Interactions in families of the European earwig (*Forficula auricularia*) - behavioural dynamics and conflicts

Inauguraldissertation

zur
Erlangung der Würde eines Doktors der Philosophie
vorgelegt der
Philosophisch-Naturwissenschaftlichen Fakultät
der Universität Basel

von

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Basel, 2010

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Basel, den 13. Oktober 2009

Prof. Dr. Eberhard Parlow, Dekan

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PhD-Thesis – Ralph Dobler

"Nothing in biology makes sense except in the light of evolution."

Theodosius Dobzhansky

Contents

Summary

Interactions in families and their stability are often discussed on an evolutionary background only. However, the evolutionary stability of an interaction tells only half of the story. It is further necessary to have knowledge about the behavioural stability of such an interaction in a family. What is the value of an evolutionarily stable strategy (ESS) when the behavioural dynamics that actually happens does not allow the interaction to reach or to be expressed at the evolutionary optimum? It is therefore important to know whether a behavioural interaction has an equilibrium and if so, whether and how this equilibrium can be attained behaviourally. To know whether an interaction has an equilibrium and whether this equilibrium is behaviourally attainable or not provides information about the behavioural stability of an interaction. This knowledge is important for behaviours where the behavioural stability is questioned, for example in siblicide. The knowledge of how the equilibrium is reached allows to draw conclusions about who has the behavioural control in an interaction.

In the first part of my thesis (chapter 2) I investigated the stability of behavioural interactions and whether they are compatible with ESS. In a basic two player model with repeated sequential interactions I found, that only half of the behavioural interactions lead to stability and therefore represent a behaviourally stable strategy (BSS). Testing the compatibility of BSS and ESS I found, that indeed a considerable number of ESS were not compatible with any BSS.

In the second and in the third part of my thesis (chapters 3, 4 & 5) I performed lab experiments with earwigs to assess how behavioural interactions can be influenced by external (environmental) and internal (individual) factors. In a first experiment I manipulated the nutrition levels of nymphs and females and hence also their hunger states. Combining nymphs and females from different or equal nutrition levels (cross-fostering) allowed me to conclude how nymphs and females react to the hunger state of the other (environment) and how this reaction is influenced by their own hunger state. Results showed, that the behaviour of the female depends on their own hunger state only and that the behaviour of the nymphs is influenced by their own hunger state and the hunger state of the female. In a second experiment I investigated whether nymphs can recognise related individuals and how relatedness influences the killing (siblicide) and cannibalism behaviour in nymphs. I found that individuals can recognise kin and that the killing and cannibalism behaviour is influenced by the relatedness of two interacting individuals.

All three parts of my thesis point out, that the interactions between individuals of a family are important, because they affect their behavioural and evolutionary stability. Over the course of time the stability of behavioural interactions rules the evolutionary stability of a strategy. Selection can only act on BSS because only these strategies have an attainable equilibrium which is necessary for evolutionary stability. It is therefore absolutely necessary to have knowledge about the behaviour (how interact two individuals, who has the behavioural control) and its stability (e.g., siblicide) to draw any conclusions about evolutionary stability.

Zusammenfassung

Interaktionen in Familien und deren Stabilität werden oft nur in evolutionärem Zusammenhang diskutiert. Die evolutionäre Stabilität enthält jedoch nur die halbe Wahrheit. Es ist ebenfalls notwendig über die Verhaltensstabilität solcher Interaktionen innerhalb von Familien Bescheid zu wissen. Was ist der Nutzen einer evolutiv stabilen Strategie (ESS = evolutionarily stable strategy), wenn die zu Grunde liegende Verhaltensdynamik der Interaktion es nicht erlaubt das evolutive Optimum zu erreichen oder auszudrücken? Es ist daher auch wichtig zu wissen ob eine Verhaltensinteraktion ein Gleichgewicht hat und falls ja, ob und wie dieses Gleichgewicht über Verhalten erreicht werden kann. Zu wissen ob eine Interaktion ein Gleichgewicht hat, und ob dieses Gleichgewicht über Verhalten erreicht werden kann oder nicht, liefert Informationen über die Verhaltensstabilität der Interaktion. Dieses Wissen ist wichtig für Verhalten bei denen die Verhaltensstabilität in Frage gestellt werden kann, zum Beispiel bei Brudermord (engl. siblicide). Das Wissen darüber wie ein Gleichgewicht erreicht wird erlaubt es Rückschlüsse zu ziehen, wer die Kontrolle über die Verhaltensinteraktion besitzt.

Im ersten Teil meiner Arbeit (Kapitel 2) untersuchte ich die Stabilität von Verhaltensinteraktionen und ob diese mit ESS kompatibel sind. In einem einfachen Zwei-Spieler Modell mit wiederholten, nacheinander abfolgenden Interaktionen habe ich herausgefunden, dass nur die Hälfte der Verhaltensinteraktionen zu Stabilität führen und damit auch eine verhaltensstabile Strategie (BSS = behaviourally stable strategy) repräsentieren. Bei Kompatibilitätstest zwischen BSS und ESS fand ich heraus, dass tatsächlich eine beträchtliche Anzahl von ESS mit keiner BSS kompatibel waren.

Im zweiten und dritten Teil meiner Arbeit (Kapitel 3, 4 & 5) führte ich Laborexperimente mit Ohrwürmern durch, um abzuschätzen wie Verhaltensinteraktionen durch externe (umweltbedingte) und interne (individuelle) Faktoren beeinflusst werden können. In einem ersten Experiment manipulierte ich das Nahrungsniveau von Nymphen und Weibchen und damit einhergehend deren Hungerzustand. Kombinierung von Nymphen und Weibchen aus verschiedenen und gleichen Nahrungsniveaus (Vertauschungsexperiment; engl. cross-fostering) erlaubte es mir Rückschlüsse zu ziehen wie Nymphen und Weibchen auf den Hungerzustand des Anderen (Umwelt) reagieren, und wie stark diese Reaktion durch den eigenen Hungerzustand beeinflusst wird. Die Resultate zeigten auf, dass das Verhalten der Weibchen nur auf ihrem eigenen Hungerzustand beruht und dass das Verhalten der Nymphen sowohl von ihrem eigenen als auch vom Hungerzustand des Weibchens abhängt. In einem zweiten Experiment untersuchte ich ob Nymphen verwandte Nymphen erkennen können und ob Verwandtschaft das Tötungs- und Kannibalismusverhalten der Nymphen beeinflusst. Ich fand heraus, dass Nymphen verwandte Nymphen erkennen können und dass sowohl Tötungs- als auch Kannibalismusverhalten von der Verwandtschaft zweier interagierender Nymphen beeinflusst wird.

Alle drei Teile meiner Arbeit zeigen auf, dass Interaktionen zwischen Angehörigen einer Familie wichtig sind, weil diese ihre eigene Verhaltensstabilität und evolutive Stabilität beeinflussen. Im Verlaufe der Zeit können Verhaltensinteraktionen die evolutionäre Stabilität von Strategien bestimmen. Selektion kann nur auf BSS wirken, weil diese ein über Verhalten erreichbares Gleichgewicht besitzen, welches für evolutive Stabilität notwendig ist. Es ist daher von grundlegender Wichtigkeit Wissen über Verhalten (auf welche Art und Weise interagieren zwei Individuen, wer hat die Kontrolle über das Verhalten) und dessen Stabilität (z.B. beim Brudermord) zu haben um Rückschlüsse über dessen evolutionäre Stabilität ziehen zu können.

Chapter 1

Introduction

Interactions in families

A variety of ways exist for how members of a family can socially interact. Interactions can be intra- (i.e., between siblings or between parents) or intergenerational (i.e., between parents and offspring), they can take place between two or more individuals (sequentially), they can be symmetrical or asymmetrical, one-off or repeated. However, there are two things that these kinds of interactions have in common. First, an interaction only occurs between two individuals (an actor and a reactant). Interactions between more than two individuals are the outcome of multiple sequential interactions performed within pairs. Second, the social interaction requires communication (Hansell 2005) (between a sender and a receiver), which can be auditory, visual, olfactory or tactile. An interaction always has an initiator (i.e., actor or sender) and a reacting individual (i.e., reactant or receiver).

When individuals interact, they interact for a particular reason, which may or may not be the same for actor and reactant. An offspring, for example, begs to get food provisioned by the parents, while a male approaches a female to mate. The outcome of the interaction can be either positive, negative or neutral and can be categorised based on the consequences for the actor and the reactant (see Table 1.1). When the interaction has a negative outcome for either the actor or the reactant, the interaction leads to a conflict. When the interaction is positive for one of them and neutral for the other, no conflict arises. Finally, when the consequences are positive for both, the interaction leads to cooperation.

Table 1.1: Overview over the different possible outcome of interactions between an actor and a reactant. The interaction has three possible outcomes (positive(+), negative(-) or neutral(0)) for the actor and the reactant, respectively. The resulting outcome combinations can be categorised as presented here.

		Actor		
	Effect	+	0	-
Reactant	+	Cooperation	Acceptance	Exploitation
	0	Acceptance	—	Competition
	-	Exploitation	Competition	Competition

Although it is not always obvious at first sight, the actor initiates the interaction to receive a reward. Workers (e.g., in social insects, see Wenseleers et al. 2004; Ratnieks & Wenseleers 2008 for reviews) and helpers (reviewed in Bshary & Bergmueller 2008) for example seem to invest a lot for the good of the family (e.g., bring food to the nest, protect the hive or take care of offspring) without any immediate personal reward. However, in the light of Hamilton's rule (Hamilton 1964a,b) it becomes clear that workers and helpers receive a pay-off for their investment in terms of inclusive fitness (the benefits of indirect fitness gain outweigh the costs of direct fitness losses). According to Hamilton's rule (or the inverse Hamilton's rule, depending on the applied context) the behaviour of the actor should only imply so much costs (either to itself or the reactant, depending on the context) to the interaction, that the inclusive fitness is still positive (Hamilton 1964a,b; Yamamura & Higashi 1992). This rule is also fulfilled in the parent-offspring conflict (e.g., Trivers 1974; Clutton-Brock 1991; Mock & Parker 1997) or in the case of siblicide (and cannibalism) (e.g., Fox 1975; O'Connor 1978; Pfennig 1997; Mock & Parker 1998), although it seems not to be case at a first sight.

Parent-offspring conflict

The interaction between begging offspring and care-giving parents is one of the most conspicuous interactions in a family. Each offspring tries to obtain more care (e.g., food) from the parents than its nest mates, because the offspring's own value (in a reproductive or genetic sense) is higher compared to the value of a nest mate (Hamilton 1964a,b). However, the parents try to distribute their care in equal shares among the offspring, because each offspring has the same value for the parents (Hamilton 1964a,b). Obviously, this leads to a conflict over food allocation between the offspring and the parents, where offspring demand far more resources than parents should provide (Trivers 1974).

Game theoretical models provide possible evolutionarily stable strategies (ESS) for how to resolve the conflict between parents and offspring (e.g., Parker & Macnair 1979; Parker 1985; Godfray 1991; Godfray & Johnstone 2000; Parker et al. 2002). For the sake of simplicity, these models assume that only a single interaction or multiple independent interactions occur between parents and offspring in each generation (Maynard-Smith 1982; Parker 1985; Houston et al. 1988; Godfray 1999; McNamara et al. 1999; Godfray & Johnstone 2000; Royle et al. 2002). However, in reality parents and offspring interact repeatedly in each generation, generating new behavioural dynamics that are likely to influence the outcome of both the current and future interactions (McNamara et al. 1999; Godfray & Johnstone 2000). It is therefore important to not only understand the necessary conditions for the evolutionary resolution of the conflict itself (e.g., Takada & Kigami 1991; Rodríguez-Gironés et al. 1998; McNamara et al. 1999), but also the required behavioural conditions for a stable conflict resolution (Dobler & Kölliker 2009). In **chapter 2** I present a formal model to derive the behavioural stability conditions for repeated dynamic parent-offspring interactions on a single generation level. I further apply the derived behavioural stability conditions to Parker's 'scramble competition' ESS model (Parker 1985; Mock & Parker 1997; Parker et al. 2002) in order to investigate the behavioural stability of proposed evolutionary conflict resolutions. Evolutionary and behavioural stability conditions have to be met for an ESS in a stricter sense.

According to the game theoretical models it is possible to predict whether parents or offspring are in control over food allocation at evolutionary equilibria. In the 'scramble competition' model it is the offspring that gain control over food allocation (e.g., Parker & Macnair 1979; Parker 1985), in the 'honest signalling' model it is the parent keeping the control over food allocation (e.g., Godfray 1991; Godfray & Johnstone 2000). Recently, the predictions of these studies have been challenged. Jeon (2008) argues that parents do not necessarily lose the control over food allocation in the case of 'scramble competition', but that parents allocate more food to the offspring with a higher reproductive value (Fisher 1930). These results question the assumption of equal offspring value to the parents in the 'honest signalling' model. Empirical studies support the argument of Jeon (e.g., Royle et al. 2002; Mas et al. 2009), but it is not yet clear whether parents and offspring adjust their behaviour according to their own, to each others (parents on offspring and *vice versa*) or to both nutritional states. Thus it is not known who controls the food allocation, the parents or the offspring. In **chapter 3** I present the results from an experiment in which I investigated how females and offspring adjust their foraging behaviour (i.e., provisioning, begging or self-foraging) to their own nutrition state and to the nutrition state of each other. In addition I explored whether females or offspring have control over the foraging behaviour. In this study I used families of the European earwig (*Forficula auricularia*) for lab experiments where I interchanged females between clutches from equal or different food level treatments. Results demonstrated that earwigs adjust their foraging behaviour to changes in nutritional states and suggest there is evidence that the offspring have the control over the foraging behaviour.

Siblicide and cannibalism

Siblicide (and consequent cannibalism) represents one of the most extreme intrafamilial interactions (along with all the other interactions where one family member kills another). Applying the principle of Hamilton's rule (Hamilton 1964a,b) to siblicide (the inverse Hamilton's rule, Yamamura & Higashi 1992) yields the prediction that an individual should only kill a sibling when the direct fitness benefits outweigh the costs due to indirect fitness losses (Mock & Parker 1997; Pfennig 1997). However, our understanding of quantitative fitness consequences due to siblicide and cannibalism is still limited. According to a substantial body of theoretical work on the evolution and stability of siblicide and cannibalism (e.g., O'Connor 1978; Mock & Parker 1998; Pexton & Mayhew 2002; Nishimura & Isoda 2004; Perry & Roitberg 2005), kin recognition is predicted to be a key factor in the evolution and stability of these extreme behaviours (Mock & Parker 1997, but see Crozier 1986; Fletcher & Doebeli 2009). Still there is little empirical data on how kin recognition interacts with siblicide and cannibalism. In **chapters 4 & 5** I present the results from a comprehensive siblicide and cannibalism experiment with nymphs of the European earwig (*F. auricularia*). I demonstrate that siblicide actually occurs in earwig nymphs and carries significant costs to the victims and that cannibalism has benefits to the survivors. As expected if this behaviour was shaped by kin selection, I further demonstrate that European earwig nymphs have the ability to recognise kin, which allows them to potentially avoid the loss of inclusive fitness arising when killing a related individual.

The European earwig (*Forficula auricularia*)

The European earwig (*Forficula auricularia* Linnaeus (Insecta: Dermaptera: Forficulidae)) is a nocturnal (sub)-social species, native to Europe, western Asia and the northern rim of Africa (van Heerdt 1946). It has been (accidentally) introduced to the temperate zones in both hemispheres and is nowadays established in most countries in these regions (Lamb & Wellington 1975). Although the European earwig is primarily a terrestrial species (Chant & McLeod 1952) they can also be found in shrubs and trees where they forage (Lamb & Wellington 1975).

The life-cycle of *F. auricularia* has six stages: the egg stage, four immature instars and an adult stage (e.g., Lamb & Wellington 1975). The egg stage and the first instar can be grouped as the nesting phase (in a subterranean burrow), the other instars and the adult stages as the free-foraging phase (Lamb & Wellington 1975). Eggs hatch between late March and early May and first instars stay in the nest (Lamb & Wellington 1975). Already as first instars they start to leave the nest to forage but return to the nest during the day (e.g., Vancassel 1984; Kölliker 2007) although food is also provided by the caring mother during this period (e.g., Lamb 1976; Vancassel & Forasté 1980; Kölliker & Vancassel 2007; Kölliker 2007; Staerkle & Kölliker 2008). On an average of twelve days after hatching the nymphs moult and enter the second instar (unpublished data R Dobler) and start to migrate to the surface and become independent of maternal care (Lamb & Wellington 1975; Moerkens et al. 2009). After approximately 28 days, nymphs moult a second time and enter the third instar (unpublished data R Dobler). In this stage a second migration starts into the trees (Moerkens et al. 2009) where they moult again when they are approximately 50 days old (unpublished data R Dobler). Around day 70 after hatching, the fourth instars moult again and become adults (unpublished data R Dobler). As an adult, males and females mate in summer and fall (Costa 2006). The female (sometimes with a male) builds the nest in late autumn (Costa 2006). Male earwigs normally die during or at begin of winter (Lamb & Wellington 1975; Gingras & Tourneur 2001, but see Lamb 1975). Females lay a clutch of eggs (20 to 80) between late autumn and early spring (e.g., Lamb & Wellington 1975; Vancassel 1984; Wirth et al. 1998; Gingras & Tourneur 2001). Some females lay a second clutch in early spring after the nymphs of the first clutch entered the second instar (e.g., Lamb & Wellington 1975; Tourneur & Gingras 1992; Wirth et al. 1998). Females guard the clutch and protect the eggs by cleaning them against fungal spores and other pathogens (Weyrauch 1927; Costa 2006). Females die in spring, normally after nymphs entered the second instar.

Two female reproductive strategies represent adaptation to local climate conditions. Females in regions with long and cold winters lay one clutch at the beginning of winter (Vancassel 1984; Tourneur & Gingras 1992; Wirth et al. 1998) and females in regions with temperate winters lay two clutches, one at the end of winter and one in early spring (Weyrauch 1927; Beall 1932; Lamb & Wellington 1975; Wirth et al. 1998). Recent molecular studies suggest that *F. auricularia* is a complex of two sibling species with different life-history strategies (Wirth et al. 1998; Guillet et al. 2000a,b). Wirth et al. (1998) demonstrated with breeding experiments that a postzygotic barrier may exist, because the clutches of crosses between the two sib-species had a very low hatching success. The earwigs I used for my experiments were collected in Opfershofen (Thurgau, Switzerland) and belonged the subgroup A (*sensu* Wirth et al. 1998) where females lay only a single clutch at the beginning of winter.

Clutches of the European earwig have a diverse genetic background because females mate multiply (mixed paternity, Guillet 2000) and because hatched offspring can join another another clutch, especially (but not exclusively) when the female dies (clutch-joining/adoption after hatching, Kölliker & Vancassel 2007). Therefore this is an ideal study system to investigate kin recognition effects. Kin recognition is assumed to play an important role in the evolution and stability of siblicide (Mock & Parker 1997) and this nest mate killing behaviour (siblicide) has also been observed in the European earwig (personal observations R Dobler, F Mas and M Kölliker). Likewise, that females provide food to their offspring, but the offspring also tend to forage by themselves makes this system suitable to address the question of whether the mother or the offspring have the behaviour control over food allocation and whether this behaviour depends on hunger levels and/or competition levels.

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Chapter 2

Behavioural attainability of evolutionarily stable strategies in repeated interactions

Published as: Dobler, R. & Kölliker, M. 2009. Behavioural attainability of evolutionarily stable strategies in repeated interactions, *Anim. Behav.*, **77**, 1427–1434.

