival times. The effect was present in the beginning, up to day 10 in the sibling treatment (Figure 1a), and up to day 11 in the nonsibling treatment (Figure 1b). Conversely, and as expected when cannibalism occurred and had benefits for the survivor, the observed survival curves were significantly above the simulated curves, an effect detectable after day 10 in both treatments (Figure 1).

Kin recognition

We hypothesized selection for kin-recognition abilities and predicted that victims in pairs of unrelated nymphs should die earlier than victims in sib pairs. Comparing the victims and the survivors between the 2 treatments (S and N) revealed a significant difference in the survival of the victims but not in

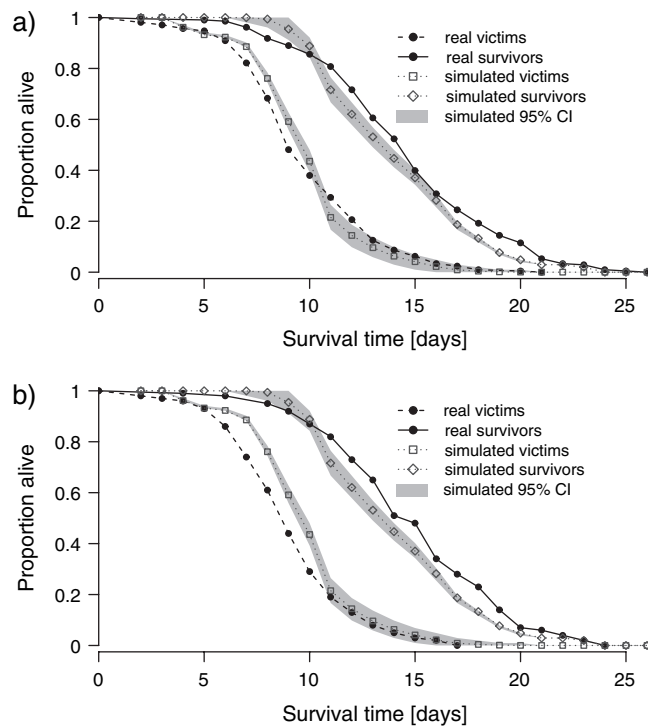


Figure 1
Effects of siblicide and cannibalism on survival. Overlay of simulated survival data and observed survival data. Simulated data are based on virtual pairs of singly held control individuals (for details, see MATERIALS AND METHODS). (a) Graph includes the data from the unmarked sib pairs. (b) Graph based on the data of the unmarked nonsib pairs. In both cases, victims survive for less time than expected by simulation and survivors survive longer than expected by simulation. This indicates costs of siblicide (or killing) to the victims. The survivor gets benefits from siblicide and/or cannibalism.

the survivors (Table 1). Thus, relatedness had the expected effect of increasing the survival of the related victim, but contrary to expectation, the increase in survival of the unrelated survivor was statistically not significant. Furthermore, the summed survival time of a pair did not differ between related and unrelated pairs (Kruskal–Wallis rank sums: $\chi^2 = 0.150$, $df = 1$, $P = 0.697$).

To analyze the kin effect also in relation to individual weight among interacting nymphs, a similar analysis was carried out using the replicates with marked individuals (treatments SM and NM) where we could assign the weight to victim and survivor. Including individual weight in the analysis showed

Table 1
Effect of relatedness on survival of victims and survivors. Parametric survival fit, Weibull distribution

Source	likelihood-ratio χ^2	Estimate \pm SE ^a	df	P
Victims (S–N)				
Relatedness	4.863	0.041 \pm 0.018	1	0.027
Survivors (S–N)				
Relatedness	0.040	–0.003 \pm 0.015	1	0.840
Victims (SM–NM)				
Relatedness	6.027	0.055 \pm 0.022	1	0.014
Survivors (SM–NM)				
Relatedness	0.161	–0.007 \pm 0.017	1	0.690

^a Positive estimates indicate related individuals survived longer.

a significant overall correlation between survival time and weight (Spearman's $\rho = 0.382$, $P < 0.001$). Statistically controlling for this relationship did not change the previously described effect of relatedness on the survival of victims and survivors (see Tables 1 and 2, Figure 2).

