Males choose to keep their heads: Preference for lower risk females in a praying mantid

Esteban Avigliano [a,1], Romina C. Scardamaglia [a], Fabián M. Gabelli [b], Lorena Pompilio [a,b,*]

[a] Departamento de Ecología, Genética y Evolución & IEGEBA-CONICET, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina
[b] Facultad de Psicología, Universidad de Buenos Aires, Argentina

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ABSTRACT

Male reproductive success is obviously mate limited, which implies that males should rarely be choosy. One extreme case of a reproductive (or mating) cost is sexual cannibalism. Recent research has proposed that male mantids (*Parastagmatoptera tessellata*) are choosy and not complicit in cannibalism and that they modify behavior towards females based on the risk imposed by them. Since female cannibalism depends on females' energetic state (i.e. hunger) we investigated whether male mantids are capable of using environmental cues that provide information regarding the energetic state of females to make their mate choices. Under laboratory conditions, males were confronted individually with three options: a female eating a prey, a female without a prey, and a male eating a prey (as a control for the presence of prey). Each subject comprising a choice was harnessed and placed in the corners of a triangular experimental arena at an equidistant distance from the focal male. The prey was a middle size cricket that subjects ate in approximately twenty minutes. The behavior of focal males was recorded for six hours. Females were under the same deprivation regime and, in line with previous studies, consuming one cricket did not significantly increase females' abdomen girth. Male mantids significantly preferred females that were eating a prey. In all cases choices were made after the females consumed the whole prey. This suggests that males did not use the prey as a direct way to avoid being cannibalized by keeping the female busy. The preference for females that had recently fed may have evolved because of the potential reduction in sexual cannibalism.

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1. Introduction

Sexual cannibalism is a co-evolutionary puzzle found in many different taxa: spiders (Andrade, 1996; Schneider, 2014), scorpions (Peretti et al., 1999), and praying mantids (Kynaston et al., 1994; Maxwell, 1999a). Females of sexually cannibalistic species are known for their voracity during mating, since they may consume their mates either before, during or after the sexual encounter. The costs and benefits of sexual cannibalism for each sex depend on its timing. Sexual cannibalism before copulation can only benefit the cannibalistic female, while sexual cannibalism during or after

sperm transfer can benefit both the female and male (Elgar and Schneider, 2004), depending on the future mating opportunities for the male and the effect his consumption has on the production of offspring (Andrade, 1996; Barry et al., 2008; Johnson, 2001).

There are different (although not mutually exclusive) hypotheses that may explain sexual cannibalism. Non-adaptive hypotheses include the aggressive spillover hypothesis (Arnqvist and Henriksson, 1997), which suggests that sexual cannibalism may have evolved as a by-product of selection for high and non-discriminate aggression in the juvenile stage, when aggressiveness results favorable in the foraging context. The mate choice hypothesis (Elgar and Nash, 1988), on the other hand, suggests that sexual cannibalism is an extreme form of mate choice, where females copulate with high quality or preferred males and cannibalize lower quality males before fertilization. The life-history strategy hypothesis (Schneider and Elgar, 2002) states that sexual cannibalism may be a side effect of an increased foraging vigor of females that mature at a smaller size and body mass.

When cannibalism occurs during or after sperm transfer females obtain clear benefits from the consumption of a mate-turned-into-

* Corresponding author at: Laboratorio de Ecología y Comportamiento Animal, Departamento de Ecología, Genética y Evolución & IEGEBA-CONICET, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EGA Buenos Aires, Argentina.
E-mail addresses: rscardamaglia@yahoo.com (R.C. Scardamaglia), lopompilio@yahoo.com.ar (L. Pompilio).
[1] Present address: Instituto de Investigaciones en Producción Animal (INPA-CONICET-UBA), Facultad de Ciencias Veterinarias, Argentina.

prey: they not only procure the sperm to fertilize their eggs, but they also get a meal in the process. From the males' perspective, the costs outweigh the benefits in many species (but see Andrade, 1996), since becoming their partner's meal translates into null future reproductive success. As a result, males have evolved counter-adaptations such as risk avoidance behaviors (Barry et al., 2009; Fromhage and Schneider, 2004; Lelito and Brown, 2006; Maxwell et al., 2010). In turn, risk avoidance behaviors can favour the evolution of new techniques for females to lure males (Barry, 2015), creating an 'arms race' between the sexes.