Abstract

Theory for the evolution of social interactions based on continuous strategies often assumes for simplicity that expressed behaviours are independent from previous encounters. In reality, however, such dependencies are likely to be widespread and often strong, generating complex behavioural dynamics. To model this process and illustrate potential consequences for the evolution of behavioural interactions, we consider the behavioural dynamics of the interaction between caring parents and their demanding offspring, a prime example for long series of interdependent and highly dynamic interactions. These dynamics can be modelled using functions describing mechanisms for how parents and their offspring respond to each other in the interaction. We establish the general conditions under which the behavioural dynamics converge towards a proximate equilibrium and refer to such converging interactions as behaviourally stable strategies (BSSs). We further demonstrate that there is scope for behavioural instability under realistic conditions; that is, whenever parents and/or offspring 'overreact' beyond some threshold. By applying the derived condition for behavioural stability to evolutionary models of parent-offspring conflict resolution, we show by numerical simulations that evolutionarily stable strategies (ESSs) of current models are not necessarily behaviourally stable. Because behavioural instability implies that expressed levels of behaviours deviate from the ESS, behavioural stability is required for strict evolutionary stability in repeated behavioural interactions.

Introduction

Conspicuous offspring behaviours and displays to demand resources from their parents can be observed in most animal species with parental care (Clutton-Brock 1991). According to parent-offspring conflict (POC) theory, offspring are usually selected to demand more resources from their parents than the parents should provide (Trivers 1974). This phenomenon can be evolutionarily explained in terms of the outcome of the POC over resource distribution, where offspring begging and parental provisioning strategies reflect an evolved resolution of this conflict (Trivers 1974; Parker 1985; Godfray 1995; Kilner & Johnstone 1997; Mock & Parker 1997; Royle et al. 2002). There are two main types of game-theoretic approaches to modelling conflict resolution. The 'scramble competition' model assumes that offspring control parental food allocation (Parker & Macnair 1979; Parker 1985; Parker et al. 2002). The 'honest signalling' model assumes, that parents control food allocation (Godfray 1991; Godfray & Johnstone 2000). Both types of models can explain the evolution of condition-dependent, conspicuous and costly offspring begging and parental response.

These models generally assume for simplicity a single interaction, or equivalently multiple independent interactions, between parent and offspring (Maynard-Smith 1982; Parker 1985; Houston et al. 1988; Godfray 1999; McNamara et al. 1999; Godfray & Johnstone 2000; Royle et al. 2002; but see Johnstone 1996 for a two-step exception) and the evolving strategies are taken to be adequately represented by the behavioural outcome of a one-off interaction. However, in reality the interactions between parents and offspring are behaviourally very dynamic and typically involve repeated encounters that are interdependent (McNamara et al. 1999; Godfray & Johnstone 2000). The issue of stability has been thoroughly explored in conflict resolution models from the perspective of evolutionary stability (e.g. Takada & Kigami 1991; Rodríguez-Gironés et al. 1998; McNamara et al. 1999). But it is not known whether, and under what conditions, the behavioural dynamics of repeated parent-offspring interactions allow the behaviours actually to be expressed according to the idealized strategies in the evolutionary models.

Here, we model the repeated parent-offspring interaction using a behavioural reaction norm approach (Smiseth et al. 2008) in an expanded negotiation model framework (Moore et al. 1997; McNamara et al. 1999; Taylor & Day 2004; Johnstone & Hinde 2006), where a demand function defines how offspring adjust their begging to variation in parental provisioning, and a supply function defines how parents adjust their provisioning to variation in offspring begging (Fig. 2.1; Hussell 1988). These functions define how parents and offspring react to each other, and the resulting dynamics can be considered as a negotiation process. Under this perspective, evolutionary strategies can be represented by the slopes and/or shapes of these functions, mediate the behavioural dynamics of the interaction (Smiseth et al. 2008). In his graphical model, Hussell (1988) focussed on the expected behavioural equilibrium over multiple interdependent parent-offspring interactions (see also Kölliker 2003). This equilibrium represents the behavioural strategies considered in the game theoretic conflict resolution (Godfray 1991; Mock & Parker 1997; Parker et al. 2002) and quantitative genetic coadaptation models (Wolf & Brodie 1998; Kölliker et al. 2005). However, given a pair of supply and demand functions, the behavioural dynamics of the repeated parent-offspring interactions may, or may not, lead to this equilibrium. Thereby, the shapes of the supply and demand functions affect the stability of the behavioural equilibrium (Samuelson 1976). Understanding the conditions under which the behavioural equilibrium is actually reached in the interaction is critical, because only a stable behavioural equilibrium can adequately represent strategies in current evolutionary resolution models (see Samuelson 1976 for an economical context).

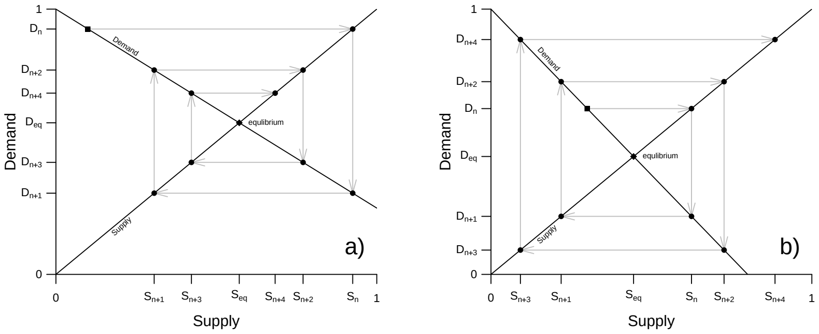

Figure 2.1: Dynamics of repeated interactions. By superimposing the demand function and the inverted supply function the repeated interdependent parent-offspring interaction can be graphically visualized. Starting at a demand level D_n (filled square) leads over repeated interactions to the supply level S_{n+4}. The equilibrium (S_{eq}, D_{eq}, solid diamond) represents the point of behavioural matching between parents and offspring over supply and demand level, respectively. a) A behaviourally stable parent-offspring interaction converges toward the equilibrium. b) An interaction that diverges away from the equilibrium is behaviourally not stable.

We provide a formal model and results from numerical analyses exploring the stability of behavioural equilibria and behavioural strategies in parent-offspring interactions for different shapes of supply and demand functions. We also show for a range of realistic conditions that current conflict resolution models predict evolutionarily stable strategies (ESSs) that are behaviourally not stable.

The Model

Behavioural equilibria

The offspring behavioural reaction norm for demand (Taylor & Day 2004; Smiseth et al. 2008) is defined by the demand function $D = f(S)$, describing the dependence of offspring begging on parental provisioning. The parental behavioural reaction norm for supply (Taylor & Day 2004; Smiseth et al. 2008) is defined by the supply function $S = g(D)$, describing the dependence of parental provisioning on offspring begging. The interdependence of the two recursive functions can be used to model the behavioural dynamics over repeated interactions of parents and offspring (Fig. 2.1).

To display and formalize this feedback and find the behavioural equilibrium, the arguments of the two functions need to be expressed in the same currency. This can graphically be achieved by inverting the supply function and superimposing it on the demand function (Hussell 1988). The intersection point of the two functions represents the behavioural equilibrium. Formally, the behavioural equilibrium is derived by inverting the supply function, setting it equal to the demand function:

$$f(S_{eq}) = g^{-1}(S_{eq}).$$

Then solving for S_{eq}, where S_{eq} is the equilibrium value for the supply and setting S_{eq} in the demand function yields the equilibrium value for demand D_{eq} (Kölliker 2003).

Stability of behavioural equilibria

To address the behavioural stability of the equilibria, the dynamics of parent and offspring behaviours over repeated interactions need to be explored explicitly. Only when repeated parent-offspring interactions converge towards the equilibrium, the equilibrium and the strategies are behaviourally stable (Fig. 2.1a). At such an equilibrium we refer to the pairs of strategies as behaviourally stable strategies (BSSs), represented by the slopes and/or shapes of the supply and demand functions. When repeated parent-offspring interactions diverge away from the equilibrium, the equilibrium and the strategies are behaviourally not stable (Fig. 2.1b). We used the standard mathematical techniques based on discrete-time dynamics to address the stability of behavioural equilibria (Otto & Day 2007, pp. 163 - 169). In our model, discrete time steps are from one specific interaction (offspring demands, parent provides) to the next and the process is started with an offspring begging event.

Our model in principle explores a behavioural negotiation process between parents and offspring (e.g. McNamara et al. 1999; Taylor & Day 2004; Johnstone & Hinde 2006) in which parent and offspring interact according to their behavioural reaction norms. In contrast to previous models (e.g. McNamara et al. 1999; Taylor & Day 2004; Johnstone & Hinde 2006), we focus on the behavioural process and allow for asymmetric functions, as we have parental supply and offspring demand in our model, which are represented by response mechanisms for different kinds of behaviour.

Numerical analyses

To further explore the behavioural dynamics of parent-offspring interactions explicitly, we also used numerical simulations for the changes of demand (begging) level and supply (provisioning) level over a series of 2000 time steps for a given set of supply and demand functions (Fig. 2.1). For the first time step the initial demand level D_0 was given and for subsequent steps the value of the supply function was used as argument of the demand function and vice versa. The initial demand level was randomly chosen within 10% around the equilibrium D_{eq}. This choice increased the likelihood of reaching the equilibrium with 2000 interactions even when the process of convergence was slow. But any initial demand level could have been chosen. There was no effect of initial condition on the outcome (stability/instability) of the interaction (see Results). Values for supply and demand were represented on a standardized scale from 0 (minimum) to 1 (maximum). The functions we used for supply and demand were strictly monotonic (see below). A maximum level of demand was set at the point of no supply, resulting in intercepts of 1 for the demand function and 0 for the supply function. The interactions between parents and offspring were assumed to be error free. That is, the dynamics of the behavioural interaction strictly followed the supply and demand functions without any deviation. For simplicity we assumed a single offspring interacting with a single parent (Hussell 1988; Godfray 1991; Kölliker et al. 2005).

Specific function types

We numerically investigated the impact of two different types of functions on behavioural stability. Linear functions are the simplest and usual way to represent the parent-offspring interaction. They are standard in quantitative genetic maternal effect (Kirkpatrick & Lande 1989) and coadaptation models (Wolf &

Brodie 1998; Kölliker 2003; Kölliker et al. 2005), and reflect the local gradients in game-theoretic conflict resolution models (Godfray 1991; Parker et al. 2002). In addition, to simulate the consequences of slightly more complex responses on the behavioural dynamics, we used power functions (Smiseth et al. 2008), for which the slopes are not constant but change with the level of supply and demand. This may have important consequences for the behavioural dynamics and stability of the parent-offspring interaction.

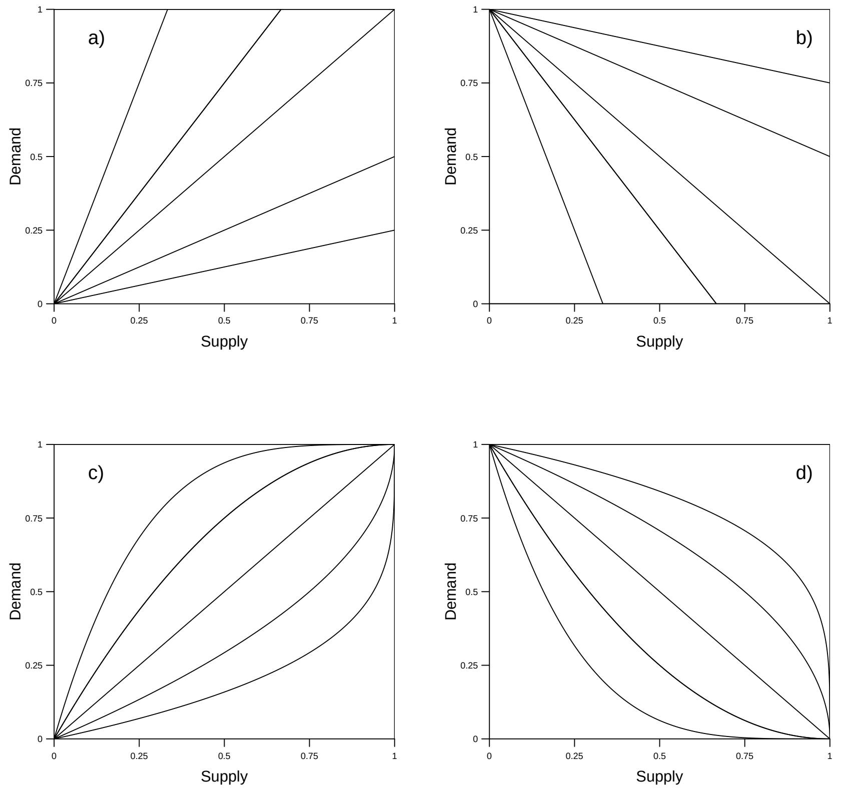

Figure 2.2: Illustration of the used supply and demand function types (behavioural reaction norms). a) Inverted linear supply functions (to superimpose with the demand function) for different slopes. b) Different slopes for linear demand functions. c) Several different inverted supply power functions (to superimpose with demand functions). d) Different demand power functions.

In the linear case, the supply function was defined as $S = g(D) = aD + y$, with slope a and intercept $y = 0$ (Fig. 2.2a). The demand function was defined as $D = f(S) = bS + x$, with slope b and intercept $x = 1$ (Fig. 2.2b). The intercepts reflect the previously mentioned assumption of maximal begging in the absence of provisioning. The slopes a of the supply function could vary between zero and infinity ($0 < a < \infty$) and the slopes b for the demand function between minus infinity to zero ($-\infty < b < 0$).

In the case of power functions, the supply function was defined as $S = g(D) = 1 - (1 - D)^k$ (Fig. 2.2c) and the demand function was defined as $D = f(S) = (1 - S)^l$ (Fig. 2.2d). The parameters k and l define the corresponding strength and direction of the curvature and could both range from zero to infinity ($0 < k < \infty$, $0 < l < \infty$).

Numerical application to ESS models

The link between behavioural dynamics and evolutionary stability was explored by applying our BSS condition to an already existing ESS model in a numerical sensitivity analysis. We chose the scramble competition resolution model, for which the role of supply and demand functions has been made explicit (Parker 1985; Mock & Parker 1997; Parker et al. 2002). But our analysis in principle also applies to honest signalling models (Godfray 1991; Godfray & Johnstone 2000), although this is based on a different (i.e. additive rather than multiplicative) fitness model. Scramble competition models assume that parents have a fixed quantity of resources available for reproduction. A unit of investment in a given offspring enhances that offspring's survival chances, but at the expense of other offspring the parent can produce. Offspring survival chances follow a curve of diminishing returns with respect to the parental resources obtained (Smith & Fretwell 1974; Parker 1985). Further, for evolutionary stability, offspring begging has to be costly. For simplicity, we assume that offspring survival decreases linearly with increased begging (Parker et al. 2002). To allow direct comparison with the evolutionary model, the dimensionless level of supply in our behavioural model can be interpreted in units of parental investment.

The scramble competition ESS is defined via the local gradients of supply and demand functions at the ESS (Parker 1985; Mock & Parker 1997 ; see Appendix), which are parameters in the model and assumed to be nonevolving. We carried out a broad numerical sensitivity analysis, varying the gradients (i.e. the slopes) of the supply and demand functions and the parameters p and q of the associated cost and benefit functions of begging and provisioning, respectively (see Parker et al. 2002 and Appendix for details of the functions), to test for the behavioural stability of the ESS for specific sets of supply and demand functions (with known slopes and intercepts) and, hence, whether they are BSSs or not.

To explore numerically the parameter space of the scramble competition ESSs for converging behavioural dynamics we performed the following steps: 1) We generated a behavioural equilibrium grid for the supply and demand function pairs (1'000'000 behavioural equilibria; 1'000 demand levels and 1'000 supply levels, evenly distributed) in the parameter range of our model. 2) We calculated the ESSs according to the scramble competition model (Parker & Macnair 1979; Parker 1985; Parker et al. 2002) in terms of a demand and supply function pairs (according to Eqs A-2 and A-3). 3) For all of these function pairs we checked whether the intercept of the demand function was close to 1 and that for the supply function close to 0 to fulfil the assumptions we made to derive the BSS conditions. Intercepts were deemed close enough when they deviated by less than 0.005. 4) The equilibria of those funtion pairs which satisfied these criteria were matched to the behavioural equilibrium grid generated before (see step 1). We took the numerical values for the behavioural equilibrium and the evolutionary equilibrium to be equal when they were within a margin of ± 0.001, which corresponds to the resolution of the behavioural equilibrium grid. 5) In cases where we found more than one function pair that numerically satisfied our matching conditions, we chose the one with the smallest mismatch to be the 'true' one, as we expected only one ESS per parameter combination p and q. Choosing another pair did not alter the final result (i.e. whether an ESS was behaviourally stable or not). 6) For the slope combinations where behavioural and evolutionary equilibrium matched, we checked whether or not the equilibrium was also behaviourally stable. For this we applied the stability conditions of our formal model.

We ran our model for 90 different fitness parameter value combinations p and q in the cost and benefit functions of the scramble competition model (see Parker et al. 2002 and Appendix for details of the functions). Variation in these fitness parameters may have an impact on the outcome of the behavioural stability of the POC resolution, because different slopes for demand and supply functions are required to reach the ESS.

We used R version 2.4.0 (2006-10-03) and Mathematica 6.0.1.0 for the analyses and simulations (R Development Core Team 2006; Wolfram Research, Inc. 2007).

Results

Stability of behavioural equilibria and numerical analyses

We calculated the stability index λ following Otto & Day (2007) for discrete-time dynamics systems. λ allows us to determine if a dynamic system that is close to an equilibrium converges towards, or diverges away from, this equilibrium from one time-step to the next. In our case, it is the derivative of the function describing the begging level at the next time step, which is a combination of the supply and demand function. In our model this is

$$\lambda = f'(S_n),$$

where $f(S_n) = D_{n+1}$ is the begging level after one interaction when starting at D_n, with

$$D_{n+1} = f(S_n) = f(g(D_n)).$$

S_n is the supply level and $f(S_n)$ the demand function. $f(g(D_n))$ is again the demand function, expressed as a function of the demand level one interaction before. The resulting value for λ is

$$\lambda = f'(S_n) = f'(g(D_n))g'(D_n) = f'(S_n)g'(D_n).$$

(Note that $g(D_n) = S_n$).

For linear demand and supply functions we get

$$f(S_n) = D_{n+1} = b(aD_n + y) + x,$$

where x and y are the intercepts of the demand and supply function, respectively. And for λ we get

$$\lambda = ab.$$

A value of λ between -1 and 1 indicates a stable dynamic equilibrium (Otto & Day 2007). So the general stability condition for the behavioural interaction between a parent and its offspring is

$$\lambda = |ab| < 1. \tag{2.1}$$

For the case of linear supply and demand functions, this condition is for local and global stability; it is not only valid at/near the equilibrium but for any initial begging level D_n, because the functions involved are linear and the slopes a and b apply over the whole range. This stability condition can also be proven by using the convergence criteria for infinite repeated interactions between parent and offspring (see Appendix).