The weight asymmetry Δw of the 2 individuals in a pair ($\text{weight}_{\text{survivor}} - \text{weight}_{\text{victim}}$) was significantly smaller in the sib treatment than in the nonsib treatment (Kruskal–Wallis rank sums: $\chi^2 = 17.632$, $df = 1$, $P < 0.001$; median sib: 0.16 mg, median nonsib: 0.23 mg), an effect easily explained by the strong family effect on hatchling weight (see MATERIALS AND METHODS).

To test for kin effects on sibicide and cannibalism, although controlling for weight asymmetries, we used the weight differences Δw and compared them with the survival differences between survivor and victim, respectively ($\Delta s = \text{survival}_{\text{survivor}} - \text{survival}_{\text{victim}}$). Our null expectation for the relation between Δs and Δw was again generated using the simulation approach based on the control individuals. The average weight difference Δw across 1000 permutations was significantly and positively related to the survival difference Δs ($F_{1,100} = 854.460$, $P < 0.001$). The simulated intercept was not significantly different from 0 ($P = 0.403$; Figure 3), indicating that control individuals with the same weight showed no difference in survival time in the absence of interactions. In the real pairs, Δw was significantly positive related with Δs ($F_{1,300} = 27.737$, $P < 0.001$) and the intercepts deviated significantly from 0 ($F_{1,300} = 6.079$, $P = 0.014$). This latter result demonstrates a difference in survival time independent of weight asymmetry with a significant effect of relatedness on Δs (higher Δs in unrelated pairs). There was further no significant interaction between relationship and weight asymmetries ($\Delta w \times \text{relatedness}$ $F_{1,300} = 0.038$, $P = 0.845$; Figure 3). Integrated over the whole observed Δw range, nonsibs showed a $27.2 \pm 10.0\%$ higher Δs value than sibs (means \pm SE: Δs sibs, 4.466 ± 0.250 days; Δs nonsibs, 5.680 ± 0.386 days; Figure 3).

The frequency of cannibalized victims in the nonsib treatments (N, NM) was significantly higher compared with the sib treatments (S, SM; Fisher's Exact test: $P = 0.013$; nonsib, $n = 200$, 93.5% cannibalism; sib, $n = 412$, 86.7% cannibalism).

To further analyze potential benefits of cannibalism correlations between the rate of cannibalism and survival of victims and survivors were carried out. Δs was significantly larger when the victim was cannibalized (Kruskal–Wallis rank sums: $\chi^2 = 49.9$, $df = 1$, $P < 0.001$). Whether a victim was cannibalized or not was not significantly related to the survival time of the victim (Kruskal–Wallis rank sums: $\chi^2 = 0.153$, $df = 1$, $P = 0.695$) but positively to the survival time of the survivor (Kruskal–Wallis rank sums: $\chi^2 = 47.52$, $df = 1$, $P < 0.001$).

Table 2

Effect of relatedness on survival of victims and survivors, including weight as a covariate. The interactions relatedness \times weight were not significant (victims: $P = 0.054$; survivors: $P = 0.731$) and were therefore removed from the analysis. Parametric survival fit, Weibull distribution

Source	likelihood-ratio χ^2	Estimate \pm SE ^a	df	P
Victims (SN–NM)				
Relatedness	4.442	0.042 ± 0.019	1	0.027
Weight	41.183	0.477 ± 0.071	1	<0.001
Survivors (SM–NM)				
Relatedness	0.721	0.012 ± 0.014	1	0.384
Weight	95.770	0.491 ± 0.047	1	<0.001

^a Positive estimates indicate related or heavier individuals survived longer.

