Kin recognition in a butterfly: inferences about its heritability

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Some animal species are able to recognise their relatives, cannibalising mostly non-kin individuals, as happens with the caterpillars of the butterfly Heliconius erato phyllis. Here, we established a breeding programme where adults had different coefficients of relatedness (r = 0 and r = 0.5; offspring, respectively with F = 0 and F = 0.25). The caterpillars cannibalised or did not cannibalise sibling eggs, which was used to make inferences on the kin recognition inheritance of non-cannibals, and to estimate its heritability. The parents had both cannibal and non-cannibal phenotypes; crosses were done for all combinations of these phenotypes, which were divided into outbred and inbred. Caterpillars were grown in the laboratory until the adult stage, and were classified as cannibal or non-cannibal after a test with three sibling eggs. The results showed that the mean number of non-cannibal siblings, those that recognise their kin, is larger in inbreds, above 60%, regardless of their parents’ behaviour. Among non-inbred individuals the mean frequency of non-cannibal siblings was around 38%; these differences were statistically significant. The heritability was estimated by four methods. For F = 0 it was around 0.24 ± 0.11, and for F = 0.25 it was around 0.20 ± 0.17. These results, taken together, were discussed in terms of a threshold character: above this threshold the expression of the non-cannibal phenotype is allowed. As for the low values for heritabilities, they were discussed in terms of the theory of traits relevant to both fitness and the resource allocation priority hypothesis.

KEY WORDS: cannibalism, caterpillar-egg kin recognition, Heliconius erato phyllis, Lepidoptera, inbreeding.

INTRODUCTION

Kin recognition is the ability of an individual to recognise and associate preferably with genetically related individuals (Holmes & Sherman 1982; Green et al. 2008).

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Kin recognition is fundamental in altruistic interactions, where the altruist sacrifices something of its individual fitness to benefit the receptor. The evolution of altruism by kin selection requires that interacting individuals be more related than any two unrelated individuals in the population.

Direct kin recognition can be mediated by three mechanisms: (1) social learning (or previous association); (2) phenotype matching; and (3) allele recognition, also known as the “green-beard effect” (Dawkins 1976; Blaustein 1983). Only the last two mechanisms allow a true recognition, as the phenotypical cues reflect an individual genotype (Lizé et al. 2006). According to Lehmann and Perrin (2002), natural selection should favour the evolution of an optimal acceptance threshold (a level of similarity above which parents are recognised), that minimises the errors of treating a relative like an unrelated individual, and of treating a non-relative like a related individual.

Kin discrimination based on genetics has been found in groups of colonial marine organisms (Crozier 1986; Grosberg & Quinn 1986). Mice also have histocompatibility genes (MHC) for cooperation (Manning et al. 1992) and to avoid inbreeding (Potts et al. 1991). Olsén et al. (1998) studied MHC in Arctic char Salvelinus alpinus and its relation with smells used in kin recognition. Cannibal larvae of the tiger salamander Ambystoma tigrinum use genetically based kin-specific olfactory signals to feed non-relatives, distinguishing different categories of relatives (Pfennig et al. 1994). Blumstein et al. (2013) studied alarm calls, a characteristic associated with kin recognition, in Marmota flaviventris, concluding that it is heritable. Genetic components of recognition also have been found in arthropods, such as subsocial isopods, Coleoptera (Coccinelidae), eusocial bees, ants and termites. However, environmental components of colony recognition have been evidenced in several social species, including ants, wasps and bees (reviewed by Lehmann & Perrin 2002).

The ability for kin recognition may be expressed as a binary notation: an individual recognises relatives or not. Several other characteristics are expressed as one or few discrete phenotypes. Some examples in animals include paedomorphosis, paedomogenesis and cyclomorphosis; trophic dimorphism in amphibians and fishes; wing dimorphism in insects; diapause, reproductive strategies (semelparity and iteroparity) and reproductive behaviour (Roff 1998a); helping behaviour in birds (Charmantier et al. 2007); dimorphism in cricket wings of Gryllus firmus (Roff 1990); and division of labour in colony hygienisation in Apis mellifera (Oxley et al. 2010). In some instances, the different ways are determined by simple Mendelian mechanisms, or, when the Mendelian models do not fit, the threshold one is the alternative (Roff 1997). The key to understanding the inheritance of such traits is the concept that the character has an underlying continuity (liability), with a threshold that imposes a discontinuity on the visible expression (Falconer 1989). Both polygenic and single-locus systems can be analysed within this framework (Roff 1986). The estimation of heritability of threshold traits (binary) is well discussed, for instance in Robertson and Lerner (1949), Dempster and Lerner (1950), Robertson (1951), Elston (1977) and, more recently, Voordouw and Anholt (2002) and Charmantier et al. (2007).

Several studies have found evidence of kin recognition through differential cannibalism of relatives and non-relatives, some of them in arthropods (Nummelin 1989; Dickinson 1992; Agarwala & Dixon 1993; Joseph et al. 1999; Beavis et al. 2006; De Nardin & Araújo 2011; Parsons et al. 2013). Newly hatched caterpillars of the butterfly Heliconius erato phyllis in experimental conditions can discriminate siblings from non-siblings, usually cannibalising the latter (De Nardin & Araújo 2011). This finding is important knowing that females of H. erato phyllis inspect carefully the apical meristem of the host plant, which is a limiting resource, to be sure that is free of eggs (Gilbert 2011).
When only sibling eggs are available, the frequency of cannibalism is significantly lower than when only non-sibling eggs are available. The source of information for kin recognition is located in the egg chorion (De Nardin et al. 2015). The objective of this paper was to analyse the behaviour (as cannibal or non-cannibal caterpillars) of the offspring with different inbreeding coefficients (F = 0 and F = 0.25), and to estimate, for each inbreeding coefficient, the heritability of kin recognition. Initially, our objective was to estimate the heritability of cannibalism; however, given our results we had to change the objective (see Results section).