Numerical simulations

Our numerical simulations deal only with a subset of all possible functions, namely a supply function with a positive slope a (parent increases supply level with increasing demand level) and a demand function with a negative slope b

(offspring decreases demand level with increasing supply level) (Figs 2.2a and b). This assumption is also made in scramble competition models (Parker et al. 2002). The stability condition under these assumptions and for linear supply and demand functions is

$$-1 < ab < 0.$$

This solution is a partial solution of the conditions for general stability derived earlier (Eq. 2.1), confirming the result of our formal model. The product of the two parameters a and b defines the behavioural stability of linear parent-offspring interactions. When ab has a value between -1 and 0 ($-1 < ab < 0$), then the repeated interactions of parent and offspring converge towards the equilibrium and reflect a BSS. In all these cases the two functions intersect at a demand level between 0.5 and 1 ($0.5 < D_{eq} < 1$, Fig. 2.3a), under the assumptions of our model (i.e. slopes of the functions are of opposite sign and the intercepts are 0 and 1, respectively). The threshold level of 0.5 can be derived analytically (see Appendix, A-1). That half of the function pairs that intersect above a demand level of 0.5 represent a BSS. The half of the function pairs that intersect below a demand level of 0.5 represent behaviourally not stable strategies, resulting in divergence of the behavioural interaction.

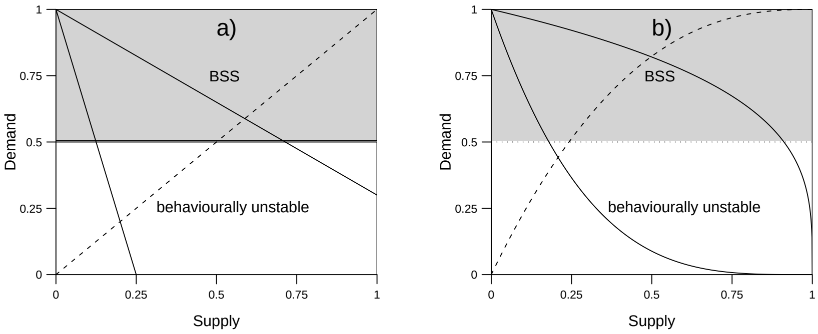

Figure 2.3: Supply (dashed) and demand (solid) functions which intersect in the grey shaded area represent behaviourally stable strategies (BSS). Function pairs with an intersection in the white area represent a behaviourally unstable strategy. a) Linear response functions. One supply function and two different demand functions. One combination leads to a BSS, the other is behaviourally not stable. The threshold level of 0.5 was derived analytically. b) Same as in a) but with power functions and threshold level according to the results of our numerical simulations. In a) and b) the inverted supply function is drawn to superimpose the two functions.

For the power functions (Figs 2.2c and d), the local stability conditions follow the general rule

$$-1 < f'(S_{eq})g'(D_{eq}) < 1. \tag{2.2}$$

$f'(S_{eq})$ is the derivative (local gradient) of the demand function at the equilibrium and $g'(D_{eq})$ is the derivative of the supply function at the equilibrium.

According to the results of our simulation, this stability condition seems not only valid at the equilibrium but over the whole value range of possible initial demand levels (data not shown). So we can state the general stability conditions for the power functions within the value range of our numerical simulation as follows:

$$-1 < f'(S)g'(D) < 0.$$

This is equivalent to the stability condition for linear functions, but generalized to the case of non-linear power functions. The behavioural stability of the parent-offspring interaction depends only on the derivatives (the slopes) of the describing functions of demand and supply. Again, under the assumptions of our model, all supply and demand function pairs that intersect at a level of demand between 0.5 and 1 ($0.5 < D_{eq} < 1$) have a behaviourally stable equilibrium (Fig. 2.3b), whereas those that intersect between 0 and 0.5 ($0 < D_{eq} < 0.5$) do not.

Numerical application to ESS models

For 17 out of the 90 simulations the ESS was outside the considered parameter space or the intercepts deviated too much from 1 (for the demand function) or 0 (for the supply function). For 73 simulations we found ESSs inside the considered parameter space where the intercepts of the functions matched to 1 and 0, respectively. For 16 cases the difference between ESS and BSS was larger than our matching criteria (i.e. the difference in either demand level or supply level was larger than 0.001 (our grid resolution) and the function pair could hence not be clearly assigned to one grid point). Out of the remaining 57 cases where the intercepts fulfilled our matching criteria, 33 turned out to be behaviourally stable (BSS) and 24 were behaviourally not stable (Table 2.1).

ESSs were behaviourally stable in the lower range of explored begging costs (q ranging from -0.1 to -0.35), representing higher numerical values for ESS levels of demand. For higher begging cost parameter values, and the correspondingly lower values for ESS levels of demand, the ESSs were behaviourally not stable. The parameter p, determining the benefit of parental supply for offspring survival, was not associated with behavioural stability (Table 2.1). for the begging cost parameter predicted ESSs that are also BSSs, and higher values

Table 2.1: Simulation results for behavioural and evolutionary stability for different parameter combinations p and q in the cost and benefit functions.

Provisioning benefit parameter q	Begging cost parameter p									
	-0.05	-0.1	-0.15	-0.2	-0.25	-0.3	-0.35	-0.4	-0.45	-0.5
0.5	NA	YES	NA	NA	NA	NA	NA	NA	NA	NA
1	NA	YES	Yes	Yes	YES	YES	YES	No	No	No
1.5	NA	YES	Yes	Yes	YES	YES	YES	No	No	No
2	NA	YES	Yes	Yes	YES	YES	YES	No	No	No
2.5	NA	YES	Yes	Yes	YES	YES	YES	No	No	No
3	NA	YES	Yes	Yes	YES	YES	YES	No	No	No
3.5	NA	YES	Yes	Yes	YES	YES	YES	No	No	No
4	NA	YES	Yes	Yes	YES	YES	YES	No	No	No
4.5	NA	YES	Yes	Yes	YES	YES	YES	No	No	No

NA: parameter combinations with no evolutionary equilibrium in the parameter range of our simulation. YES: parameter combinations with evolutionary equilibria which are also behavioural equilibria. Yes: parameter conditions with evolutionary equilibria that are also behavioural equilibria but where the difference of the two is larger than 0.001 (our grid resolution) in at least one dimension (supply or demand). No: parameter combinations with evolutionary equilibria which are no behavioural equilibria. Begging cost increases from left to right. Provisioning benefit increases from top to bottom. The reason why we could not clearly assign some evolutionary equilibria to unique grid points in our simulation (p values of -0.15 and -0.2) is, that the sum of the deviations of the intercepts for the two functions was in these cases larger then the grid resolution, although taken separately each intercept fulfilled our matching criteria. Hence, our inability to assign these evolutionary equilibria is a result of our matching criteria for the intercepts rather than a methodological problem in the simulation of repeated interactions. Therefore, it is likely that these evolutionary equilibria represent the proper behavioural equilibria.

for the begging cost parameter lead to predicted ESSs that are behaviourally not attainable (Table 2.1).

Discussion

Behavioural interactions based on continuous strategies generate complex dependencies and behavioural dynamics over time, raising the question of behavioural stability. To define a condition for behavioural stability in repeated interactions we proposed the novel concept of the behaviourally stable strategy (BSS): a BSS is characterized by behavioural dynamics of repeated interactions that converge towards the behavioural equilibrium. While the BSS is a proximate condition for the outcome of behavioural interactions, it has repercussions on evolutionary stability in a stricter sense. Non converging behavioural dynamics imply deviation from the expressed behavioural levels that would represent the ESS. Thus, by definition, behaviourally unstable strategies lead to deviation from the single-interaction or negotiation ESS (see below) and to corresponding fitness penalties. To illustrate this argument further, we have shown by simulations that there are realistic conditions under which ESSs for parent-offspring conflict resolution are behaviourally not stable. While this analysis is based on scramble competition resolution models (Parker et al. 2002), in principle the same basic conclusion apply to honest signalling models (Godfray 1991) because neither type of model incorporates the dynamics of repeated interactions.

Negotiation models (McNamara et al. 1999; Taylor & Day 2004; Johnstone & Hinde 2006) and quantitative genetic models of interacting phenotypes (Moore et al. 1997; Kölliker 2003) both assume $|\lambda|$ to be smaller than 1 and thereby ensure behavioural stability in the predicted evolutionary outcomes. Our model provides the biological rationale for this critical assumption in negotiation and interacting phenotype models.

Behavioural stability

The behavioural stability of parent-offspring interactions at the equilibrium depends only on the derivatives (the change rates) of the supply and demand function. The absolute value of the product of the two derivatives has to be smaller than 1 (Eq. 2.2). Samuelson (1941, 1976) found analogous results for linear demand and supply functions in economics for the equilibrium prices of products. This result can be biologically interpreted such that the stability condition is likely to be violated when at least one interactant reacts too sensitively (i.e. it 'overreacts') to a behavioural change in the other interactant, leading to unsteady (oscillating) dynamics.

Under the assumptions of an intercept of 0 for the supply and of 1 for the demand function, the equilibrium is behaviourally stable for linear response functions as well as for power response functions, when the begging level at the equilibrium is larger than 0.5 (i.e. generally speaking the average between the minimum and maximum level, see Appendix). We present the derivation for the linear case, although an equivalent solution can be shown for power functions (G. Nöldeke, personal communication; R. Dobler and M. Kölliker, unpublished results).

The increased complexity in the response functions from a linear to a power function had no impact on the outcome of the behavioural stability in our simulations. Nevertheless, we cannot reject the possibility that response functions with a more elaborate complexity (e.g. logistic functions, quadratic functions or higher order functions) may influence the behavioural stability, including the possibility of multiple alternative behavioural equilibria (i.e. more than one intersection point). In such more complex cases the stability may not only depend on the response functions and their derivatives but also on the starting conditions, adding another level of complexity to the model. For such models it would not only be interesting to find stability conditions but also to find possible conditions and circumstances that allow the interaction to change from one behavioural equilibrium to another. Under such more complex conditions, behaviourally stable equilibria may not always be attainable.

Communication errors and shifting response functions (e.g. due to changing environmental conditions or offspring age) may make the behavioural equilibrium shift over time, which would constantly reintroduce behavioural dynamics, likely rendering even stronger the expected selection pressure on behavioural reaction norms that allow fast behavioural convergence. In future models it would be interesting to incorporate perception errors, time lags and developmental/plastic function adjustments (Johnstone & Grafen 1992; Johnstone 1994), and to study such plasticity in experimental work (e.g. Hinde & Kilner 2007). Such inclusions would add realism and specificity to the model, but our major conclusion that the behavioural dynamics need to be addressed for an understanding of evolved strategies in repeated social interactions will most likely not be affected.

So far, empirical studies on behavioural dynamics mainly focused on the average effect which a change in behaviour (experimental or natural) of an interactant has on the behaviour of another interactant (e.g. Smith et al. 1988; Kilner 1995; Ottosson et al. 1997; Kilner et al. 1999). Although these studies give valuable insight on the overall adjustment (change rate) and plasticity of behaviour s, they do not address the underlying dynamics leading to the observed behavioural outcome. Experiments where a supposedly equilibrated system is deviated temporarily and the subsequent interaction-to-interaction dynamics analysed explicitly could provide the data required to determine to what degree a behavioural reaction norm (i.e. response rule) approach can actually be used to model the behavioural dynamics in repeated interactions (Roulin 2002; Hinde & Kilner 2007; Smiseth et al. 2008). Behaviourally stable strategies (BSSs) are expect to stabilise back to the initial equilibrium after the temporary disturbance.

Application of the BSS concept

Applying our BSS model to scramble competition resolution models (Parker 1985; Mock & Parker 1997; Parker et al. 2002) confirms that predicted ESSs of single-interaction models are not necessarily behaviourally stable strategies. Some are either outside the parameter range or they represent a behaviourally unstable equilibrium. In both cases, what would be the ESS can behaviourally never be reached, regenerating selection in the interactions. Under the specific conditions of the chosen intercepts, and from a perspective of behavioural stability, intermediate to high begging levels should be favoured over the course of selection, because only these can be the result of convergent behavioural dynamics. This may appear counterintuitive at first sight, as one would associate higher begging levels with increased costs, which should be evolutionarily unfavourable (Moreno-Rueda 2007). However, higher begging costs also imply lower evolved begging levels at the ESS (Parker 1985 ; see Appendix) and when ESS begging levels exceed the level for behavioural stability, instability ensues (Table 2.1). Thus, there are behavioural stability constraints in parent-offspring interactions, which would favour evolutionary conflict resolutions with relatively high levels of begging and, hence, relatively low associated begging costs. In addition to the well-studied selection for optimal conflict resolution, we suggest selection on behavioural reaction norms that enhance the likelihood for behaviourally stable repeated interactions.

Conclusions

The importance of behavioural stability is not restricted to the functional context of parent-offspring interactions, but may include any context where fast-responding short-term interactions are involved (e.g. dominance interactions (Matsumura & Kobayashi 1998), biological markets (Noe & Hammerstein 1994, 1995), cell interactions (Hofmeyr & Cornish-Bowden 2000), negotiation over care (McNamara et al. 1999; Taylor & Day 2004; Johnstone & Hinde 2006)).

There are usually many BSSs that are not an ESS. Many interactions behaviourally converge but yield behavioural levels with suboptimal fitness consequences. This is not surprising, since behavioural stability alone tells us nothing about fitness. More revealing are the cases where a predicted ESS (in terms of a pair of slopes for the supply and demand reaction norms) is not a BSS. We could show for the scramble competition model (Parker 1985; Mock & Parker 1997; Parker et al. 2002) that behaviourally unstable ESSs are predicted when begging costs are of greater than some intermediate level. BSS and ESS are two conditions to evaluate the stability of repeated interactions that deal with the proximate and ultimate dimension of repeated interactions, respectively. Both need to be met for evolutionary stability in a stricter sense.

Acknowledgments

We thank Andreas Dobler, Flore Mas, Georg Nöldeke and two anonymous referees for helpful comments on this manuscript. The study was financially supported by the Swiss National Science Foundation (grant no. 3100A0-111969 to M.K.)

Appendix

Alternative proof of the behavioural stability conditions for linear behavioural reaction norms

The change in begging over one time step is

$$D_{n+1} = b(aD_n + y) + x.$$

The change of begging level over n time steps is therefore

$$D_n = a^n b^n D_0 + a^{n-1} b^n y + a^{n-1} b^{n-1} x + a^{n-2} b^{n-1} y + a^{n-2} b^{n-2} x + ... + abx + by + x.$$

Factoring out $a^i b^i$ for $0 \leqslant i \leqslant (n-1)$ leads to

$$D_n = a^n b^n D_0 + (x + yb) \sum_{i=0}^{i=n-1} a^n b^n.$$

The second term on the right hand side is a geometric series that for $n \to \infty$ only converges, when $|ab| < 1$. For this case ($|ab| < 1$) the first term on the right hand side converges to 0. From this we can conclude that the repeated interaction only converges towards the equilibrium (D_{eq}) when $|ab| < 1$. Otherwise the interaction diverges.

The demand level at the equilibrium D_{eq} (for $|ab| < 1$) is:

$$D_{eq} = \lim_{n \to \infty} a^n b^n D_0 + (x + yb) \sum_{i=0}^{i=n-1} a^n b^n = \frac{x + yb}{1 - ab}.$$

For the linear case in our simulation we have $x = 1$ and $y = 0$, resulting in

$$D_{eq} = \frac{1}{1 - ab}. \tag{A-1}$$

This proves that the behavioural equilibrium is only stable if and only if $D_{eq} > 0.5$ (because $|ab| < 1$).

More generally, the threshold level for stability/instability D_{eq} for any intercepts x and y is

$$D_{eq} = \frac{x + y}{1 - ab} = \frac{x + y}{2}.$$

Because $1 - ab < 2$, the lowest value for D_{eq} is the mean of the two intercepts x and y, representing the threshold demand level for BSS.

Details of the scramble competition model

Following Mock & Parker (1997) and Parker et al. (2002), we used the following functions for cost and benefit. For the costs of begging we used the survival probability κ:

$$\kappa(D) = pD + 1,$$

with p as the parameter (slope) for the cost of begging ($-1 < p < 0$) and an intercept of 1. As the costs reduce the net benefit, the intercept of 1 indicates no costs when there is no begging. Values of p close to 0 indicate a weak begging cost which becomes higher the more p diverges from 0. With $p = -1$, maximal begging results in a survival probability of 0. For the benefit (μ) of supply we used

$$\mu(S) = 1 - e^{-q(S-0.1)},$$

with the parameter q for the benefit of supply bigger than 0 ($q > 0$). Applying these functions to the ESS conditions of the scramble competition model (Parker 1985, Eqs 2 and 3; Mock & Parker 1997) with

$$\beta = \frac{0.5v}{v-1}$$

for the case of 'true monogamy' (see Parker 1985) and

$$\alpha + \beta = 1.$$

α and β are coefficients assigned to special levels of sib competition, parental care and mating system. v is the product of the two gradients of the supply and demand functions (Parker et al. 2002)

$$v = g'(D_{eq})f'(S_{eq}).$$

This leads to

$$D_{ESS} = \beta\frac{\kappa(D_{ESS})}{\kappa'(D_{ESS})} = \left(\frac{0.5ab}{ab-1}\right)\frac{pD_{ESS}+1}{D_{ESS}} \tag{A-2}$$

as the stability condition for demand and

$$S_{ESS} = \alpha\frac{\mu(S_{ESS})}{\mu'(S_{ESS})} = \left(1 - \frac{0.5ab}{ab-1}\right)\frac{1-e^{-q(S_{ESS}-0.1)}}{e^{-q(S_{ESS}-0.1)}k} \tag{A-3}$$

as the stability conditions for supply. This are the two strategies offspring and parents, respectively, should play to solve the POC from an evolutionary perspective.

Note: v (see Parker et al. 2002) is equivalent to λ in our condition for behavioural stability.

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Chapter 3

Effects of clutch size and food level on maternal and offspring foraging in the European earwig (*Forficula auricularia*)

Manuscript: Dobler, R. & Kölliker, M. Effects of clutch size and food level on maternal and offspring foraging in the European earwig (*Forficula auricularia*).

Abstract

Theory predicts, that there is a conflict over resource allocation between parents and offspring in species with obligate parental care. In species with partial begging (i.e., when the offspring can beg for food and feed for themselves) the offspring can potentially escape this conflict by self-foraging. This depends on who has the control over foraging behaviour, the mother or the offspring. In an experiment with the European earwig (*Forficula auricularia*), a social insect species with partial begging, we addressed the questions, how clutch size, as well as the food levels experienced by offspring and female affect offspring and female foraging behaviour, respectively. We manipulated clutch size and the food level of nymphs and females. Subsequently, we exchanged females between treatments for observation trials. Each female and each clutch was used once in one of two identical experiments carried out on independent earwig samples and at different ages of nymphs. We found that nymphs of *F. auricularia* forage themselves at high rates and adjust their foraging behaviour on the own food level status as well as on the food level status of the female. The females adjusted their foraging behaviour only to their own food level status. We therefore conclude, that offspring of the European earwig have the control over the foraging behaviour with limited influence by the female.

Introduction

Based on the work of Hamilton (1964a,b), Trivers (1974) was the first to point out why the conflict between parent and offspring over parental care allocation exists. Since then the parent-offspring conflict (POC) has been the subject of many theoretical and empirical studies. The relatedness of a caring parent is usually equal to all its offspring, hence it should distribute care (i.e., in most of the cases provisioning of food) equally among all of them. However, each offspring is more closely related to itself than to its siblings. Therefore, it should try to acquire more care from its parents than its siblings. Mainly two theoretical models exist about how this conflict can be solved. The 'honest signalling' model by Godfray (1991, 1995) proposes that the offspring signal their real need to the parents and the parents distribute care accordingly to this signals. In this model the parents 'win' the conflict, as they keep the control of how to allocate resources to the offspring (i.e., adjusted to the individual need). The 'scramble competition' model by Parker and Macnair (Parker & Macnair 1978; Macnair & Parker 1978, 1979; Parker 1985) assumes that offspring do not display their real need when begging, but try to out compete their sibs. In this model, the offspring (or more precisely some of the offspring) 'win' the conflict because a strong offspring can acquire more food than the weak one and hence potentially undermine the parents optimal investment. However, Jeon (2008) argued, that even under scramble competition parents may still be under resource allocation control. Parents may allocate more food to the offspring with the higher reproductive value (Fisher 1930), which might be the one that begs more. An extension on Parker's model (Parker et al. 1989) where offspring with different need were assumed suggests that begging can contain honest information about 'need' in scramble competition models, although it did not evolve as an honest signal of need (Parker et al. 2002).