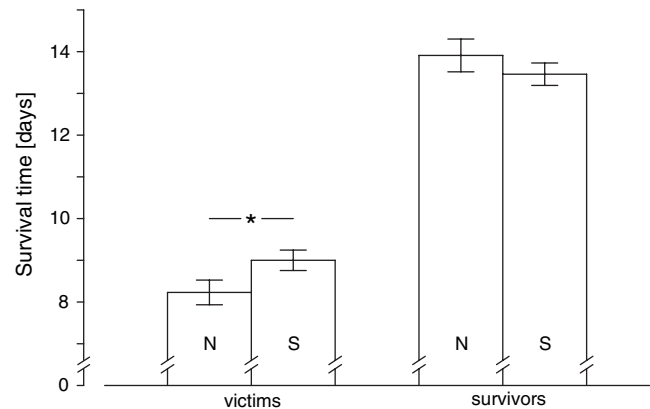


Figure 2

Survival of victims and survivors in related (S) and unrelated (N) pairs. The unrelated victims live for significantly less time than the related victims (mean \pm SE, nonsibs: 8.23 ± 0.29 days, sibs: 9.00 ± 0.24 days). But there is no significant difference in survival between related and unrelated survivors (mean \pm SE, nonsibs: 13.91 ± 0.39 days, sibs: 13.46 ± 0.29 days).

Aggregation did not significantly differ between the sib and nonsib treatments (Kruskal–Wallis rank sums: $\chi^2 = 0.001$, $df = 1$, $P = 0.991$) and was not significantly correlated with the occurrence of cannibalism (logistic fit: $\chi^2 = 0.461$, $df = 1$, $P = 0.496$).

DISCUSSION

It is not trivial to experimentally demonstrate whether victims truly die due to nest-mate killing or whether they just starve and are then cannibalized. Killing events are typically rarely observable, although we did make the observation in a few cases (Dobler R, Kölliker M, personal observation; see also Supplementary Material). Broods of European earwigs contain

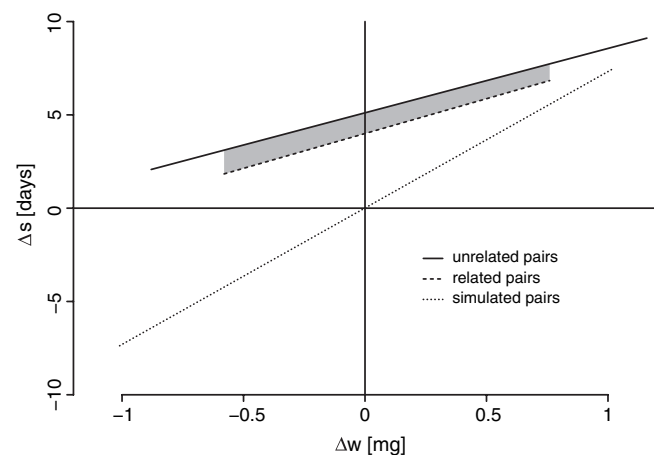


Figure 3

Relation between Δs (difference in survival time between survivor and victim) and Δw (weight difference between survivor and victim). The area shaded in gray represents Δ^2_s , this is the difference between unrelated (solid line) and related (dashed line) pairs for any given weight asymmetry. The value of Δ^2_s can be used to estimate the relative relatedness difference between nonsib and sib pairs (for details, see text). The dotted line is the expected effect of Δw on Δs when the 2 individuals from a pair do not interact, based on the simulated data. Line length represents the range of observed values.

offspring from diverse genetic backgrounds (mixed paternity [Guillet 2000] and brood joining/adoption after hatching [Kölliker and Vancassel 2007]), which sets the stage for kin selection to potentially favor kin recognition in nest-mate killing and cannibalism. The predictions from the hypothesis of kin-selected siblicide and filial cannibalism were mostly supported by our results. Victims died earlier than expected by chance, survivors lived longer than expected by chance, and victims in related pairs lived longer than victims in unrelated pairs. However, the expected effect that unrelated survivors should survive longer than related survivors (because unrelated individuals could benefit more from killing and cannibalizing the victim earlier) was not statistically significant. Nevertheless, a role for the expected kin recognition in cannibalism and associated benefit was suggested by the significantly higher rate of cannibalism in unrelated pairs of nymphs and a positive association between the survival time of the survivor and the incidence of cannibalism.