In praying mantids, the behaviors that reduce the risk of cannibalism include slow approaches of males towards females, which can take from several minutes to hours (Lelito and Brown, 2006; Maxwell, 1999b; Prokop and Václav, 2005; Scardamaglia et al., 2015); males freezing upon sight of a female in order to avoid detection (Barry et al., 2009; Lawrence, 1992; Roeder, 1935) and avoiding mating with hungry (Lelito and Brown, 2006; Maxwell et al., 2010) or aggressive (Brown et al., 2012; Scardamaglia et al., 2015) females.

The balance between costs and benefits for males (and thus male behavior) may vary due to factors such as accessibility to sexual partners throughout life: males that experience a higher encounter rate with females are more cautious than those that experience a low mate encounter rate (Brown et al., 2012). In the same way, males approach females more cautiously at the beginning than at the end of the season, in association with the risk of cannibalism: mantids that mature earlier are bigger and more cannibalistic than those that mature later in the season (Prokop and Václav, 2008). Evidence suggests that female cannibalism depends on females' energetic state: the hungrier the female the higher the probability of sexual cannibalism (Barry et al., 2008; Maxwell et al., 2010), and that males may use female activity or environmental cues to predict the risk of cannibalism (Gemeno and Claramunt, 2006; Scardamaglia et al., 2015). Gemeno and Claramunt (2006), for example, found that *Mantis religiosa* males approach females more quickly when they capture a prey item. In the same line, Scardamaglia et al. (2015) found that *Parastagmatoptera tessellata* males may cue on the female predatory strike and avoid aggressive and thus riskier females. In this work, we examined male behavior in response to potential indicators of the risk of cannibalism in praying mantids that occur in the province of Buenos Aires, Argentina. We presented *P. tessellata* males with three different options in a laboratory-controlled experiment: one female that was observed whilst consuming a prey (hereafter 'female with prey'), one female that did not get access to a prey (hereafter 'female without prey'), and a male that was observed consuming a prey (control for the presence of prey, hereafter 'control male'). Specifically, we studied whether males are sensitive to cues that provide information on female energetic state and whether they show risk avoidance behavior. Contrary to Gemeno and Claramunt (2006), we presented the options simultaneously rather than focusing on male behavior when presenting the options independently. The current experimental design has the advantage of allowing males to choose between females, providing direct evidence of their preference. We hypothesized that males would behave so as to reduce their risk of being cannibalized and we predicted that they would prefer females they had seen consuming a prey recently.

2. Methods

2.1. Collection and rearing

The praying mantids were raised in the laboratory from oothecae collected from wild populations in Buenos Aires province, Argentina. Oothecae were incubated at 27–31 °C until egg hatching, which occurred after 24–45 days. Nymphs were reared individually in 150 ml plastic containers during the first three or four instars and then transferred to 450 ml plastic containers. Wooden sticks were placed inside the rearing containers, providing a substrate for perching. Mantids were fed *Drosophila melanogaster* ad libitum and misted with water daily, and after about 8 weeks the diet was switched to two juvenile crickets (*Acheta domesticus*) three times a week. Adult emergence occurred 13–15 weeks after hatching (mean ± SD: 93.03 ± 2.48 days for males, N = 33, and 108.96 ± 3.61 days for females, N = 33). The adults were visually isolated from each other by placing sheets of paper between the rearing containers to avoid the development of any preference prior to the experiment. Both male and female adults were fed two juvenile crickets three times per week, which constitutes an abundant diet for this species. Room temperature (25 ± 1 °C) and photoperiod (12:12 h light:dark) were maintained constant during rearing.

The praying mantids used in the choice experiments were all sexually mature and virgin adults. We used males and females older than 21 days post adult emergence. Individuals were deprived of food for 2 days before the experiment to homogenize their energetic state.