Two main factors are important in the POC. First, the clutch size which may directly influence the competition level between the offspring in a clutch (Godfray & Parker 1992). Second, the availability of food or to be more precise, the amount of food the parents provide to the offspring. The clutch size should be optimised that the product of the number of offspring and the fitness of each offspring is maximised (Lack hypothesis) (Lack 1947a,b; Lack & Wynne-Edwards 1964). However, females produce often more eggs than expected by this hypothesis (Mock & Forbes 1995). Additional eggs may be unfertilised and just serve as nutrition for the hatchlings (trophic eggs, Gobin & Ito 2000; Kim & Roland 2000). Alternatively, additional eggs may give the parents the possibility to increase their fitness in cases of food surplus. There is the possibility for adaptive brood reduction (i.e., selective mortality of the least likely to survive offspring) and in times of food shortage the additional offspring can serve as food for the other offspring (Alexander 1974; Godfray & Parker 1992). However, parents do not always invest in the additional offspring even in times of abundantly food but provide more care to offspring in good condition (e.g., Royle et al. 2002; Mas et al. 2009). A possible reason for it is, that these offspring have a higher reproductive value for the parents (Fisher 1930) despite the abundant food.

Empirical work on birds provides evidence for both conflict resolution models (i.e., the 'honest signalling' and the 'scramble competition' model, respectively). For example, Kacelnik et al. (1995), Kilner (1995) and Price et al. (1996) demonstrated, that offspring begging reflects the feeding history of the individual offspring, giving support for the 'honest signalling' model of Godfray (1991, 1995). Smith & Montgomerie (1991) and McRae et al. (1993) (as examples) found evidence for 'scramble competition' among offspring in terms of begging behaviour and positioning in the nest, respectively. Moreover, and probably related to both models, it appears that parents adjust their investment not only according to the begging intensity of the individual offspring but also to the begging intensity of the whole clutch (e.g., Ottosson et al. 1997; Kilner et al. 1999). Furthermore, Bateson (1994) made the point, that mothers (or parents) should adjust their care to their own state as well as to the state of the offspring to maximise the reproductive success. Similarly, offspring should adjust their begging behaviour to their own state and the status of the mother (parents) to maximise their chance to reach reproductive age. Female (parent) status is a measure of the cost per unit provisioning, this is the effort it takes a female (parent) to provide what offspring ask for. If this cost is high, theory predicts lower amounts of provided and demanded effort.

The majority of studies on parental care used birds and mammals as model organism, but for about two decades, family interactions have also been investigated in insects (e.g., Wyatt & Foster 1989; Scott 1990; Nalepa & Bell 1997; Smith 1997; Smiseth & Moore 2002; Costa 2006; Kölliker et al. 2006; Staerkle & Kölliker 2008). A particularity of insects is that partial begging can occur (Smiseth et al. 2003). This is, that the offspring may have the option to forage independently of the parents (e.g., burying beetles (*Nicrophorus vespilloides*), Smiseth & Moore 2002; Smiseth et al. 2003 or European earwigs (*Forficula auricularia*), Vancassel 1984; Kölliker 2007). This gives the offspring the opportunity to avoid the 'scramble competition' for parentally provided resources via self-foraging when the food supply through the parents is not sufficient or the competition level for the provided resources is to high (Smiseth et al. 2007). According to the argument of Bateson (1994) the decision to self-forage might not only depend on the status of the offspring but also on the parental status.

We used the European earwig (*Forficula auricularia*) and established two clutch treatments (normal and reduced clutch size, respectively) and two food treatments (high (*ad libitum*) and low food, respectively). This manipulated the hunger levels of nymphs and females (food treatment) as well as the competition level for the nymphs (clutch treatment). With cross-fostering experiments we tested how the hunger levels of nymphs and females interacted to affect the foraging behaviours of nymphs and females in different sized families.

We expect more nymphs with food intake in normal clutch treatments and low nymph food treatments than in reduced clutch treatments and high nymph food treatments. Former are expected to be hungrier and should therefore beg more (and hence get more food provided by the female) or self-forage more than the latter. We also expect that females from low food treatments provide less food to the nymphs because it is more costly for her to provide food than to eat it herself. We can not make any clear predictions about how the interaction of offspring and maternal state may affect their foraging behaviours. But based on the results we will be able to draw conclusions about the behavioural control over foraging in the European earwig.

Material & Methods

Study animals

We collected 2$^{\mathrm{nd}}$, 3$^{\mathrm{rd}}$ and 4$^{\mathrm{th}}$ instar nymphs of the European earwig (*F. auricularia*) at an organic orchard near Opfershofen (Thurgau, Switzerland) in May 2007. *F. auricularia* is a group living social insect with a one year generation time. After promiscuous mating during summer and early autumn, females start to lay clutches into burrows in autumn. On average a clutch has about 50 eggs (ranges from 20 to 80) and the female cares for the eggs during winter to protect them against pathogen infections and predation. Males normally die before winter. Offspring (1st instar nymphs) hatch in early spring and get food provisioning by the mother for up to then days but they have also the ability to self-forage (Kölliker 2007) (partial begging, Smiseth et al. 2003). After about ten days offspring become 2nd instar nymphs and start to disperse. The social family structure comes apart and individuals band together in bigger groups. The individuals become adult after the 4th instar stage.

The collected nymphs were set-up together in Petri-dishes (∅ 15 cm) in groups of ten with humid sand as substrate and a half-cut plastic tube as shelter. Fresh food (vegetables, fruits, pollen and oatmeal) was provided twice a week.

Experiment set-up and design

Two successive experiments were carried out, which differed in the age at which the mother-nymph interaction was tested. In the first experiment, nymphs were tested at age 5-7 days, in the second experiment at age 3 days. For clarity, the two experiments are presented according to the age of the nymphs, rather than the chronological order of the experiments.

Experiment at age 3 days

Note: this experiment will hereinafter be referred to as Experiment '3'. One half of the nymphs were kept under standard rearing conditions (14:10 h L:D, 20 °C, 50% rel. humidity). When becoming adults (5^{th} stage) individuals were sorted within four days and kept in male and female groups of ten. As soon as the majority of the nymphs in each rearing regime became adult, pairs of males and females were set-up for mating. Pairs were kept in smaller Petri-dishes (∅ 10 cm) but otherwise the same way as described above. When the female started to lay the eggs, the male was removed and the female put to winter conditions (first to 10 °C in completely darkness and then (in cohorts twice a month) to 5 °C in completely darkness). Clutches were regularly checked for egg development, female survival and the humidity of the sand was checked. Clutches with dead females were discarded. As soon as most of the eggs in a clutch were well developed the clutch was transferred to experimental conditions (16:8 h L:D, 20 °C:15 °C, 50% rel. humidity) to provide suitable hatching conditions.

We established two different clutch treatments and two food treatments in our experiment. Clutch treatment was either the normal clutch size ('N') or a clutch size reduced to one half of the original size ('R'). Food was either high ('H') where the individuals had access to *ad libitum* food or low ('L') where the individuals had only food access every other day, starting with a day with food. We used pollen pellets as food as described elsewhere (Kölliker 2007). Combining clutch treatments and food treatments we got four set-up treatments: normal clutch with high food ('NH'), normal clutch with low food ('NL'), reduced clutch with high food ('RH') and reduced clutch with low food ('RL').

We set-up 12 NH, 10 NL, 13 RH and 9 RL replicates for Experiment '3'. Clutches were randomly assigned to one of the four possible treatments after the first nymph hatched, but in a way that always two successive set-up were from the same clutch treatment. The females of these two set-ups were then exchanged reciprocally for the observation trials (see below). Like this we did not get the possible full factorial design because we only crossed offspring and female food treatment originating from the same clutch treatment (i.e., female

Table 3.1: Overview with all possible female x nymph combinations for the observation trials. The females from two families were always exchanged reciprocally. Like this females were always together with unfamiliar nymphs from either the same food treatment or the other food treatment. Families were not exchanged between the two clutch treatments. H indicates families from the high food treatment, L families from the low food treatment.

clutch treatment	families		observation trials	
	family A	family B	female B x nymphs A	female A x nymphs B
reduced clutch	H1	H2	H2 x H1	H1 x H2
	H3	L1	L1 x H3	H3 x L1
	L2	H4	H4 x L2	L2 x H4
	L3	L4	L4 x L3	L3 x L4
normal clutch	H5	H6	H6 x H5	H5 x H6
	H7	L5	L5 x H7	H7 x L5
	L6	H8	H8 x L6	L6 x H8
	L7	L8	L8 x L7	L7 x L8

x nymph: HxH, HxL, LxH and LxL in the normal clutch treatment and in the reduced clutch treatment, respectively)(Table 3.1). The *a priori* reason we did so was because we wanted to test how clutch size affects food level effects in females and nymphs.

Set-ups for observation trials were placed in Petri-dishes (∅ 15 cm) on humid sand as substrate. Two watch glasses (∅ 4 cm) on top of each other (the upper painted with black acrylic paint) covered an artificial burrow (approx. ∅ 3 cm) which the females used as nest. All replicates were checked daily and food was changed/removed. The pollen pellets were weighed before and after food changing in a standardised manner, this means the pellets were dried in a oven beforehand to standardise the amount of humidity in the pellets. Daily food consumption of each replicates was calculated as the weight change of the pollen pellets over 24 hours.

Experiment at age 5-7 days

Note: this experiment will hereinafter be referred to as Experiment '5'. After bringing the caught nymphs from the field to the lab, the other half of them were kept under short day conditions (10:14 h L:D, 20 °C:15 °C, 50% rel. humidity) to speed up development. Otherwise the procedure was the same as in Experiment '3'. We established the same clutch treatments and food treatments as described for Experiment '3' above. 12 NH, 14 NL, 12 RH and 12 RL replicates were set-up for Experiment '5' in the same way as the set-ups in Experiment '3' (Table 3.1).

Hatching success (proportion of hatched eggs) was not different between experiment '3' and experiment '5' clutches (ANOVA: $F_{1,65}=0.917$, $p=0.341$; Experiment '3': 0.668±0.030, hatch prop Experiment '5': 0.634±0.031). However, number of eggs and number of hatchlings was significantly higher in Experiment '3' clutches (egg number: ANOVA: $F_{1,65}=15.024$, $p<0.001$; Experiment '3': 60.457±2.074; egg number Experiment '5': 48.906±2.136; hatch number: ANOVA: $F_{1,65}=8.982$, $p=0.003$; Experiment '3': 40.028±2.259, hatch number Experiment '5': 30.843±2.040).

Observation trials

Experiment '3'

Observation trials of Experiment '3' took place at day 3 after set-up from February to April 2008. We shifted the observations from days 5-7 in Experiment '5' (see below) because a lot of nymphs were found outside the nest after the observation trials in Experiment '5'. This may be due to a high nymphal activity on days 5-7, an age when the nymphs become increasingly mobile and independent of maternal care. We expected the nymphs to stay more in the nest at day 3 and that the females hence provide more food to the nymphs in the nest. Only families with more than ten nymphs were used for the observation trials, because smaller families do not provide reliable data. We further excluded pairs of replicate when one female died before the observation trial. We had to exclude six families due to size and 12 due to dead females. This resulted in 26 replicates in Experiment '3' (8 NH, 6 NL, 8 RH and 4 RL).

We removed the food of all replicates in the morning on the observation day to increase the probability that the nymphs were hungry during the observation trial in the afternoon/evening. About three hours before the observation trial the females were put to the nymphs of the other matching set-up (i.e., from the same clutch treatment, see above, Table 3.1) to get used to them and *vice versa*. Therefore, we put a small Petri-dish over the nest to force the nymphs and the female to stay together. The food for the observation trial was also weighed and already placed on the Petri-dish, but the individuals had no access to it. We used blue dyed pollen pellets (Staerkle & Kölliker 2008) for the observation trial prepared in the same manner as described above. The dyed food allowed us to count the number of nymphs with food intake during the trials because the dyed pollen is easy to see in the stomach and gut of 1^{st} instar nymphs (Staerkle & Kölliker 2008). At the start of the observation trial the small Petri-dish was taken from the nest and the watch glass painted with black acrylic paint was taken from the unpainted lower watch glass. This allowed us to observe the behaviour in the nest without too much disturbance as the nest was still covered.

After the observation trial the pollen pellet were removed and weighed (the pellet was first dried again). The weight change of the food ($\Delta_{Food} = \text{food}_{after} - \text{food}_{before}$) during the observation trial was calculated as a measure of consumed food during the observation trail. We further counted the number of nymphs with dyed pollen in the gut or stomach (nymphs with food intake) and how many nymphs were outside the nest.

Experiment '5'

The procedure for Experiment '5' was the same as for Experiment '3' except for two things: observation trials took place between days 5-7 seven (rather than at day 3) after set-up and from November to December 2007. Observation trials took place between days 5-7 after set-up to maximise sample size. In Experiment '5' we had to exclude 19 families due to size and six due to dead females. This resulted in 25 replicates in Experiment '5' (8 NH, 7 NL, 4 RH and 6 RL).

Observation trial set-up

Up to four female-nymphs groups were set-up at once for an observation trial. Each trial lasted for three hours and took place in darkness at room temperature. Start was either at 1500 h, 1800 h or 2100 h, depending on the number of replicates to observe per day, the first always starting at 1500. Behaviour was recorded with camcorders (Sony Handycam DCR-HC90E) equipped with infra red sources to make night vision movies. To cover three hours of behaviour tapes had to be changed after 90 minutes under red light conditions to avoid disturbance of the animals. One camera per replicate was focussed on the nest to observe the behaviour in the nest. The camera was about 50 cm above the nest and the view angle was about 70 °. An additional camera was focussed on the four food pellets (centred between the other four cameras, view angle 90 °) to record the time the females and the offspring spent on the food.

The video tapes were analysed after the experiments and the following behaviour were recorded: in the nest: i) time the female was not in the nest, ii) number of nymphs leaving the nest, iii) number of nymphs entering the nest, iv) mouth-to-mouth contact (female and a nymph have contact with the mandibles). Outside the nest: v) time the female spent on the food and vi) time the nymphs spent on the food. We used the sum of ii) and iii) to estimate the activity of the nymphs during the three hours of observation.

Statistics

We used JMP 7.0.2 (JMP Version 7.0.2. 1989-2007) and R version 2.9.1 (2009-06-26) (R Development Core Team 2009) for statistical analyses. We present parametric statistical tests and models if the residuals were normally distributed, and non-parametric tests otherwise. Stepwise multiple regression models (mixed direction to find minimal model) were used to find behaviour with significant effects. P-values were corrected for multiple testing in the analysis of the behavioural data according to the Benjamini-Hochberg method (Benjamini & Hochberg 1995) (multtest-package in R (Pollard et al. 2009)). Adjusted p-values are indicated with p_A, raw p-values with p. Mean values are always given ± standard error.

Nymphs in the two experiments were of different age when the observation trials took place and their mothers were kept under different environmental conditions after they were brought to the lab. Therefore, the two experiments were analysed separately, but then also combined to test for consistent differences and similarities across experiments.

Results

Experiment '3'

In the experiment where nymphs were 3 days old clutch treatment had no significant effect on any of the behavioural measurements (i.e., number of nymphs outside the nest, time the female spent outside the nest, nymph activity, time female spent on food, time nymphs were on food and the number of mouth-to-mouth contacts between female and nymphs) (Wilcoxon Rank Sums: all $|Z|<1.517$, all $p_A>0.360$). Food treatment of the nymphs had no significant effect on any of the behavioural measurements (Wilcoxon Rank Sums: all $|Z|<1.397$, all $p_A>0.576$) and female food treatment had also no significant effect on any of the behavioural measurements (Wilcoxon Rank Sums: all $|Z|<2.609$, all $p_A>0.063$).

In a model with clutch treatment, food treatment of the nymphs, food treatment of the females and the interaction between the two food treatments as factors none of the factors had a significant effect on the number of nymphs with food intake (ANOVA: all factors: $F<1.582$, $p>0.222$; full model: $F_{4,21}=1.073$, $p=0.395$). In model with clutch treatment, food treatment of the nymphs, food treatment of the females and the interaction between the two food treatments as factors none of the factors had a significant effect on the amount of consumed food (ANOVA: all factors: $F<3.143$, $p>0.091$), but the overall model was marginally significant (ANOVA: full model $F_{4,21}=2.8646$, $p=0.049$).

Table 3.2: Correlations between behavioural measurements in Experiment '3' (3 days old nymphs). Spearman's ρ below the diagonal, significant interactions after correction for multiple testing (Benjamini & Hochberg 1995) are indicated with an asterisk (*).

	nymphs out[a]	female out[b]	nymphs activity[c]	female on food[d]	nymphs on food[e]	mtm contacts[f]
nymphs out	—					
female out	0.5675*	—				
nymphs activity	0.4537*	0.5126*	—			
female on food	0.5366*	0.7499*	0.4715*	—		
nymphs on food	0.4871*	0.5733*	0.6656*	0.4362*	—	
mtm contacts	-0.2697	-0.4135*	0.0336	-0.3300	0.0559	—

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[a] number of nymphs outside the nest after the observation

[b] time the female spent outside the nest during the observation

[c] amount of nymphs leaving and entering the nest

[d] time the female spent on the food

[e] time offspring were on the food

[f] mouth-to-mouth contacts

Exploring behavioural measures predicting the number of nymphs that consumed food, stepwise linear regression revealed that the time nymphs were on the food had a positive relationship (time nymphs were on food: F=18.922, $p<0.001$; all other $F<1.715$, $p>0.157$; full model: $F_{6,19}$=10.495, $p<0.001$). The time nymphs were on the food and the time the female spent on the food associated both positive with the amount of consumed food during the observation trial (time female spent on food: F=20.470, $p<0.001$; time nymphs were on food: F=18.469, $p<0.001$; all other $F<1.420$, $p>0.248$; full model: $F_{6,19}$=15.172, $p<0.001$).

There were significant positive correlations between all the measured behaviours, except the mouth-to-mouth contacts which were significantly negatively correlated with the time the female was outside the nest (see Table 3.2).

Experiment '5'

In the experiment where nymphs were 5-7 days old, clutch treatment had no significant effect on any of the behavioural measurements (i.e., number of nymphs outside the nest, time the female spent outside the nest, nymph activity, time female spent on food, time nymphs were on food and the number of mouth-to-mouth contacts between female and nymphs) (Wilcoxon Rank Sums: all $|Z|<0.880$, all $p_A>0.977$). Food treatment of the nymphs had no significant effect on any of the behavioural measurements (Wilcoxon Rank Sums: all $|Z|<2.536$, all $p_A>0.068$) and female food treatment had also no significant effect on any of the behavioural measurements (Wilcoxon Rank Sums: all $|Z|<1.991$, all $p_A>0.211$).