Our experiments were designed to elucidate the functional context of nest-mate killing during the time of maternal care in the European earwig and to quantify fitness costs and benefits to victim and survivor, respectively. Previous research explored the role of kin in mediating forms of cannibalism mostly in nonsocial animals (but see Bilde and Lubin 2001). For instance, Pfennig et al. (1993) observed direct siblicide and cannibalism in their study on polyphenism in tadpoles of the spadfoot toad (*Scaphiopus bombifrons*), and they found that carnivores consume significantly fewer siblings than nonsiblings. A majority of studies report indirect evidence for cannibalism by observing that individuals disappeared and remaining bodies or body parts (dragonfly larvae *Aeshna juncea* and *Tramea carolina* [Van Buskirk 1989, 1992]; damselfly larvae *Megaloprepus coerulatus* [Fincke 1994]; wolf spiders *Pardosa amentata* [Hvam et al. 2005]), not allowing the discrimination between nest-mate killing and cannibalism and the associated fitness consequences. With the simulation of the survival of victims and survivors in control individuals, that is, noninteracting “pairs,” we created the distribution of expected survival probabilities for victims and survivors under the null hypothesis. Only with such controls is it usually possible to determine the occurrence of nest-mate killing (albeit indirectly) and to quantify the fitness consequences for the victims and the survivors.

In *F. auricularia*, nest-mate killing is at least partially driven by the nutritional benefit obtained from cannibalism. We showed that survivors lived longer than expected and that victims lived for less time than expected, indicating that the survivors killed the victims to cannibalize them. In addition to this nutritional benefit, the evolutionary function of earwig nest-mate killing to relax competition between nymphs for maternal food provisioning (Stanback and Koenig 1992) cannot be ruled out. A previous study showed that the survival of individual nymphs is higher in small broods (Kölliker 2007), indicating a potential benefit of nest-mate killing in terms of reduced competition. This may increase the survival probability of the survivor beyond the one reported in this study. Given the large earwig brood sizes (Kölliker 2007), a relatively high rate of nest-mate killing would probably be required to generate a biologically relevant benefit from reduced competition, but this needs further investigation.

Although we cannot fully rule out the possibility, it is unlikely that the reduced life span of victims in our experiments is due to stress induced by the interaction with the survivor and not the result of active killing. If this was the case, an effect of kin would not be expected as we kept all individuals under identical conditions, and our observations of nest-mate killing (see above) also document this behavior directly. There was no evidence for a difference in aggregation behavior between related and unrelated pairs, and aggregation did not signifi-

cantly correlate with the rate of cannibalism. These results suggest that related and unrelated nest mates behaviorally interacted to a similar degree and that siblicide and cannibalism are not indirectly mediated by differential aggregation. It should be noted, however, that our measure of aggregation based on daily scan observations was rather rough and may not have picked up finer grained behavioral dynamics potentially underlying kin recognition in this species.