On the previous day to the beginning of the trials, all sexually mature females from our laboratory-reared population were briefly anaesthetized (∼30 s) with CO_2 following the procedure of Prokop and Václav (2005) and measurements of their body mass (accurate to 0.1 mg) and body length (accurate to 0.1 mm) were taken. The index of physical condition (IPC) was calculated following Lawrence (1992) as body mass/body size^3. We matched females for each trial according to their similarity in body mass (mean ± SE: 1.48 ± 0.04 g female with prey; 1.47 ± 0.05 g female without prey; N = 18), body length (3.62 ± 0.04 cm female with prey; 3.60 ± 0.04 cm female without prey; N = 18), IPC (0.011 ± 0.003 g female with prey; 0.011 ± 0.002 g female without prey; N = 18). Each individual was used only once.

We carried out pilot tests to evaluate whether the ingestion of a prey (i.e. a middle sized cricket) affected females' abdomen girth (which could in turn affect male choice, Barry et al., 2010; Maxwell, 1999a). To that end, we selected 10 females that were 21–24 days post-eclosion at random from our laboratory-reared population. They were tethered and fed simulating the conditions in the experiment (see below). We measured abdomen girth with callipers both before and after the ingestion of the prey. Mean time of manipulation and ingestion of the prey was 17.6 ± 1.7 min (N = 8). There were no differences in abdomen girth before or after the ingestion of the prey (0.72 ± 0.063 cm before and 0.71 ± 0.063 cm after ingestion of prey, Wilcoxon matched-pairs test: W = 91, p = 0.81, N = 9).

2.2. Experimental choice arena

We used a triangular arena (68 × 68 × 14 cm, base × height × depth) to carry out the choice experiments (Fig. 1). The arena had a translucent cover through which the trials could be video recorded and was divided into three sections: (1) female 1 area; (2) female 2 area; (3) control male area. Each individual was tethered to one of the corners of the arena to prevent them from approaching the focal male, ensuring that the choice was made exclusively by the latter. The choice arena was covered with a black curtain to allow the researcher to carry out manipulations without disturbing the animals. A second arena, identical to the experimental one, was constructed in order to habituate the females and control male separately from the focal male, avoiding any interactions between them before the experiment. Both arena surfaces were wiped with ethanol between trials to eliminate any possible olfactory cues.
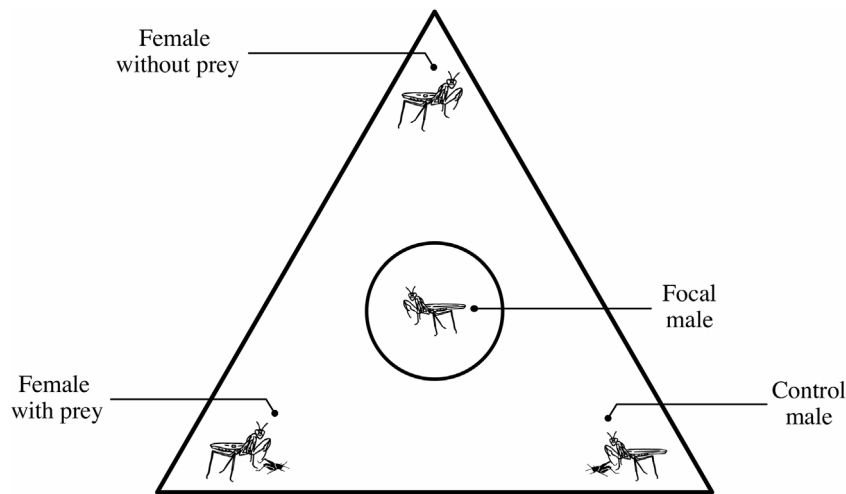
Fig. 1. Experimental setup. Focal males were presented with three options in a triangular choice arena: a female that was eating a prey, a female that did not get access to a prey, and a male that was eating a prey (control male). The focal males were released from a delimited area in the arena.

2.3. Experimental design

Each trial comprised a habituation session and an experimental session. Before the beginning of each trial, the females and the control male were briefly anaesthetized with CO_2 and the tether was attached to them. The tether consisted of a 5 cm S-shaped piece of wire that was fastened with double-coated tape (3M, St Paul, MN, U. S. A.) to the pronotum of the mantid. The distal end of the piece of wire could be easily inserted or removed from a socket placed in each corner of the arena. Except for eliminating prothorax movements when they were tethered, mantids could groom, orient towards prey, strike, capture and eat. The use of the double-coated tape allowed releasing the animals with no harm immediately after each trial.