In a model with clutch treatment, food treatment of the nymphs, food treatment of the females and the interaction between the two food treatments as factors, food treatment of the nymphs had a significant effect on the number of nymphs with food intake (ANOVA: food treatment nymphs: F=8.375, p=0.009, more nymphs with food intake in the low food treatment; all other factors: $F<2.210$, $p>0.153$; full model: $F_{4,20}$=3.084, p=0.039). In a model with clutch treatment, food treatment of the nymphs, food treatment of the females and the interaction between the two food treatments as factors, food treatments of the nymphs had a significant effect on the proportion of nymphs with food intake (ANOVA: food treatment nymphs: F=12.542, p=0.002, more nymphs with food intake in the low food treatment; all other factors: $F<2.961$, $p>0.101$; full model: $F_{4,20}$=5.065, p=0.006). In a model with clutch treatment, food treatment of the nymphs, food treatment of the females and the interaction between the two food treatments as factors, food treatment of the nymphs had no significant effect on the amount of consumed food but the overall model was not significant (ANOVA: food treatment nymphs: F=5.468, p=0.030, more consumed in the low food treatment; all other factors: F<3.148, p>0.091; full model:$F_{4,20}$=2.692, p=0.061).

Exploring behavioural measures predicting the number of nymphs that consumed food, stepwise linear regression revealed that the number of nymphs with food intake was associated with the time nymphs were on the food (positive; F=9.004, p=0.008), the number of nymphs outside the nest (positive; F=14.652, p=0.001) and the nymph food treatment (partial r^2=0.274, more nymphs with food intake in the low food treatment; F=7.078, p=0.016) (all other F<3.540, p>0.076; full model: $F_{6,18}$=10.570, p<0.001). The proportion of nymphs with food intake showed a relationship with the time nymphs were on the food (positive; F=16.693, p<0.001) and the nymph food treatment (partial r^2=0.543, a higher proportion of nymphs with food intake in the low food treatment; F=6.828, p=0.017) (all other F<2.245, p>0.136; full model: $F_{5,19}$=10.570, p<0.001). The time nymphs were on the food and the time the female spent on the food were both positive associated with the amount of consumed food (time nymphs were on food: F=5.519, p=0.012; time female spent on food: F=5.223, p=0.029; other F<1.991, p>0.081; full model: $F_{7,17}$=4.618, p=0.005).

Correlations between the measured behaviours were made to find possible connections between them. There were significant positive correlations between nymph activity and the time the female spent outside the nest (Spearman's ρ=0.623, p_A=0.011) and between nymph activity and the time nymphs were on the food (Spearman's ρ=0.665, p_A=0.008) (Table 3.3). All other correlations were not significant (p_A>0.122).

Experiment '3' and Experiment '5'

Comparing the two experiments showed that the two experiments differed significantly in the number of nymphs with food intake (Experiment '3': 15.539±2.892 nymphs, Experiment '5': 8.880±1.556 nymphs; Table 3.4), the amount of consumed food during the observation trial (Experiment '3': 6.657±1.018 mg, Experiment '5': 3.724±0.373 mg; Table 3.4) and the time the female was on the food (Experiment '3': 15.523±3.129 min, Experiment '5': 10.932±2.186 min; see Table 3.4 for further details). The proportion of nymphs with food intake and the other behavioural measurements were not significantly different between the experiments (see Table 3.4).

Over both experiments, clutch treatment had a significant effect on the number of nymphs outside the nest (normal clutch: 16.241±3.004 nymphs, reduced clutch: 6.090±1.505 nymphs; Table 3.4). Food treatment of the nymphs had a

Table 3.3: Correlations between behavioural measurements in Experiment '5' (5-7 days old nymphs). Spearman's ρ below the diagonal, significant interactions after correction for multiple testing (Benjamini & Hochberg 1995) are indicated with an asterisk (*).

	nymphs out[a]	female out[b]	nymphs activity[c]	female on food[d]	nymphs on food[e]	mtm contacts[f]
nymphs out	—					
female out	0.3159	—				
nymphs activity	0.4361	0.6225*	—			
female on food	0.0432	0.0591	0.0397	—		
nymphs on food	0.4140	0.3869	0.6654*	0.0917	—	
mtm contacts	-0.2601	-0.1889	-0.2354	-0.1864	-0.4300	—

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[a] number of nymphs outside the nest after the observation
[b] time the female spent outside the nest during the observation
[c] amount of nymphs leaving and entering the nest
[d] time the female spent on the food
[e] time offspring were on the food
[f] mouth-to-mouth contacts

Table 3.4: ANOVA overview for the combined data from both experiments. Effects of nymph age at the experiment (nymph age), clutch treatment (clutch), food treatment of nymphs (nymph food), female food treatment (female food) and the interaction between food treatment of females and nymphs (female food x nymph food) on the number of nymphs with food intake, the amount of consumed food, the proportion of nymphs with food intake and the measured behaviours.

dependent	factor/treatment	df	F	p
nymphs with food intake	full model	5	2.952	0.022
	nymph age	1	6.681	0.013
	clutch	1	1.458	0.234
	nymph food	1	4.845	0.033
	female food	1	2.919	0.094
	female food x nymph food	1	0.084	0.773
proportion nymphs with food intake	full model	5	3.835	0.006
	nymph age	1	1.843	0.181
	clutch	1	1.092	0.302
	nymph food	1	8.775	0.005
	female food	1	6.720	0.013
	female food x nymph food	1	0.812	0.372
consumed food	full model	5	4.525	0.020
	nymph age	1	10.944	0.002
	clutch	1	2.107	0.153
	nymph food	1	3.512	0.067
	female food	1	5.075	0.029
	female food x nymph food	1	1.115	0.297
nymphs outside the nest	full model	5	3.029	0.019
	nymph age	1	1.887	0.176
	clutch	1	6.840	0.012
	nymph food	1	1.698	0.199
	female food	1	0.041	0.841
	female food x nymph food	1	2.838	0.099
nymph activity	full model	5	1.029	0.413
	nymph age	1	1.427	0.239
	clutch	1	0.735	0.396
	nymph food	1	1.246	0.271
	female food	1	2.246	0.141
	female food x nymph food	1	0.301	0.586
nymphs on food	full model	5	3.588	0.008
	nymph age	1	0.016	0.900
	clutch	1	0.174	0.678
	nymph food	1	3.378	0.073
	female food	1	5.163	0.028
	female food x nymph food	1	5.879	0.019
mouth-to-mouth contacts	full model	5	2.044	0.091
	nymph age	1	0.282	0.598
	clutch	1	0.661	0.421
	nymph food	1	1.321	0.257
	female food	1	6.985	0.011
	female food x nymph food	1	0.074	0.787
female outside the nest	full model	5	1.895	0.114
	nymph age	1	0.770	0.385
	clutch	1	0.658	0.421
	nymph food	1	0.254	0.617
	female food	1	3.601	0.064
	female food x nymph food	1	2.284	0.138
female on food	full model	5	2.703	0.032
	nymph age	1	4.058	0.050
	clutch	1	1.794	0.187
	nymph food	1	0.616	0.437
	female food	1	5.826	0.020
	female food x nymph food	1	0.653	0.423

significant effect on number of nymphs with food intake (high food: 9.536±2.342 nymphs, low food: 15.609±2.370 nymphs; Table 3.4) and the proportion of nymphs with food intake (high food: 0.332±0.069, low food: 0.612±0.077; Table 3.4). Female food treatment had a significant effect on the amount of consumed food (high food: 4.234±0.634 mg, low food: 6.517±1.014 mg; Table 3.4), the proportion of nymphs with food intake (high food: 0.359±0.071, low food: 0.589±0.080;Table 3.4), the time females were on the food (high food: 6.888±1.702 min, low food: 16.002±3.702 min; Table 3.4), the time nymphs were on food (high food: 50.418±10.488 min, low food: 87.457±10.844 min; Table 3.4) and the number of mouth-to-mouth contacts (high food: 2.926±0.667, low food: 0.682±0.311; see Table 3.4 for details).

The interaction between food treatment of females and nymphs had a significant effect on the time nymphs were on food ($F_{1,45}$=5.880, p=0.019; Figure 3.1). The time nymphs from the low food treatment were on the food was not significantly influenced by the female food treatment but high food treatment nymphs spent significantly more time on the food when together with a low food treatment female than when together with a high food treatment female.

Discussion

Our experiments were designed to test whether foraging behaviour in the European earwig is under the control of the nymphs, under control of the female or whether both have control about foraging to some degree. Clutch treatment and both food treatments had no significant effects in Experiment '3' and only food treatment of the nymphs in Experiment '5'. All treatments had some significant effects when we analysed the pooled data. A possible reason why we did not find more significant treatment effects was the low statistical power we had due to the sample size and the high variation between families (personal observation R Dobler). In both experiments we found a positive association between the number of nymphs with food intake and the time the nymphs were on the food, a positive association between the amount of consumed food and the time the nymphs were on the food and the amount of consumed food was in a positive relationship with the time the female spent on the food. This indicates, that nymphs and females consumed food directly at the source and that the number of nymphs with food intake was hence a result of self-foraging by the nymphs and most likely not caused by female food provisioning.

The treatment manipulations (i.e., food level of the nymphs, food level of the females and clutch size) had no significant effects in Experiment '3' and only nymph food treatment had significant effects in Experiment '5'. The absence of

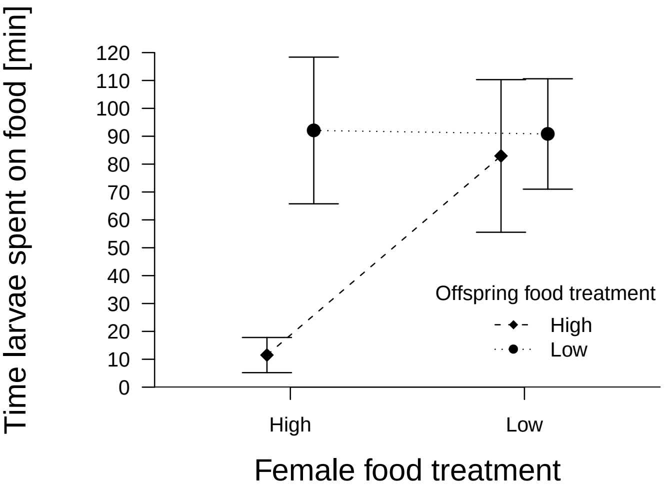

Figure 3.1: Effect of female and offspring food level treatment on the time nymphs were on food over the 3 hour observation period. The interaction between the two treatments is significant (see text). The time nymphs from the low food treatment spent on the food was not affected by the food level of the female. Nymphs from the high food treatment spent significantly more time on the food when together with a female from the low food treatment than when together with a female from the high food treatment. High female x high offspring: 11.512±6.303 min, high female x low offspring: 92.072±26.307 min, low female x high offspring: 82.933±27.372 min, low female x low offspring: 90.812±19.800 min.

any significant treatment effects in Experiment '3' may indicate that the time was too short to establish the treatments. Although we found no significant treatment effects, the other results (including the correlations) are mostly consistent with the hypothesis, that nymphs attained food mainly by self-foraging and not by female provisioning. The significant effects of the food treatment of the nymphs in Experiment '5' showed, that the nutritional condition of nymphs had a significant effect on the foraging behaviour of the nymphs, but not on the foraging behaviour of the female. Only nymph-related attributes (i.e., nymphs with food intake and amount of consumed food) were significantly affected by the food treatment of the nymphs but no female-only related attributes. Further, the food intake of nymphs was only affected by or associated with other nymph-related attributes (i.e., food treatment, nymphs outside the nest and time nymphs on the food). This suggests that nymphs have the control over their foraging behaviour and that they cover their dietary needs to a large extent by self-foraging at least when access to food is easy, as in our experimental set-up. This suggestion gets further support by the results from the overall analyses where we found that mostly the food treatment of the nymphs influences the food intake of the nymphs (food treatment of the females influenced the proportion of nymphs with food intake). A similar control for the foraging behaviour was found by Smiseth et al. (2003) for the nymphs of the burying beetle (*N. vespilloides*), another insect species with partial begging.

However, the female may still have an important role in the foraging behaviour of the nymphs, at least when nymphs are young. In Experiment '3' we found a significant positive correlation between the time the female spent on the food and the time the nymphs were on the food, which both were also positively associate with the amount of consumed food. There was no significant correlation between the time the female spent on the food and the time nymphs were on the food in Experiment '5', but both had a positive relation with the amount of consumed food. A possible interpretation is, that the female guides the nymphs (3 days old) to the food source, because they would not find it by themselves. The older nymphs (5-7 days old), however, possible find the food by themselves, as there is no significant association between the time the female spent on the food and the time the nymphs were on the food. Maybe this is based on experience (learning) of the nymphs. This interpretation finds also support from the results in the pooled data as females in Experiment '3' spent more time on the food than females in Experiment '5'. What has already been shown is, that nymphs growing up without a tending female have a smaller survival probability than nymphs growing up with a tending female (Kölliker 2007). Therefore, the female seems to have an important role for the survival of the nymphs, but we can not conclude from our experiment whether this is related to the foraging behaviour or to some other features. So far this bases all on indices and further experiments are needed to address the question whether the female guides the nymphs to the food or not.

When testing the two experiments together we found, that the age of the nymphs at the experiments had a significant effect on the number of nymphs with food intake, the amount of consumed food and time the female spent on the food. That we found more nymphs with food intake at day 3 than on days 5-7 can be explained by the absolute higher amount of food that was consumed at day 3 compared to days 5-7. As the study of Kölliker (2007) showed, the absolute food consumption of European earwigs is highest at day 3 after hatching and decreases then over the next days. That females spent more time on the food in Experiment '3' than in experiment '5' can be interpreted in two ways. First, it fits in the pattern that more food is consumed at day 3 than on days 5-7 and the female therefore likely has to spend more time on the food to consume more food. However, according to the results of Kölliker (2007) a female without nymphs does not consume more food on day 3 than on days 5-7. But this can not directly be compared with our experiment, because the foraging behaviour of a single female may be completely different from a female tending nymphs. The second interpretation, that the female guides the nymphs to the food is a possible mechanism which could explain this result, that has already been discussed above.

In the pooled data, clutch treatment had a significant effect on the number of nymphs outside the nest. Significantly more nymphs were outside the nest in the normal clutch treatment than in the reduced clutch treatment but the proportion of nymphs was similar. If competition had increased the pressure on nymphs to forage independently, a disproportionately higher number of nymphs would be expected outside the nest in the larger clutches. However, this difference can already be explained by the difference of the clutch size *per se* and we can therefore not conclude that the difference was a result of a elevated competition level in the larger clutches. That clutch size had no other significant effect is a bit surprising because clutch size is expected to have an effect on the competition level which again should have an effect on the foraging behaviours (e.g., Fox 1975). A possible explanation is that the *ad libitum* access to food decreased competition level below a value where differences between the clutch sizes were detectable

Overall, the food level treatment of the female had significant effects on food consumption, the proportion of nymphs with food intake, the time the nymphs were on the food and the number of mouth-to-mouth contacts. These all were nymph-related attributes that were significantly affected by the female food level. The time the female spent on the food, the amount of consumed food and the number of mouth-to-mouth contacts were female-related attributes where the food level treatment of the female had a significant effect on. Not surprisingly, females from a low food treatment spent more time on the food (because females are expected to be hungry) and more food was consumed in this treatments. This matches with the predictions of Bateson (1994) that females should adjust their foraging according to their hunger level. A significantly higher proportion of nymphs with food intake was observed at low food treatment of the female. That nymphs in this case were for significantly more time on the food is further support, that nymphs control their foraging behaviour. This is also supported by the significant effect of the interaction between the food level of the female and the food level of the nymphs on the time nymphs were on the food. When nymphs were from a low food treatment, the time they were on the food was not significantly affected by the food treatment of the female. However, when nymphs were from a high food treatment, they were significantly longer on the food when the female was from the low food treatment compared to when the female was from the high food treatment. This also goes along with the predictions of Bateson (1994) which states, that nymphs should adjust their foraging behaviour not only to their own hunger level but also to the hunger state of the female. As argued above, a female from a low food treatment should provide less food to the offspring than a female from a high food treatment. Nymphs together with a low food female should therefore forage more themselves, because they should not get food provisioning by the females in this case.

Through out our experiments, we could not find any evidence for female food provisioning mediating the observed effects or correlations. The only significant effect we found related to female food provisioning was the negative effect the food level of the female had on the number of mouth-to-mouth contacts. Although, mouth-to-mouth contact *per se* is no evidence for female food provisioning. Females from the low food treatments had less mouth-to-mouth contacts then females from the high food treatments. This was as expected, as it would be costlier for the female to provide food to the nymphs than to forage herself. But this difference in mouth-to-mouth contacts can not be taken as an evidence for a change in female provisioning rate, because we scored the mouth-to-mouth contacts only in the nest. It is possible that mouth-to-mouth contacts took place outside the nest. If this happened, our measure of mouth-to-mouth contacts was incomplete. However, although possible, it is unlikely that nymphs leave the nest to get food provided by the female when they have the ability to self-forage. We have to stress, that our result disagrees with two previous studies on female provisioning in earwigs. Staerkle & Kölliker (2008) and Mas et al. (2009) found that females provide food to the nymphs. Yet, in their experiments the nymphs did not have the possibility to forage themselves because only the mother had access to food for a limited time. While in this experiment, nymphs and females were freely allowed to forage and interact. Further, in their study Mas et al. (2009) kept the nymphs for two days without food in the low food treatment, we kept them without food every second day. A direct comparison between those studies and our experiment is therefore not possible due to the different experimental conditions.

To summarise, our results suggest that nymphs of the European earwig are under control of the foraging behaviour as they adjust it to their hunger level and the food state of the tending female. Further, our results indicate that the nymphs cover their dietary needs to a large extent by self-foraging. Clutch size manipulation had only small effects on the foraging behaviour of females and nymphs. Overall, our results and findings point out a number of perspectives for further experiments to investigate the dynamics of foraging behaviours between mothers and offspring.

Acknowledgement

We thank Anja Studer, Nicolas Boileau and Urs Stiefel for excellent lab assistance. We further thank Tim Janicke, David Duneau, Peter Sandner, ... and x anonymous referees for helpful comments on this manuscript. The study was financially supported by the Swiss National Science Foundation (grant no. 3100A0-111969 to M.K.)

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Chapter 4

Kin selected siblicide and cannibalism in the European earwig

Published as: Dobler, R. & Kölliker, M. 2010. Kin selected siblicide and cannibalism in the European earwig. *Behav. Ecol.*, **21**, 257–263.

Abstract

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.

Introduction

In social animals where caregivers (e.g., workers or parents) invest continuously essential resources for juveniles 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 & Parker 1997). Under very intense competition selection may favor very aggressive interactions among juveniles (i.e., siblings), which may go as far as siblicide (O'Connor 1978; Mock & Parker 1997). There are many anecdotal reports, 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 & Lubin 2001), snails (Baur 1992), amphibians (Pfennig et al. 1993, 1994), fish (FitzGerald & Whoriskey 1992) and mammals (Fox 1975). Importantly, this occurs not only under harsh environmental conditions (Fox 1975) and it 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 is 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 & 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 & West 2007), and it should only occur when the direct fitness benefits outweigh the costs due to indirect fitness losses (Hamilton 1964a,b; Mock & 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 & Bilde 2008). As expected it was generally found that siblicide reduced density and competition, and that cannibalism to 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 & Parker 1998; Pexton & Mayhew 2002; Nishimura & Isoda 2004; Perry & Roitberg 2005). In these models, kin recognition is predicted to be a key factor (Mock & Parker 1997 , but see Crozier 1986; Fletcher & Doebeli 2009). Although, genetic kin recognition is observed at much lower frequencies than expected (Gardner & West 2007), probably because this form of kin recognition is often evolutionarily not stable (Rousset & Roze 2007), indirect phenotypic mechanism of kin membership are widespread. An added component of selection for kin recognition specific to the evolution of cannibalism may be due to the 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 earwig (*Forficula auricularia*, Dermaptera). In this species, nymphs of one brood (nest mates) stay together during the first juvenile instar (about ten days). Diversity in kinship among family members of one brood can be high because offspring of one brood are typically sired by multiple males (Guillet 2000) and nymphs may join other family groups (Kölliker & 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 were generated by using survival data from control nymphs held singly under identical conditions, and pairing them virtually in computer simulations.