We observed cannibalism in 86% and more of the pairs (depending on treatment) in *F. auricularia* nymphs. This high rate of cannibalism may partly be due to the lack of alternative food sources in our experiment, but it is consistent with our general observation that dead nymphs are almost always cannibalized also in intact broods with sufficient food. The differential occurrence of cannibalism in related versus unrelated pairs showed that earwig nymphs evolved mechanism to avoid cannibalizing closely related dead nymphs. Thus, kin recognition and cannibalism may be functionally linked not only through siblicide but also through an additional mechanism. Pfennig (1997) argued that related individuals may avoid to cannibalize each other to prevent pathogen transmission despite the benefits of cannibalism to the survivor. This hypothesis is at the current stage speculative in the case of *F. auricularia* and needs further study. More generally, cannibalism in earwigs is not restricted to the period of maternal care (i.e., first instar larvae) but seems to be characteristic for other life stages as well, having potentially substantial consequences for population dynamics and selection on kin-recognition abilities across life stages. Moerkens et al. (2009) showed that whole age classes of *F. auricularia* can disappear in natural populations when densities are high and argue that cannibalism is the most likely explanation for this phenomenon.

In our experiments where no alternative food sources were provided, the direct benefit to own survival outweighed at some stage the indirect costs of killing a related individual and siblicide occurred despite the ability of recognizing kin. According to the “inverse Hamilton’s rule” (Yamamura and Higashi 1992), an individual should not kill a related individual before $B > rC$ (the benefits “B” to the survivor has to be bigger than the implemented costs “C” to the victim devalued by relatedness “r”). Because the cost of killing a related individual probably stayed quite constant during the course of our experiment, but the benefit of killing the related individual steadily increased over time, the likelihood that this condition was met gradually increased during the course of the experiment. To estimate the relatedness among nymphs that must have prevailed in the evolution of earwig siblicide and nest-mate killing if kin selection was involved (which we denote as \bar{r} in the following), we could use the values for Δs as approximation to a combined value of B and C ($\Delta s \approx B - C$). Taking the Δs value of the nonsib pairs as the baseline reference ($r = 0$), the difference in Δs between nonsib and sib pairs ($\Delta^2 s = \Delta s_{\text{nonsibs}} - \Delta s_{\text{sibs}}$) could be used to estimate the difference (expressed as a proportion) in relatedness between the treatments as $\bar{r} \approx (\Delta^2 s / \Delta s_{\text{nonsibs}})$. Based on the obtained $\Delta^2 s$ value, this estimate was approximately 27%, which fits the expected relatedness of earwig families given multiple paternity (Guillet 2000) and brood joining (Kölliker and Vancassel 2007) quite well. In our study, relatedness ranged from 0.25 to 0.5 in sib pairs (multiple but unknown paternity) and was 0 for the nonsibs. Nevertheless, the obtained estimate will need quantitative confirmation using molecular parentage analysis.

Kin recognition in its strict (i.e., genetic) sense can often be confounded with group recognition (Grafen 1990). In our experiments, hatched larvae from one brood were together for approximately 24 h before setup for the experiment. This might have been enough time for “filial imprinting” and offspring of one brood would therefore recognize each other as

familiar due to group recognition instead of kin recognition. Separating eggs before hatching in future experiments would allow to separate the potential filial imprinting from a direct kin-recognition effect (Gardner and West 2007; Schneider and Bilde 2008).

Conspecific killing, siblicide, and cannibalism are common behaviors for invertebrates (e.g., Fincke 1994; Bilde and Lubin 2001; Hvam et al. 2005) and these behaviors occur also in vertebrates (e.g., O'Connor 1978; Pfennig 1997). However, clear experimental separation for killing and siblicide and their fitness consequences (i.e., whether cannibalized individuals got killed or whether they died for another reason) is still scarce, probably partly due to the difficulty of observing the killing events per se.

Furthermore, selection on kin-recognition abilities may often not only be purely due to rivalry and conspecific killing but also due to other components of social living. For example, it may be beneficial to associate with related individuals during foraging because of reduced competition and enhanced foraging efficiency (e.g., Ruch et al. 2009). Further study is needed to better understand the components (e.g., relatedness, group size, and resource availability) shaping selection on siblicide and cannibalism and how selection on kin-recognition abilities in different functional contexts combine to favor particular mechanisms and their specificity.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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