The habituation session lasted 24 h. The focal male was habituated in the experimental arena (i.e. the actual arena where the choice test was carried out), while the females and control male were habituated in a second arena, identical to the experimental one. The habituation session for the females and the focal male was mainly intended to habituate them to being tethered. To do this, we attached the tethers immediately before the start of the habituation session and placed them in the corners of the alternative arena. Once the habituation session ended, the females and the control male were transferred to the experimental arena. The design of the tether allowed for rapid transference of the individuals, with minimal disturbance.

Twenty-three males were tested as focal subjects. Each of them was presented with three simultaneous options: one 'female with prey' (i.e. a female that was given access to a prey and was observed while consuming it by the focal male), one 'female without prey' and one 'control male' (i.e. a male that was given access to a prey and was observed while consuming it by the focal male). The position of each type of option in the corners of the arena was randomized and counterbalanced between trials.

At the beginning of each trial the focal males were removed from the habituation arena and placed in the centre of the experimental arena under a clear plastic cup, which was at the same time covered by a black paper cup. Focal males remained under both cups during the transference of the harnessed individuals into the experimental arena, which precluded any disturbance to the focal male during this action. Next, the black paper cup was removed so that the focal male could observe the three options as they were given or not access to a prey and observed the beginning of prey consumption.

The three tethered mantises began the trial facing towards the focal male's position in the centre. The clear cup was then removed and the focal was free to move inside the arena.

The experimental session was video recorded and lasted 6 h. For each focal male during the experimental session we recorded the time spent in the area of each option, any mating attempts and cannibalistic events.

2.4. Data analysis

Five trials were discarded due to logistic problems such as release of the prey either by the female with prey or the control male. An additional trial was excluded from the analysis of the proportion of time spent in each area since only a section of the experimental arena was video-recorded, but was included in the mating attempts analysis. A mating attempt was defined as the event where the focal male tried to mount a female, either by jumping or climbing on top of her, independently of female acceptance of the copulation. We considered the focal males' first attempt to copulate (i.e. the first mating attempt) as the main measure of preference, and the proportion of time spent in each area as a secondary measure.

We compared the frequency of mating attempts with each type of female with a binomial test, and the proportion of time that focal males spent in each area with a repeated-measures ANOVA, followed by Tukey post-hoc tests. Data were normalized using the arcsin transformation. Additionally, we compared the number of mating attempts with each type of female that resulted in cannibalism with a Fisher's exact test. Statistical analyses were carried out using R 3.2.0 software. All tests were two tailed and differences considered significant at $P < 0.05$. Mean $\pm$ SE is reported in Results.

2.5. Ethical note

We did not observe any harmful effects associated with food deprivation: none of the individuals died and all appeared to be in good condition when we carried out the experiment. They were returned to their normal feeding regime (two juvenile crickets three times per week) immediately after the end of each trial.
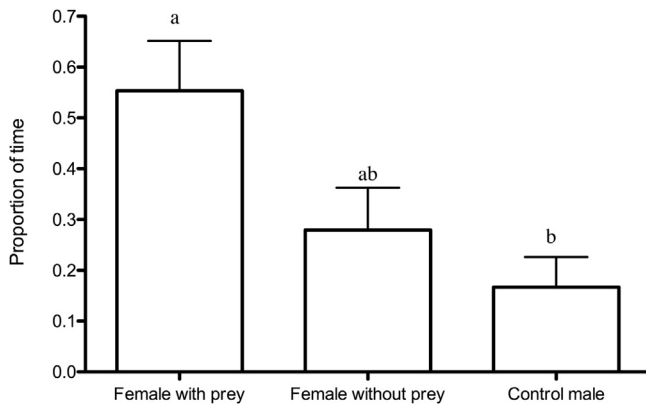
Fig. 2. Proportion of time (mean ± SE) spent by *P. tessellata* males in the area of each option.

3. Results

3.1. Mating attempts

Mating attempts were observed in 89% (16/18) of the trials. Sixty-nine percent of the mating attempts (11/16) were directed to the female with prey, while 28% (5/16) were directed to the female without prey. None of the focal males attempted to mate with the control male. Focal males did not approach or attempted to mate with any of the individuals during the time of prey ingestion. The mean latency to a mating attempt was 144 ± 23 min (N = 16). Males attempted to mate more frequently with the female with prey than with the female without prey (binomial test: p = 0.04). Nine of the mating attempts ended in copulation. Eight males copulated with the female with prey while one male copulated with the female without prey.