Material & 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 lab. *F. auricularia* is a sub-social insect species with a one year generation cycle. Females care for eggs over winter and provide newly hatched offspring with food during the first juvenile instar (Kölliker 2007).

The earwigs were set-up in Petri-dishes (∅ 10 cm) on humid sand as substrate in male-female pairs or female alone (see below). After set-up the animals were kept under standard rearing conditions (see Kölliker 2007; Staerkle & Kölliker 2008; Mas et al. 2009 for details) 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-siblings and full-siblings. Number of eggs and hatchling per family were recorded. 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) hatchling 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 hours after the first hatching in a family was observed. We paired two families hatching on the same day for one replicate and each family was only used for one replicate. Each replicate included five different treatments based on nymphs combined from the two families in different ways: a control treatment (C), a sibling treatment (S), a non-sibling treatment (N), a sibling treatment with marked individuals (SM) and a non-sibling treatment with marked individuals (NM) (see below for detailed description of treatments; Bilde & 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 polystyrole boxes (22x22x14 mm, Art. 2964, Semadeni, Switzerland) with 1.5 ml of moist sand as substrate according to their treatment. Prior to set-up, they were weighed on a Mettler-Toledo micro-balance (Mettler AT5, Greifensee, Switzerland) with an accuracy of one μg. 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: χ^2=1.336, df=4, p=0.855;

means±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: χ^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) one randomly chosen nymph of each family was set-up alone in one box. For the sibling treatment (S) two randomly chosen nymphs of the same family were set-up in one box and for the non-sibling treatment (N) two 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) 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, $p<0.001$). 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) (two-way ANOVA, 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 eight boxes (two C singlets, two S pairs, two SM pairs, one N pair and one NM pair). The eight boxes of one replicate were placed on the bottom side of a 10 cm Petri-dish lid and position of the treatments were randomized over replicates to avoid position effects. In total 107 replicates were set-up with 214 families.

After set-up each box was checked daily and water was added when necessary to prevent dry 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, but at lower frequencies (R. Dobler and M. Kölliker, 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 on 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: LL=-0.957, Pearson χ^2=1.907, p=0.167; non-sib: LL=-0.041, Pearson χ^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; 2008-12-22) (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 expected under the null-hypothesis of no siblicide and no cannibalism. The 25th and 975th value for the daily survival probabilities, respectively, were used to generate the 95% confidence interval around the expected daily mean survival probabilities.

If siblicide occurs, we predicted that real victims should die earlier than than the 'victims' in the simulated pairs because they get actively killed by the survivor. Further, 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 7.0.2. 1989-2007) and R version 2.8.1 (2008-12-22) (R Development Core Team 2009) for statistical analyses. We excluded treatment replicates where one individual died within 24 hours after set-up as we can not exclude the possibility that they died as a consequence of handling at set-up. This resulted in the following numbers of replicates in each treatment (number of set-up 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 4.1 a) as well as in the case of unrelated pairs (Figure 4.1 b). As expected if siblicide occurs and reduces 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 ten in the sibling treatment (Figure 4.1 a) and up to day eleven in the non-sibling treatment (Figure 4.1 b). Conversely, and as expected when cannibalism occurs and benefits the survivor, the observed survival curves are significantly above the simulated curves. This effect was present after day ten in both treatments (Figure 4.1).

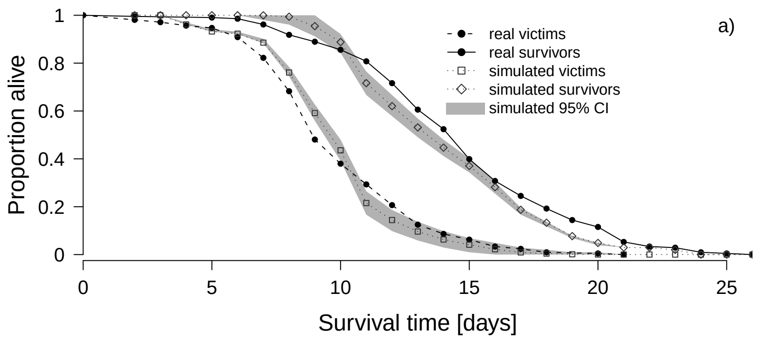
Kin Recognition

We hypothesized selection for kin recognition abilities and predicted that victims in pairs of unrelated nymphs should die earlier than victims in sibling pairs. Comparing the victims and the survivors between (S and N) revealed a significant difference in the survival of the victims but not in the survivors (Table 4.1). 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: χ^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 on the replicates with marked individuals (treatments SM and NM) where we could assign the weight of victim and survivor. Including individual weight in the analysis showed a significant overall correlation between survival time and weight (Spearman's ρ=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 Table 4.1 and 4.2, Figure 4.2).

The weight asymmetry Δw of the two individuals in a pair (weight$_{survivor}$ - weight$_{victim}$) was significantly smaller in the sibling treatment than in the non-sibling treatment (Kruskal-Wallis Rank Sums: χ^2=17.632, df=1, p<0.001; median sib: 0.16 mg, median non-sib: 0.23 mg), an effect easily explained by the strong family effect on hatchling weight (see methods).

To test for kin effects on siblicide and cannibalism while controlling for weight asymmetries, we used weight differences (Δw) and compared them with



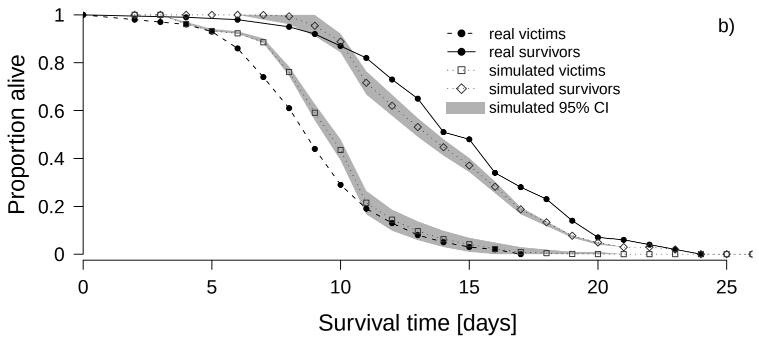


Figure 4.1: Overlay of simulated survival data and observed survival data. Simulated data are based on virtual pairs of singly held control individuals (see methods for details). a) Graph includes the data from the unmarked sibling pairs. b) Graph based on the data of the unmarked non-sibling pairs. 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.

survival differences between survivor and victim, respectively (Δs; $\text{survival}_{survivor}$ - survival_{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 survival difference Δs ($F_{1,100}$=854.460, $p<0.001$). The simulated intercept was not significantly different from zero (p=0.403)(Figure 4.3), indicating that control individuals of 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 zero ($F_{1,300}$=6.079,

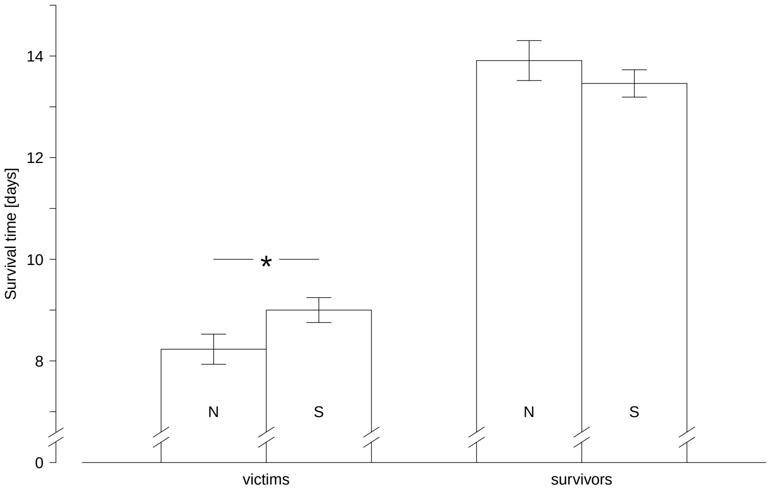


Figure 4.2: Survival of victims and survivals in related (S) and unrelated (N) pairs. The unrelated victims live for significantly less time than the related victims (mean±SE, non-sibs: 8.23±0.29 days, sibs: 9.00±0.24 days). But there is no difference in survival between related and unrelated survivors (mean±SE, non-sibs: 13.91±0.39 days, sibs: 13.46±0.29 days).

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). There was further no significant interaction between relationship and weight asymmetries (Δw x relatedness $F_{1,300}$=0.038, p=0.845) (Figure 4.3). Integrated over the whole observed Δw-range, non-siblings showed a 27.2±10.0% higher Δs value than siblings (means±SE: Δs sibs: 4.466±0.250 days; Δs non-sibs: 5.680±0.386 days)(Figure 4.3).

The proportion of cannibalized victims in the non-sibling treatments (N, NM) was significantly higher compared to the sibling treatments (S, SM) (Fisher's exact test: p=0.013; non-sib: n=200, 93.5% cannibalism, sib: n=412, 86.7% cannibalism).

To further analyse potential benefits of cannibalism correlations between 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: χ^2=49.9, df=1, p<0.001). Whether a victim was cannibalized or not had no effect on the survival time of the victim (Kruskal-Wallis Rank Sums: χ^2=0.153, df=1, p=0.695). but positively to the survival time of the survivor (Kruskal-Wallis Rank Sums: χ^2=47.52, df=1, p<0.001).

Aggregation did not significantly differ between the sibling and non-sibling

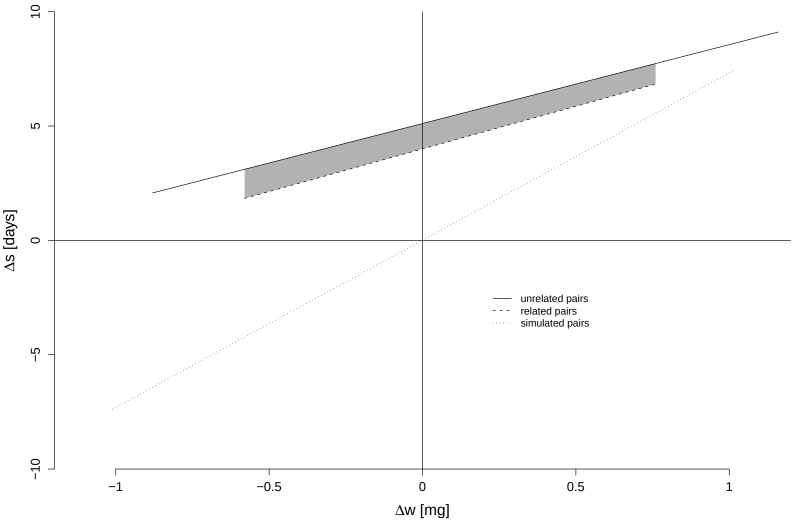


Figure 4.3: Relation between Δs (difference in survival time between survivor and victim) and Δw (weight difference between survivor and victim). The area shaded in gray represents Δ^2s, this is the difference between unrelated (solid line) and related (dashed line) pairs for any given weight asymmetry. The value of Δ^2s can be used to estimate the relative relatedness difference between non-sibling and sibling pairs (see text for details). The dotted line is the expected effect of Δw on Δs when the two individuals from a pair do not interact, based on the simulated data. Line length represent the range of observed values.

treatments (Kruskal-Wallis Rank Sums: χ^2=0.001, df=1, p=0.991) and was not significantly correlated with the occurrence of cannibalism (Logistic Fit: χ^2=0.461, df=1, p=0.496).

Table 4.1: Effect of relatedness on survival of victims and survivors. Parametric survival fit, Weibull distribution.

source	LL-ratio χ^2	estimate±SE*	df	p
victims (S-N)				
relatedness	4.863	0.041±0.018	1	**0.027**
survivors (S-N)				
relatedness	0.040	-0.003±0.015	1	0.840
victims (SM-NM)				
relatedness	6.027	0.055±0.022	1	**0.014**
survivors (SM-NM)				
relatedness	0.161	-0.007±0.017	1	0.688

* positive estimates indicate related individuals survived longer.

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 (R. Dobler and M. Kölliker, personal observation; see also supplementary online material). Broods of European earwigs contain offspring from diverse genetic backgrounds (mixed paternity (Guillet 2000) and brood-joining/adoption after hatching (Kölliker & 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 non-social animals (but see Bilde & 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 non-siblings. A majority of studies reports 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, non-interacting '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 & Koenig 1992) can not 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.

Table 4.2: Effect of relatedness on survival of victims and survivors, including weight as a covariate. The interactions relatedness x 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	LL-ratio χ^2	estimate±SE*	df	p
victims (SM-NM)				
relatedness	4.850	0.042±0.019	1	**0.027**
weight	30.572	0.477±0.071	1	<**0.001**
survivors (SM-NM)				
relatedness	0.755	0.012±0.014	1	0.384
weight	91.654	0.491±0.047	1	<**0.001**

* positive estimates indicate related and heavier individuals survived longer.

Although we can not 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 significantly 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 & 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 $\hat{r}$ 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 non-sibling pairs as the baseline reference (r=0), the difference in Δs between non-sibling and sibling pairs ($\Delta^2 s = \Delta s_{non-sibs} - \Delta s_{sibs}$) could be used to estimate the difference (expressed as a proportion) in relatedness between the treatments as $\hat{r} \approx \Delta^2 s / \Delta s_{non-sibs}$. Based on the obtained Δ^2s value, this estimate was approximately 27%, which fits the expected relatedness of earwig families given multiple paternity (Guillet 2000) and brood joining (Kölliker &

Vancassel 2007) quite well. In our study relatedness ranged from 0.25 to 0.5 in sibling pairs (multiple, but unknown paternity), and was 0 for the non-siblings. 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 hours before set-up 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 & West 2007; Schneider & Bilde 2008).

Conspecific killing, siblicide and cannibalism are common behaviors for invertebrates (e.g., Fincke 1994; Bilde & 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 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, 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.

Acknowledgement

We thank Tim Janicke, Peter Sandner, Will Cresswell and two anonymous referees for helpful comments on this manuscript and Tim Janicke and David Duneau for statistical advice. The study was financially supported by the Swiss National Science Foundation (grant no. 3100A0-111969 to M.K.).

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Chapter 5

Influence of group size, weight asymmetry and kinship on siblicidal and cannibalistic behaviour in earwigs

Manuscript: Dobler, R. & Kölliker, M. Influence of group size, weight asymmetry and kinship on siblicidal and cannibalistic behaviour in earwigs.

Abstract

In group living or social species intra-specific predation and cannibalism can lead to substantial decreases of inclusive fitness because encounters of related individuals (and hence siblicide) are more likely. Therefore, strong selection on the ability of kin-recognition to avoid losses in inclusive fitness is expected. Competition level and relatedness are two key-factors for the evolution of siblicide and cannibalism. However, our knowledge about the kinship-related temporal dynamics of cannibalism in groups of different sizes, and about the accuracy of kin-mediated siblicide and cannibalism is scarce. In an experiment with nymphs of the European earwig (*Forficula auricularia*, Linnaeus), a gregarious and (sub-)social species, we investigated whether group size had an effect on the temporal dynamics of siblicide and cannibalism and on the accuracy of the kin-recognition in groups of mixed kinship. We found that the kinship-related temporal dynamics were influenced by group size and the weight asymmetry among nymphs. Siblicide and cannibalism occurred earlier in larger groups and weight asymmetry effects were stronger between unrelated individuals compared to related individuals. These results can be best explained by enhanced competition in larger groups and the ability of individuals to recognise kin.

Introduction

Cannibalism is a widespread phenomenon among taxa (e.g., Fox 1975 and references therein) with implications for the life-histories and population dynamics of the species. Cannibalism can be favoured evolutionarily because it reduces density and, hence, competition levels (Polis 1981), but also because it provides a nutritional benefit to the cannibalistic individuals. Costs of cannibalism include injury risks (Polis 1981) or pathogen transmission (Polis 1981; Pfennig et al. 1991) and, in the case of cannibalism among relatives, a reduction in inclusive fitness (Hamilton 1964a,b; Yamamura & Higashi 1992). The probability of reduced inclusive fitness by cannibalism can increase substantially in gregarious, group living or social species where interactions among related individuals may be common (Pfennig 1997). Siblicide (i.e., to kill a full or a half sibling: Mock 1984) has been frequently reported in taxa such as predatory insects (e.g., Osawa 1992; Joseph et al. 1999; Dennehy et al. 2001; Gallucci & Ólafsson 2007; Dobler & Kölliker 2010), spiders (e.g., Bilde & Lubin 2001; Beavis et al. 2007; Schneider & Bilde 2008) amphibians (e.g., Walls & Blaustein 1995; Gabor 1996; Pfennig 1997) and birds (e.g., Anderson 1990a,b) where offspring temporarily live in groups and compete for parental care. Kin-recognition is predicted to be an important component in the evolution of this behaviour (Mock & Parker 1997), because it reduces the indirect fitness costs of siblicidal acts. Kin-recognition can be based on direct genetic mechanisms (e.g., Crozier 1986; Rousset & Roze 2007) or phenotypic mechanisms correlated with kin ship (e.g., Hamilton 1964a,b; Sherman et al. 1997) and has been demonstrated to influence the siblicidal and cannibalistic behaviour in a number species (e.g., Osawa 1989; Anderson 1990a; Pfennig et al. 1994; Michaud 2003).

Depending on the nature of the kin-recognition mechanism the possibility to compare and choose between individuals may enhance the accuracy of the information on kinship available to the cannibalistic individuals preventing unnecessary losses in its inclusive fitness.

In a previous study in the European earwig (*Forficula auricularia*) we disentangled the fitness consequences associated with siblicide and cannibalism between related and unrelated pairs of nymph (Dobler & Kölliker 2010). We showed that related individuals were killed and cannibalised later and less often, respectively. In this previous study we used pairs of either related or unrelated individuals (see also Joseph et al. 1999; Michaud 2003 for similar experimental designs). Effects of the potential to choose between related and unrelated individuals on the accuracy of kin-recognition and/or group size on the time-dynamics of siblicidal and cannibalistic behaviour were not tested.

Group size (or density) was repeatedly found to be an important factor influencing cannibalistic behaviour (e.g., Polis 1980; Dennehy et al. 2001; Michaud 2003). Because group size can influence both, the level of competition and the scope for choosing among individuals, it is critical to know how exactly density and relatedness jointly influence the temporal dynamics of siblicidal and cannibalistic behaviours related to kinship among individuals. However, detailed knowledge about the mechanisms and the fitness consequences associated with kin-recognition in groups of different sizes and kin-compositions are still scarce.

In this study, we assessed the temporal dynamics of siblicide and cannibalism in mixed-kin trios of first instar nymphs of the European earwig (*F. auricularia*). *F. auricularia* is a (sub-)social species and all life stages display gregarious behaviour. Naturally, first instar groups consist of half siblings and full siblings but are likely to be associated with orphaned unrelated nymphs (Kölliker & Vancassel 2007). Variation in relatedness among aggregating nymphs is therefore expected to be common in nature. We quantified the kinship-related time-dynamics and the associated fitness consequences for all individuals in our experiment. Comparing these data from trios with the data from our previous study using pairs (Dobler & Kölliker 2010) we tested the two non-exclusive hypotheses that the possibility to choose increases the accuracy of the kin-recognition mechanism and that siblicide and cannibalism, through an effect on competition, depend on group size in this species.

Material & Methods

Study organism

We collected females of the European earwig (*F. auricularia*) on an organic pear orchard near Opfershofen, Switzerland (47°33' N, 9°9' E) and brought them to the lab in September 2008. *F. auricularia* is a promiscuously mating (sub-)social insect species (Costa 2006). Because we caught females late in the season it is likely that all had already mated with an unknown number of sires. Therefore the offspring of one female (family) were assumed to be a mixture of full siblings and half siblings ($0.25 < r < 0.5$). Females care and protect eggs over winter and provide the hatched offspring with food (Costa 2006). We set-up females under standard rearing conditions (for details, see Kölliker 2007; Staerkle & Kölliker 2008; Mas et al. 2009) and allowed them to lay eggs.

Experimental design

We set-up newly hatched nymphs for our experimental treatments within 24 hours after the first hatched nymph in a family was observed. Each experimental replicate consisted of two families hatching on the same day, and each family was only used for one replicate. Two randomly chosen nymphs from one family and one randomly chosen nymph from the other family (and *vice versa*) were set-up together. This way each family was represented as related pair and as a unrelated single individual, respectively. Individuals were marked (see below for details) to assign the initial weight to the individual nymphs and include weight and weight asymmetries in the analyses. Treatments were set-up in transparent polystyrole boxes (22x22x14 mm, Art. 2964, Semadeni, Ostermundigen, Switzerland) with 1.5 ml of moist sand as substrate according to their treatment. Prior to set-up, nymphs were weighed on a Mettler-Toledo micro-balance (Mettler AT5, Greifensee, Switzerland) with an accuracy of 1 μg. Confirming the results of a previous study, there was a significant family effect on weight also in this sample of nymph trios (Kruskal-Wallis Rank Sums: χ^2=779.827, df=213, p<0.001; intraclass correlation coefficient=0.503 (this study), 0.49 (Dobler & Kölliker 2010)).

Two nymphs per trio were marked after weighing for individual recognition with a red or blue CD marker pen (Potaco A.quip) on their legs and/or thorax by gently immobilising them with a mosquito net on a foam-stopper. Marking was carefully randomised with respect to family of origin and relatedness status (i.e., sibling or unrelated) to prevent potential confounding effects of marking (Dobler & Kölliker 2010) on the results of our experiment. We marked siblings in one random half, and two unrelated individuals in the other random half of replicates. Marking *per se* had no significant effect on the average survival time of individuals in trios (Kruskal-Wallis Rank Sums: χ^2=1.823, df=1, p=0.177).

After set-up each box was checked daily and water was added when necessary to prevent desiccation of the sand. Nymphs did not receive any alternative food to precipitate the fitness consequences of nest-mate killing/cannibalism. Nest-mate killing/cannibalism also occurs when food is provided, but at lower frequencies (R. Dobler & M. Kölliker, unpublished results). Death of animals was reported daily. The first dead individual in each group was assigned the role of the 'victim', the second the role of the 'middle' and the third the role of the 'survivor'. When two or three individuals died on the same day, the roles were assigned randomly (see also Dobler & Kölliker 2010). Bodies were left in the boxes to give the other individuals the opportunity to cannibalise. Cannibalism was scored as such when the victim (and/or middle) was sucked out or body parts or the whole body were missing. When the body started to grow mould, it was removed to prevent an infection of the survivor (and/or middle).

To further assess the effect of kinship on differential aggregation behaviour when individuals have the possibility to choose in trios. We daily scored the frequencies when all three individuals, two related, two unrelated or none of the individuals had body contact.

Statistical analyses

We used the method described in Dobler & Kölliker (2010) to simulate the expected survival times of individuals in trios in the absence of behavioural interactions. Based on the survival data of nymphs in the control group, we ran 1000 permutation but changed the procedure in a way that we grouped three (rather than two) control individuals virtually in simulations to obtain expected survival probabilities for 'victims', 'middles' and 'survivors'. Observed survival probabilities outside the 95% confidence interval obtained from the simulations were considered to deviate significantly from the null-expectations.

To test for kin effects on siblicide and cannibalism in groups of three while controlling for weight asymmetries we first calculated the weight differences between related (Δw_r = weight$_{sibling1}$ - weight$_{sibling2}$) individuals and the average weight difference between the unrelated individual and the two related individuals (Δw_u = ((weight$_{sibling1}$ - weight$_{non-sibling}$) + (weight$_{sibling2}$ - weight$_{non-sibling}$))/2). Equivalently we calculated the difference in relative survival time between related (Δs_r = survival$_{sibling1}$ - survival$_{sibling2}$) individuals and the average difference in survival time between the unrelated individual and the two related individuals (Δs_u = ((survival$_{sibling1}$ - survival$_{non-sibling}$) + (survival$_{sibling2}$ - survival$_{non-sibling}$))/2). In a second step we regressed the differences in Δs_r and Δs_u ($\delta s = \Delta s_r - \Delta s_u$) on the differences of Δw_r and Δw_u ($\delta w = \Delta w_r - \Delta w_u$). The intercept of this regression is an estimate for the effect of kinship on the survival patterns in the absence of weight asymmetries, and the slope indicates an interaction between weight asymmetries and kinship. Lack of a significant slope would mean that the effect of kin on survival differences is independent of weight asymmetries. Conversely, a significant positive slope would demonstrate that the effect of kinship on survival differences increases with enhanced weight differences among the nymphs.

Because the individuals used in this study were from the same families as the individuals used in a previous study (Dobler & Kölliker 2010) and the experiments were run simultaneously it was possible to compare the results of the two studies directly.

We used JMP 7.0.2 (JMP Version 7.0.2. 1989-2007) and R version 2.10.0 (2009-10-26) (R Development Core Team 2009) for statistical analyses. Replicates were excluded (N=20) if one individual died within 24 hours after set-up due to the possibility that they died as a consequence of handling at set-up. The number of replicates for statistical analyses was N=194. Survival patterns were analysed by using a parametric survival fit (Weibull distribution). Means ± standard error (SE) are provided, unless stared otherwise.

Results

Siblicide and cannibalism

The survival curves we observed deviated at least for part of the range in survival times from the simulated curves for victims, middles and survivors (Fig. 5.1). The survival of victims was significantly reduced compared to the simulated expectation up to day ten (Fig. 5.1). Middles also died earlier than expected by the simulation. Like in victims, this effect occurred up to day ten. From day eleven to day fourteen middles had a slight tendency to survive longer then expected by the simulated data, but the effect was not statistically significant (i.e., survival times were still within the 95%-CI; Fig. 5.1). As expected for survivors the observed survival curves were over large parts significantly above the simulated curves. This effect was present after day 14 (Fig. 5.1).

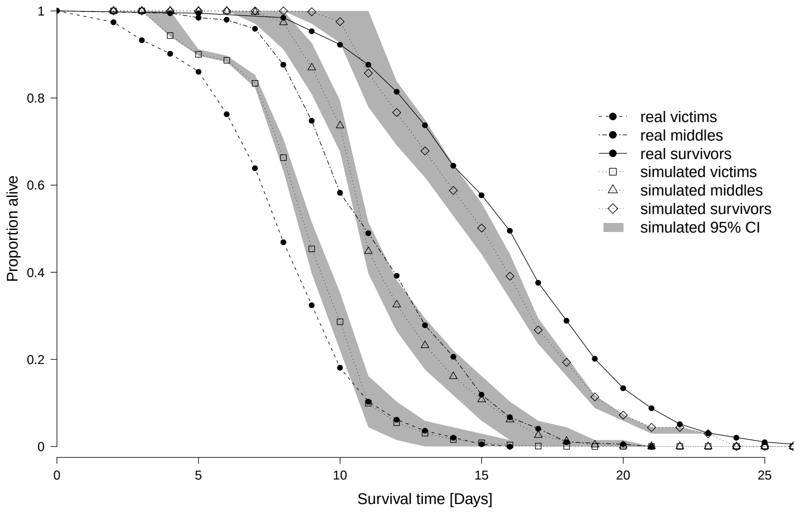

Figure 5.1: Survival of victims, middles and survivors in trios. The victims live for less time than expected, middles live for less time than expected and survivors live longer then expected.

Comparing the survival patterns in trios (this study) and pairs of nymphs (Dobler & Kölliker 2010) by using parametric survival fits with Weibull distribution revealed that victims in trios died significantly earlier than victims in pairs (-LL=1256.5, χ^2=9.45, p=0.002)(Fig. 5.2). The difference was statistically significant between trios and related pairs (-LL=752.4, χ^2=9.9, p=0.007) as well as between trios and unrelated pairs (-LL=750.7, χ^2=6.67, p=0.036). Survivors in trios lived longer than survivors in pairs (-LL=1421.7, χ^2=8.76, p=0.033)(Fig. 5.2). Although middles in trios lived significantly longer than victims from pairs (-LL=1292.3, χ^2=32.77, p<0.001), they survived for significantly less time than survivors in pairs (-LL=1370.2, χ^2=93.94, p<0.001)(Fig. 5.2).

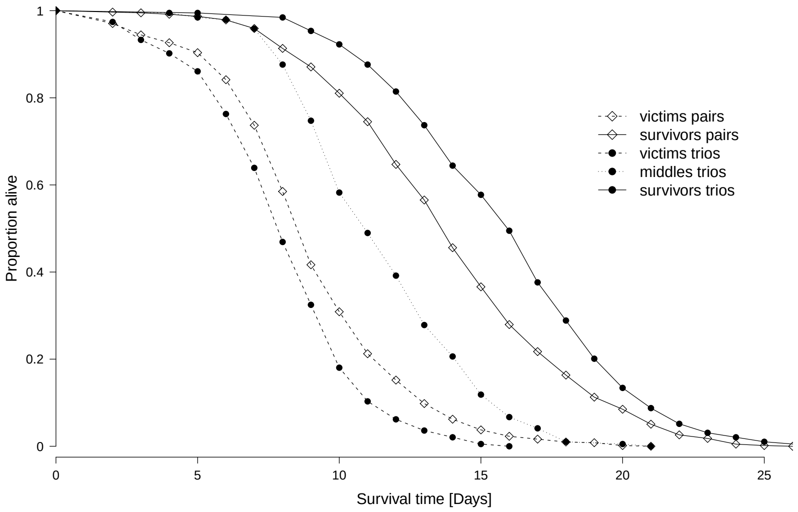

Figure 5.2: Effect of group size on the survival of individuals in pairs and trios.

Kinship-related time dynamics of siblicide and cannibalism

Whether the unrelated individual was the victim, the middle or the survivor (i.e., the death-order) was not random (Pearson χ^2=37.557, df=2, p<0.001; Fig. 5.3). Unrelated individuals were more often victim or survivor and less often middle than expected (Fig. 5.3). Considering victims separately, unrelated individuals were more often the first to die than expected (Pearson χ^2=4.766, df=1, p=0.029; unrelated frequency: expected 0.333, observed 0.407, related frequency: expected 0.667, observed 0.593).

The weight of an individual and the relatedness were both significant predictors for the role of victims (Table 5.1). Lighter and/or unrelated individuals were more often victims than heavier and/or related individuals. Related individuals were more often middles than unrelated individuals, but weight was not

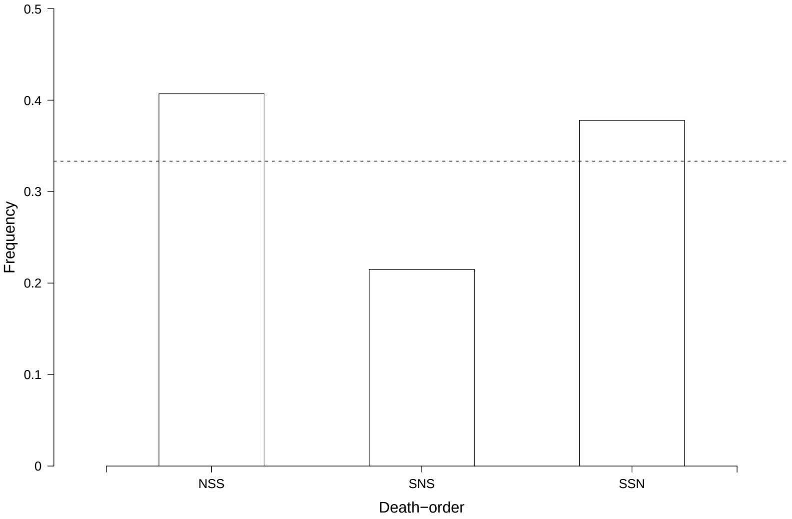

Figure 5.3: Observed and expected frequencies of the different death-orders. NSS: non-related individual was the victim; SNS: non-related individual was the middle; SSN: non-related individual was the survivor. The dashed line indicates the expected frequencies when death-orders were random.

related to the likelihood of being middle (Table 5.1). Finally, relatedness did not significantly predict if a nymph was among the survivors, but weight was strongly associated with being among the survivors (Table 5.1).

In the combined analysis of the effect of kinship and weight asymmetry the linear regression of δs on δw (δ representing the difference between the survival and weight differences among the related and unrelated individuals, respectively) showed a significant intercept (-1.344±0.286; t = -4.693, $p < 0.001$) and a significant positive slope (4.107±0.771; t = 5.330, $p < 0.001$). The significant intercept shows the difference in survival between related and unrelated individuals in the absence of weight asymmetries. This result demonstrates that unrelated nymphs were killed earlier than related individuals independent of weight. The positive slope demonstrates an interaction between weight asymmetry and kinship with a larger kin-effect in groups with higher weight asymmetries. The interaction between weight asymmetry and kinship is also significant in the linear model with separated Δs and Δw values for related and unrelated pairs, respectively ($F_{3,384} = 60.54$, $p < 0.001$; Table 5.2). Integrated over the whole observed Δw-range, non-siblings showed a 31.1±6.51% higher Δs value (as proportion $\hat{r}$, see Dobler & Kölliker 2010 for details) than siblings (Δs siblings: 4.268±0.245 days; Δs non-siblings: 5.794±0.192 days)(Fig. 5.4). The $\hat{r}$ value estimated from trios was not significantly different from the $\hat{r}$ value estimated

Table 5.1: Logistic regression model for the relationship between role (i.e., victim, middle or survivor), individual weight and relatedness. Interactions between individual weight and relatedness were all not significant (victims p=0.770; middles p=0.759; survivors p=0.953). Separate models for victims, middles and survivors.

	Coef	SE	df	Model LRχ^2	Wald Z	p
victim						
full model			2	38.73		<0.001
relatedness	0.532	0.189	1		2.81	0.005
weight	-1.889	0.354	1		-5.33	<0.001
middle						
full model			2	21.16		<0.001
relatedness	-0.886	0.204	1		-4.34	<0.001
weight	-0.282	0.320	1		-0.88	0.378
survivor						
full model			2	42.91		<0.001
relatedness	0.326	0.191	1		1.70	0.088
weight	2.000	0.328	1		6.11	<0.001

Model LRχ^2: model likelihood ratio chi-square

from pairs (Dobler & Kölliker 2010) (t = 0.327, df = 426, p = 0.744).

Bodies of unrelated individuals were cannibalised in 89.94% of the cases, bodies of related individuals in 94.94% of the cases. When the victim was a related individual it was not possible to distinguish whether the body was eaten (in 95.65% of the cases) by the related or the unrelated middle or survivor. Therefore, kin selected patterns of cannibalism cannot be directly inferred from these frequencies. Nevertheless, when assuming that the middle was never cannibalising the victim (i.e., only the survivor may cannibalise because we observed no increased survival of middles), 90.5% of the related bodies get cannibalised and 95.8% of the unrelated bodies get cannibalised, which would then be consistent with previous results (Dobler & Kölliker 2010), although the difference would not be statistically significant (χ^2=2.935, df=1, p=0.087).

Table 5.2: Linear regression model for the relationship between survival difference (Δs), weight asymmetry (Δw) and relatedness.

Coef	Estimate	SE	t	p
Intercept	-4.092	0.345	-11.884	<0.001
Δw	2.561	1.180	2.171	0.031
relatedness	3.962	0.477	8.300	<0.001
Δw x relatedness	6.526	1.515	4.309	<0.001

Individuals aggregated mostly in groups of three (51.59%) or did not aggregate at all (22.33%) (Kruskal-Wallis Rank Sums: χ^2=296.752, df=3, $p<0.001$). Individuals aggregated in related groups of two in 10.14% of the cases and in 15.97% of the cases the aggregated in unrelated groups of two (Wilcoxon signed rank test: V=2522.5, $p<0.001$). The frequency of two related individuals being aggregated was significantly and positively associated with the probability that the unrelated individual was the victim in the trio (Related pair: χ^2=4.871, p=0.027). The frequencies of the other aggregation types were not significantly associated with the relatedness of the victim (all $p>0.270$).

Discussion

In this study, we could demonstrate that group size (or density) and kinship had significant effects on the temporal dynamics of siblicidal and cannibalistic behaviours in European earwig nymphs. Victims in trios died earlier then related and unrelated victims in pairs. The latter result indicates that the larger group size increased competition among nymphs and lead to different survival patterns for victims. Furthermore, and confirming our previous main finding (Dobler & Kölliker 2010), we could show that nymphs exert kin discrimination and preferentially kill/cannibalise unrelated individuals also when the nymphs are in trios of mixed kinship. On average, the estimated accuracy of the kin-recognition mechanism was not affected by the possibility to choose among related and unrelated individuals (trios: this study), and similar in the two studies. Nevertheless, in trios of mixed kinship where choices were possible, kin effects on survival patterns increased with weight asymmetries among the nymphs , which was not the case in pairs (Dobler & Kölliker 2010). Furthermore, we found that earwig nymphs recognised kin in behavioural terms when choosing is possible, preferentially aggregating with unrelated individuals, the individuals preferentially cannibalised.

We showed that victims and middles died earlier than expected and that survivors lived longer than expected. This indicates that victims and middles got, most likely, killed by the survivor. Otherwise we would have expected that middles also benefit from the victim, but this was not observed. It is hence the unrelated and/or smaller individuals (i.e., the eventual 'victims' and 'middles') that ultimately pay the cost of aggregation and interactions in trios. This argument is supported by the fact that survivors in trios lived longer then survivors in pairs. We further found similar levels of cannibalism frequencies among related and unrelated nymphs, respectively, in trios as we previously found in pairs (Dobler & Kölliker 2010).