3.2. Proportion of time in each area

Focal males spent $55 \pm 10\%$ of the time in the female with prey area, $28 \pm 8\%$ of the time in the female without prey area and $17 \pm 6\%$ of the time in the control male area (Fig. 2). A repeated measures ANOVA showed a significant effect of the type of option ($F_{2,15} = 4.88$; p = 0.023). Tukey post-hoc tests indicated that the proportion of time that focal males spent in the area of the female with prey was significantly higher compared to that of the control male (p = 0.01). However, no significant differences were found between the control and the female without prey (p = 0.62) and between the female with prey and the female without prey (p = 0.10).

3.3. Sexual cannibalism

We recorded events of sexual cannibalism in 22.2 per cent (2/18) of the trials. In both cases the male was cannibalized by the female with prey during the copulation. For males mounting a female with prey 2/11 mating attempts resulted in cannibalism, while 0/5 mating attempts resulted in cannibalism for males mounting a female without prey (Fisher's exact test: p = 1.00).

4. Discussion

Male praying mantids (*P. tessellata*) preferred females that had recently fed on a prey, the option that can potentially reduce cannibalism, when confronted with three different options in choice tests carried out in a controlled laboratory environment. Whether under natural conditions the consumption of a single prey decreases males' chances of survival may depend on many factors (such as

previous female condition and prey size). However, there is no doubt that if the consumption of a prey has an effect, this effect must go in the direction of decreasing the chances of cannibalism. Thus, if the two confronted females are similar in other relevant variables, then the best decision for the male is to choose the option potentially associated to a lower cannibalism risk. If the consumption of a single prey was biologically irrelevant, then males should be indifferent between both females. We found, however, that males are sensitive to the presence of a female eating a prey, meaning that the experimental manipulation was enough to create differences between the females.

The main measure of preference used in the present work was mating attempts, since the cost of making a mistake can lead to the death of the male. Males showed to be risk averse: they attempted to mate more frequently with the females they had seen consuming a prey than with those that had not had access to a prey. In previous studies, Prenter et al. (1994) found that in the cannibalistic spider *Metellina segmentata* males initiate courtship and approach when females capture prey. Similarly, Gemeno and Claramunt (2006) found that when *Mantis religiosa* males are exposed to a single female they approach more quickly when the females capture a prey item, suggesting that they can assess the females' activity state. Approaching a female once she has started feeding may then be a male strategy to reduce the risk of cannibalism (Gemeno and Claramunt, 2006; Prenter et al., 1994). The present study had the advantage of allowing males to choose between females, providing direct evidence of males' preferences. Instead of approaching quickly, our males exhibited a long latency to choose their mate (more than 2 h for a target located in a maximum ratio of 68 cm). In all cases, they mounted females after the consumption of the whole prey, which in average took 17.6 min. Thus, males did not use the prey as a direct way to avoid being cannibalized by keeping the female busy. Before making their choice all males approached each female and spent a considerable time in each area, suggesting that they carefully evaluate each of their potential mates when confronted with more than one option. Another reason that can contribute to such a long latency may be the frontal position of both females (associated with an increment of cannibalism; Maxwell, 1999b) and the impossibility of mounting them from the back because they were harnessed close to the arena corners.

The secondary measure of preference (the proportion of time that males spent in the area of each option) showed that focal males spent a greater proportion of time in the female with prey area than on the control male area, indicating they approached the individuals due to an interest in them as mates rather than to get access to the prey they were eating. However, there were no significant differences in the proportion of time that males spent in the area of each type of female. As mentioned before, the fact that males approached both females before making their choice suggests that they could be assessing other female traits (such as mating status, age, etc.).