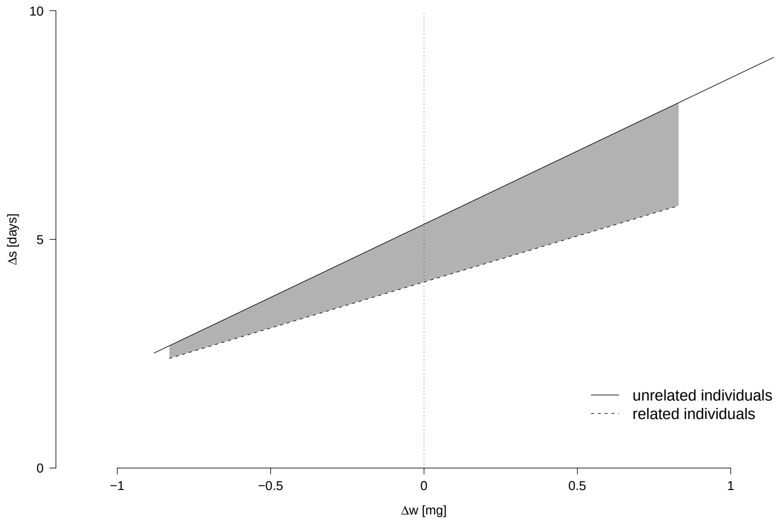

Figure 5.4: Relation between Δs (difference in survival time between survivor and middle, survivor and victim and middle and victim, respectively) and Δw (weight difference between survivor and middle, survivor and victim and middle and victim, respectively). The significantly different Δs values for related and unrelated individuals at Δw=0 (i.e., the intercept of the regression) clearly indicates that the siblicidal and cannibalistic behaviour between related and unrelated individuals is different also in the absence of a weight asymmetry. The area shaded in grey represents Δ^2s, this is the difference between unrelated and related nymphs for any given weight asymmetry. The value of Δ^2s can be used to estimate the relative difference of relatedness between sibling and non-sibling nymphs.

Comparing the survival patterns of trios and pairs revealed that victims in trios lived for a shorter time than victims in pairs and middles in trios lived longer than victims in pairs. This indicates that victims in trios paid higher fitness costs in the course of behavioural interactions (i.e., nest-mate killing and cannibalism) compared to victims in pairs but middles in trios had lower fitness costs than victims in pairs, but still higher fitness costs than expected. Conversely, survivors in trios lived longer than survivors in pairs but middles in trios died earlier than survivors in pairs. This indicates that survivors in trios had higher benefits from nest-mate killing and cannibalism than survivors in pairs and middles in trios (i.e., they could cannibalise two nymphs, rather than one). It seems likely that victims in trios died earlier than victims in pairs because of the potentially elevated competition due to larger group size (or density) when three individuals were kept together instead of two. Density (and/or group size) effects on the cannibalistic behaviour of insect larvae have been reported in other species. For example, Van Buskirk (1989) showed that the density of dragonfly larvae (*Tramea carolina*) had a positive effect on their cannibalistic behaviour and Tena et al. (2009) demonstrated the same effect for larvae of an endoparasitoidic hymenoptera (*Metaphycus flavus*). Similar effects were found in damselfly larvae (*Ischnura verticalis*) where aggressive behaviour towards conspecifics increased at higher densities (McPeek & Crowley 1987) and in copepods (*Tigriopus brevicornis* and *T. fulvus*), where adult cannibalism towards fresh hatched larvae increased with increasing density (Gallucci & Ólafsson 2007). Finally, for *F. auricularia* Moerkens et al. (2009) suggested that cannibalism is density dependent in natural populations.

In our study the sequence of deaths was significantly affected by kinship, with the unrelated nymph most often being the victim or survivor (Fig. 5.3). This result basically confirms our previous study. Interestingly though, kinship status *per se* only predicted significantly the likelihood to be a victim ($p<0.001$), but not to be the survivor ($p=0.088$). For the latter, the dominating predictor was body weight, which may reflect dominance, but also energy reserves for enhanced longevity.

The hypothesis that the possibility to choose increases the accuracy of the kin-recognition mechanism was not supported, at least overall. An effect on the accuracy of kin recognition is expected if cues from other individuals are compared to an own 'standard template' enabling to base decisions on relative similarities between cues of different individuals and the individuals own template (Sherman et al. 1997). In our experiments, the survival-time differences of related and unrelated individuals ($\hat{r}$, our parameter to estimate the accuracy of kin recognition) between pairs and trios did not differ significantly. The estimate for $\hat{r}$ of approximately 31% was not significantly different from the $\hat{r}$ value we previously found for pairs (Dobler & Kölliker 2010), indicating again, that accuracy of kin-recognition was not dependent on the possibility of choice on average. The intercept of the regression of δs on δw demonstrates that kinship had an influence on siblicide in the absence of weight differences among related and unrelated individuals. In the absence of weight asymmetries, unrelated individuals died approximately 1.3 days earlier than related individuals. To survive for the same time as a related individual, an unrelated individual needed a weight advantage of about 0.325 mg, which is about 20% of the initial body weight at hatching. Thus, to overcome the kin-recognition mechanism, an unrelated individual needed a substantial weight advantage compared to the related individuals, despite the strong effect of weight on the survival of individuals *per se*.

The statistically significant positive slope of the regression between δs on δw is due to an interaction between kinship and weight asymmetry. Bigger positive weight asymmetries between individuals led to more pronounced survival-time differences between unrelated individuals than between related individuals. This result differs from the results of nymph pairs (Dobler & Kölliker 2010) where the kin effect on siblicide and cannibalism was independent of weight asymmetry. One possible interpretation of this interaction (and lack thereof in pairs) is that weight asymmetries can facilitate (or lack thereof hinder) kin recognition, but only in mixed groups when comparison is possible. A supporting argument is, that individuals from the same family are similar in weight at hatching. Weight may hence be used as one phenotypic cue for relatedness among others. Alternatively, the positive slope of the regression could indicate that kin effects are exacerbated in groups with higher degree of weight asymmetry due to enhanced competition and/or less contestable competitive/siblicidal outcomes (i.e., clearer roles for victims, middles and survivors) (e.g., Parker & Rubenstein 1981; Enquist et al. 1990). The interaction between kinship and weight asymmetry could explain why unrelated individuals in trios were at equal frequencies victims and survivors, respectively.

Finally, a potential alternative interpretation for the found patterns is that the two related individuals may have cooperated to kill their unrelated nestmate, making siblicide and cannibalism of the unrelated victim more efficient. Such kin enhancement during foraging tasks has been shown in social spiders, for instance (Schneider & Bilde 2008). However, if kin cooperation was involved in kin-selected siblicide in earwigs, we would have expected that both related individuals gain a net fitness benefit. Contrary to this prediction, the middle (i.e., one of the two related individuals) still died earlier than expected (Fig. 5.1). It therefore seems doubtful that kin cooperation favoured the earlier death of victims in trios than pairs, and the hypothesis of enhanced competition seems a more likely explanation.

The expectation that kin recognition has an important role in shaping cannibalistic interactions gets broad support from different systems in the last decade. For instance, larvae of the ladybird beetle *H. axyridis* display a similar difference in latency to cannibalise kin and non-kin, respectively (Joseph et al. 1999). Larvae of the tree-hole mosquito *Ochlerotatus triseriatus* show a density dependent cannibalism behaviour towards non-kin, but the cannibalism behaviour towards kin is not density dependent (Dennehy et al. 2001). Such kin-dependent differentiation increases the indirect fitness (Hamilton 1964a,b; Yamamura & Higashi 1992) and is hence beneficial for the acting individual. However, not surprisingly, not only relatedness but also an individuals weight at hatching was an important determinant for the death-order. The effect of size difference (which is comparable to weight difference) on cannibalistic behaviour has already been demonstrated for ladybird larvae where the size difference had a significant effect on the cannibalistic behaviour (Michaud 2003) and in wolf spiders (*Pardosa agrestis*) the weight ratio between to individuals in a pair can be used to estimate the occurrence or absence of cannibalism (Samu et al. 1999). An other explanation may be, that some families have a better 'sense' to discriminate kin from non-kin than others do. Genetic bases for such variation in abilities of kin-recognition were reported in a study on ladybird beetles (*H. axyridis*) (Wagner et al. 1999) and Stevens (1989) showed, that the cannibalistic behaviour of *Tribolium confusum* is partly genetically determined. Further studies are needed to investigate potential genetic components of kin recognition, nest-mate killing and cannibalism in the European earwig.

To summarise we found that group size had a significant effect on the kin-related temporal dynamics of siblicidal and cannibalistic behaviour in earwig nymphs, that nymphs recognised siblings independent of weight asymmetries, and that the time dynamics of siblicide and cannibalism in relation to kinship depended on weight asymmetries. These effects are best explained by an increase in competition among individuals in larger groups, although weight asymmetries may also facilitate kin discrimination, but not by a higher kin-recognition accuracy in larger groups. And we found that kin discrimination is also present when there is no weight asymmetry between the individuals.

Acknowledgement

We thank Peter Sandner, Tim Janicke, Flore Mas and ... anonymous referees for helpful comments on this manuscript and Tim Janicke and David Duneau for statistical advice. The study was financially supported by the Swiss National Science Foundation (grants no. 3100A0-111969 and PP00A-119190 to M.K.)

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Chapter 6

Synthesis

"The whole is more than the sum of its parts."
Aristotle

The importance of behavioural dynamics

In chapter 2 I assessed the stability conditions for behavioural interactions between parents and offspring in the course of provisioning and begging. I used a formal model to derive the stability conditions analytically. I applied them with numerical simulations to proof their behavioural and evolutionary relevance. As it turned out, the stability of the behavioural interactions depends crucially on how parent and offspring react to each other. This indicates that the dynamics in repeated interactions rule about the particular behaviours of parent and offspring to represent a behaviourally stable strategy (BSS) in the end. Evaluating the behavioural stability of evolutionarily stable strategies (ESS) revealed that a considerable number of proposed ESS did not fulfil the requirements of a BSS. These strategies are therefore not qualified to represent evolutionarily stability in a stricter sense. – Behavioural dynamics are important.

In chapter 3 I investigated how the foraging behaviours of nymphs and females in the European earwig are influenced by their hunger states. The results showed two things. First, nymphs and females changed (or adjusted) their foraging behaviours in different ways according to their own hunger state and/or the hunger state of the other. The foraging behaviour of the females was only affected by their own hunger state, but not by the hunger state of the nymphs. Their behaviour was 'static' in a sense, that they did not appear to adjust it to the interaction with the nymphs. However, foraging of nymphs depended not only on their own but also on the female's hunger state. The foraging behaviour of nymphs was therefore dynamic, because they adjusted it to two different hunger conditions. Second, females changed their foraging behaviour over time (i.e., when nymphs grew older). Females hence displayed a dynamic foraging behaviour as well, as they adjusted it to the age of the nymphs. Both, nymphs and females, showed therefore dynamic behaviours, although in a different context. Nymphs according to their own hunger state and the environment, females over time. – Behavioural dynamics are important.

In chapters 4 & 5 I explored the fitness costs and benefits of nest mate killing (siblicide) and cannibalism using nymphs of the European earwig. I demonstrated that the victim's death was no chance event but was caused by an active act by the survivor. Hence nest mate killing (or siblicide) implies fitness costs to the victim. Cannibalism had as expected fitness benefits for the survivor in terms of a longer survival than predicted without cannibalism. Nymphs showed the ability of kin recognition which influenced the killing behaviour of the individuals. They adjusted the killing behaviour in accordance to the relatedness. They thereby potentially increased their inclusive fitness by killing a related individual later than an unrelated individual. Killing behaviour was further matched to the actual competition level. A dynamic killing behaviour, based on the competition level and the relatedness to the potential victim, may allow the nymphs to maximise their inclusive fitness. – Behavioural dynamics are important.

As these points show up, the dynamic behaviour among members of a family can crucially affect the outcome of interactions among them. It is therefore not only important to know the final result of such interactions (e.g., Smith et al. 1988; Kilner 1995; Ottosson et al. 1997; Kilner et al. 1999), but also the intermediate steps of the behavioural dynamics. With this knowledge it will be possible to gain an insight as to how an interaction leads to the observed outcome and it might be possible to draw conclusions about why the interactions took place (Wright et al. 2002). It is further important to incorporate behavioural dynamics into so far 'static' models on the evolutionary stability of behavioural interactions (McNamara et al. 1999; Godfray & Johnstone 2000; Dobler & Kölliker 2009). The model I presented can not only be used to explore the stability condition in the parent-offspring interaction of provisioning and begging, but for any kind of repeated interdependent behavioural interactions (e.g., dominance interactions (Matsumura & Kobayashi 1998), biological markets (Noe & Hammerstein 1994, 1995), cell interactions (Hofmeyr & Cornish-Bowden 2000), negotiation over care (McNamara et al. 1999; Taylor & Day 2004; Johnstone & Hinde 2006)).

To come back to the words of Dobzhansky *"Nothing in biology makes sense except in the light of evolution."* I add the remark that 'evolution' likewise needs to make sense in the light of behaviour.

The other pieces of the puzzle

Self-foraging

Game-theoretic models resolving the parent-offspring conflict (e.g., Parker & Macnair 1979; Parker 1985; Godfray 1995; Godfray & Johnstone 2000; Parker et al. 2002; Dobler & Kölliker 2009) did so far not take into account the possibility, that offspring can follow a mixed foraging strategy. In mixed strategies the offspring have the possibility to self-forage or to get food provided by the parents (partial begging, Smiseth et al. 2003). Self-foraging allows the offspring to avoid or escape scramble competition and the associated costs. Thereby offspring can potentially increase their fitness when self-foraging is successful.

Partial begging occurs not only in insects (e.g., burying beetles: Smiseth & Moore 2002; Smiseth et al. 2003 or European earwigs: Kölliker 2007) but also in some semi-precocial birds (Leonard et al. 1988). As brought up by

Smiseth et al. (2003), such systems could be used to investigate how dynamic changes in the offspring behaviour made the transition from non-signalling to signalling foraging strategies possible. Beside possible empirical approaches it is also necessary to develop new theoretical models where partial begging is incorporated, to predict how to solve the parent-offspring conflict on both, the behavioural and the evolutionary, levels.

Kin recognition

Kin recognition had significant effects on individual behaviour. However, it seemed that aggregation was not strongly influenced by the relatedness of the individuals. A possible explanation may be, that individuals did not necessarily group according to relatedness but according to their hungers state. That individuals (especially nymphs) adjust their behaviour to hunger states has been shown in my first experiment (chapter 3) so it is possible also involved in group building. Knowledge about the effects of both (i.e., kin recognition and hunger state) on the grouping behaviour would provide us with further information about the mechanisms involved in siblicide and cannibalism (e.g., Pfennig 1997; Yip et al. 2009).

The mechanism of kin recognition (Gardner & West 2007; Hvam et al. 2005; Schneider & Bilde 2008; Paterson & Hurst 2009) *per se* is not know for the European earwig to this day. It is most likely that earwigs recognise kin via hydrocarbons on their cuticle as it has been shown for other insects (e.g., ants: Lihoreau & Rivault 2009; Martin & Drijfhout 2009). Earwigs use hydrocarbons to signal their nutritional state (Mas et al. 2009) and it is therefore possible they use them as well to recognise kin. However, this hypothesis has to be confirmed experimentally.

Kin recognition may not only play an important role for earwigs in nest mate killing (siblicide) and cannibalism, as demonstrated in my experiments, but also for other interactions in families. It is known for other species that there are interactions where it is important to choose or avoid a related individual (e.g., helping in cooperative breeders (Komdeur 1994) or mate choice to avoid incest (Lihoreau et al. 2007)).

Competition level

The behaviour of individuals can also be influenced by the competition level they are faced with. In the second experiment (chapters 4 & 5) the killing behaviour was different when comparing pairs to triplets. Assuming that everything else other than group size has been equal between the two sub-experiments (which is likely as they were performed at the same time with animals from the same families kept under identical conditions on the same Petri-dish lid), competition level is the only factor that can explain the different behaviours we observed in pairs and triplets, respectively.

Adding an alternative food source reduced the competition level even when the group size increased. Nymphs in groups of ten with *ad libitum* access to food survived longer than the individuals in pairs and triplets without access to food. With this decreased competition level, there was also no longer a kin recognition effect detectable, as individuals in related groups had the same survival probability than individuals in mixed groups. This suggests, that kin recognition becomes more important when the competition level increases (e.g., Fox 1975; Bartlett 1987; Van Buskirk 1989; Bilde & Lubin 2001).

Perspectives

> "Science is always wrong, it never solves a problem without creating ten more."
>
> *George Bernard Shaw*

Following the quote of Shaw, with the assumption my science was not wrong *per se*, a lot of new questions and perspectives came up to me during writing up my thesis. Some of them I addressed already in the chapters and I will thus focus on the two issues I consider the most promising.

Theoretical models

Theoretical models are a strong tool to make predictions about how interactions end, on a behavioural as well as on an evolutionary level. However, to do so appropriately it is relevant that these models make 'realistic' assumptions. As showed, to consider behavioural stability can already change the predictions about the evolutionary outcome.

The model I used in chapter 2 can easily be adapted to more realistic assumptions. One possibility is to adjust the functions which describe the parental and offspring reaction norms based on empirical data. Another way is to incorporate a third player in the game to simulate interactions between and within generations (i.e., parents and offspring). Also the kind of communication between the player can be adjusted. So far the communication was error-free. To allow errors in the communication, or time lags in the interactions, would bring the model closer to reality.

The model could also be expanded in the way proposed by Smiseth et al. (2003), by allowing the offspring to choose between self-foraging and begging.

Empirical approaches to behavioural dynamics

To develop, expand and improve theoretical models makes only sense, when empirical work is conducted along with it. As already brought up, knowledge about the average changes in behaviours is insufficient to gain insight in the dynamics of the behaviour. Experiments where the behaviour of both players (i.e., offspring and parents) is manipulated and reported for each interaction can provide valuable data to understand the underlying mechanisms.

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Acknowledgements

"Pinky, are you pondering what I'm pondering?"
"I think so, Brain, but if the plural of mouse is mice, wouldn't the plural of spouse be spice?"
Pinky & the Brain

Well, this is my thesis, but many other people were involved in the progress and I would not have been able to reach this point without their help and support.

First, I would like to thank my supervisor Mathias Kölliker for giving me the opportunity to do my PhD with him. We had a lot of interesting scientific discussions and it was him who inspired my interest in theoretical modelling.

Thank to Adrian Baumeier, Alexandra Kuenze, Angela Keiser, Anja Studer, Anna Egger, Claudio Kugler, Flore Mas, Harris Fienberg, Laura Walther, Lilian Röllin, Lisa Schild, Mandy Schöne-Michling, M.K., Michael Staerkle, Nicolas Boileau, Regina Ruckli, Regine Salathé, Tim 'man hat's nicht einfach, wenn man's doppelt sieht' Janicke and Urs Stiefel for their assistance in rearing the earwigs in the lab. Bruno Fankhauser kindly allowed earwig-catching in his orchard.

It was great to discuss scientific (and sometimes other) problems with David Duneau, F.M., Peter Sandner, Thomas Fabbro, Thomas Zumbrunn and T.J.

Thomas Kühl and U.S. gave me an easy start in Basel...I miss playing darts and the bad jokes of T.K.

Nick Royle kindly accepted to be the external referee for my thesis.

Brigitte Aeschbach, Christine Parry, Jürgen Hottinger, Lukas Zimmermann, Markus Wymann, Viktor Mislin and Yasmin Picton for administrative and technical support and advice throughout the years.

Then, thank to all my friends and colleagues for the relaxing hours we spent together outside (and inside) of science.

Merci to Julia Lutz, Matt Hall, N.R., P.S and T.J. for their comments to improve parts of my thesis.

And last, but not least, thanks to my brother Andreas Dobler for the recreative intermezzos, the mathematical support and the helpful comments on my work as a non-biologist, and to my parents Leo and Maria Dobler for their backing and reliance in me over the years of my studies.

And also thanks to some authors, which never get cited in publications, but helped me a lot with their work!

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List of lecturers that were involved in my training and education at the University of Basel

Prof. Dr. Aleksander Berentsen

Prof. Dr. Dieter Ebert

Dr. Thomas Fabbro

Prof. Dr. Mathias Kölliker

Dr. Lukas Schärer