The experiment presented in this study was designed to investigate whether males use information related to the energetic condition of females to make their mate choices. Since cannibalism depends on females' energetic condition (Barry et al., 2008; Maxwell et al., 2010) males may reduce their chances of being cannibalized by preferring the females that had recently consumed a prey. It was not our purpose to generate significant differences in the real probability of cannibalism between the females because this would imply manipulation of their previous feeding regime, which could in turn create undesirable differences between them, such as variations in weight, abdomen size, odor release, level of activity, etc. For this reason, we carefully selected for each trial two females that were similar in age, body mass, body length, sexual condition (virgins) and feeding condition; and randomly assigned

them to one of the treatments (female with prey/female without prey).

Even when it was not our purpose to manipulate the real risk of cannibalism we measured the frequency of sexual cannibalism and found it was within the values found for mantids in captivity and in nature (Lawrence, 1992; Maxwell et al., 2010; Scardamaglia et al., 2015). However, this comparison should be taken carefully since most males chose the female with prey, suggesting either that the consumption of one cricket did not change the real probability of cannibalism, or that the consumption of one cricket had an effect but our species exhibits higher levels of cannibalism than other species. We do not discard the hypothesis that the presence of the harness could indirectly favour cannibalism by stressing females, but the results show that the harness used to prevent the females from approaching the focal male did not restrict neither the consumption of a cricket nor sexual cannibalism (see also Scardamaglia et al., 2015).

Why males chose the option potentially associated to a lower risk of cannibalism is, however, a matter of interpretation. We consider different possibilities: 1) Can these results be explained by the attraction generated by the prey itself? This hypothesis can be discarded since we included a male with a prey as a control for the attraction for the prey, and none of the focal males chose that option; 2) Can these results be explained by differences in the salience of the females generated by the movements of the females eating the prey? Previous experiments in our lab (Scardamaglia et al., 2015) showed that *P. tessellata* males prefer a quiet female over one that was observed performing predatory strikes to attack another male. Thus, we consider this explanation unlikely since female movements by themselves do not seem to attract males; 3) Can these results be explained by odor (i.e. chemical cues) secretions after the consumption of a prey? We haven't found reports showing that the consumption of a single prey stimulates the secretion of sexual pheromones in females under good nutritional condition as here. However, if this was the case, this could be the mechanistic explanation to understand why males prefer females that are potentially less cannibalistic.

Previous studies show that praying mantids rely on different cues to search for and choose mates. They use chemical cues when large distances are involved (i.e. mainly mate searching), and visual cues for short distances (i.e. mate assessment, Barry et al., 2010; Lawrence, 1992; Maxwell, 1999a, 1999b). In this experiment the main cue available to males was the sight of different individuals consuming (or not) a prey, thus, they may have used visual cues to make their decision. We cannot discard, however, the hypothesis that our treatment affected chemical cues and males were guided by these differences to choose a mate. Anyway, it was not our purpose to identify the cues that guided males to the female eating a prey. Future studies can investigate the specific mechanism and cues that guide this behavior.

Risk assessment by males in praying mantids has been studied in different species (Brown et al., 2012; Jayaweera et al., 2015; Scardamaglia et al., 2015). Similarly to the present experiment, Brown et al. (2012) found that male *Tenodera sinensis* avoided risky females: males with previous access to females seemed to discriminate between hungry/not hungry females or female orientation, approaching at a slower rate and staying farther away from riskier females. However, males that had restricted access to females approached females at a similar speed and stayed closer to them. In the present study males had restricted access to females previous to the beginning of the experiment. However, they behaved avoiding the risky option. This suggests that the use of simultaneous choice designs facilitates the exhibition of mating choice strategies. On the contrary, negative results should be taken carefully when females are presented isolated.

Scardamaglia et al. (2015) found that *P. tessellata* males were able to assess the level of risk imposed by females and avoided approaching more aggressive females (i.e. females that performed unsuccessful strikes against another male). Interestingly, the difference between these and our results could be due to the consequences of the strike. Unsuccessful strikes would be related to a higher risk of cannibalism. On the other hand, successful strikes which result in the consumption of a prey would be related to a lower risk of cannibalism. Future experiments are needed in order to understand if males are sensitive to the consequences of the strike itself or if they react differently depending on the kind of prey (a conspecific or not).

In conclusion, *P. tessellata* males preferred females that they had seen consuming a prey item over females that they had not seen consuming a prey item. The strong preference for potentially lower risk females provides further support for the hypothesis of conflict over sexual cannibalism, where males' and females' interests are clearly opposed.

Acknowledgments

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