MATERIAL AND METHODS

Breeding programme

Females of Heliconius erato phyllis were captured in nine natural populations, distant from each other by at least 2 km up to 160 km, from 2011 to 2014, all of them in the state of Rio Grande do Sul, Brazil. They were kept in open-air insectaries, with several species of plants, including Passiflora suberosa, P. misera and P. capsularis, where females lay eggs. Females were isolated in individual insectaries (2 × 2 × 3 m) and were fed with a mixture of water, honey and pollen. Their eggs were collected on a daily basis, with the assistance of a brush. The caterpillars were grown individually in cylindrical plastic pots, in a laboratory with constant temperature (25 ± 1 °C), and were fed exclusively with P. suberosa. It was the adults of these caterpillars that were used in breeding experiments with F = 0 and 0.25.

Cannibalism tests and breeding procedures

The tests to determine behaviour (cannibal/non-cannibal) were done with sibling eggs (from the same female) placed in the vertices of an equilateral triangle made with green cardboard paper with sides of 0.5 cm each in length, inside a Petri dish, following the methodology in De Nardin and Araújo (2011). As the females of this species are monandric, eggs from the same female are full siblings (Drummond III 1984). Each mating was observed by two of the authors (J. De Nardin and L. Silva), and once a female copulated she was isolated in one of the available insectaries. The first caterpillar to hatch, in each test, had its behaviour followed for 45 min; this method was used since our first paper (De Nardin & Araújo 2011) because the caterpillar has to eat its own chorion and then explore the surroundings to find the remaining sibling eggs. Afterwards, the caterpillar was removed from the Petri dish and transferred to a transparent plastic pot, over a piece of absorbent paper, and identified with the code C or NC (cannibal or non-cannibal, respectively) and a number. Caterpillars that did not cannibalise the remaining eggs in each test were able in some way to recognise the eggs; they were named altruists. Caterpillars that cannibalised one or both sibling eggs were named selfish and were eventually unable to recognise their relatives. Therefore, we grouped the individuals with extreme phenotypes: those that totally refrained from feeding and did not kill their siblings, and those that did.

Crosses were done taking into account the degree of relationship between male and female: if non-related, then F = 0 (F = coefficient of inbreeding); if male and female were siblings, then F = 0.25. For both groups, all combinations of male and female phenotypes were obtained: C × C; C × NC; NC × NC. A total of 53 crosses were obtained, 12 being discarded due to a small number of offspring (less than four). Therefore, we obtained 15 inbreeds (7 ♀C × ♂C, 5 ♀NC × ♂NC, 2 ♀NC × ♂C and 1 ♀C × ♂NC) and 26 outbreeds (4 ♀C × ♂C, 3 ♀NC × ♂NC, 8 ♀NC × ♂C and 11 ♀C × ♂NC) (see the table in Appendix I, available as Supplementary Material online). The fertilised females were kept isolated in insectaries with the same features as described above; their eggs were collected on a daily basis. Tests of cannibalism were done for each sibship, in the same way as they were done for the parents.
Inferences about the type of inheritance and heritability

The possibility of a simple autosomal mechanism of inheritance of kin recognition was discarded by the examination of the offspring from all crosses, one by one, who did not fit models of simple inheritance (one locus, two alleles), as well as a model with two loci. However, there remained sex chromosomal inheritance and the role of quantitative genes (polygenes). For the first case, we compared the frequency of non-cannibals within each cross, matched with the behaviour of their parents, cannibal or non-cannibal, and taking into account the inbreeding coefficient of the sibships. A one-way fixed factor analysis of variance (ANOVA; fixed factor: C or NC parental phenotypes) was applied to test the differences in the frequency of non-cannibalism for each inbreeding coefficient; further, a two-tailed t-test compared the means between inbreeding coefficients matched by the phenotype of both parents.

Finally, to estimate the effect of polygenes in kin recognition, estimates of heritability were done, assuming the threshold model of inheritance, which was, in fact, suggested by the frequency of non-cannibalism among the crosses with F = 0.25. We followed the methods shown in Mousseau and Roff (1989) and Roff (1997) for full siblings, designating them 1 for non-cannibal siblings (who showed kin recognition) and 0 for cannibals (who, presumably, showed no recognition). Specifically these methods were: ANOVA, \( \chi^2 \) and maximum likelihood; apart from using the 0/1 scale, we also estimated heritability for an underlying scale as in Roff (1997). Another method to estimate heritability for the observed scale was derived in Bull et al. (1982); a conversion to the underlying scale was done by the method of Lynch and Walsh (1998) (Appendix II, available as Supplementary Material online, contains details of the methods used). Moreover, as our inbred crosses were non-random (full sibs), the heritability of kin recognition could be inflated; due to this we had to use a correction, \( h^2 = 1 - \frac{4rH^2}{1+2r} \), where \( r \) is the correlation between parents and \( H^2 \) is the non-corrected heritability (Roff 1997). Another usual method to estimate heritability, the parent-offspring regression, was not appropriate for our kind of data.

RESULTS

The mean frequency of non-cannibalism (rough data in Appendix I, available as Supplementary Material online) among the outbred crosses was 0.40 ± 0.24 \((n = 26)\), and for inbred crosses, 0.60 ± 0.20 \((n = 15)\). It seems reasonable to admit that, as inbred individuals are homozygotes for many loci, some of these loci could be related to kin recognition, though our first objective was to estimate the heritability of cannibal behaviour. However, we observed, additionally, that the offspring of cannibal parents, especially in those cases of inbreeding, showed a higher frequency of non-cannibalism, and when parents were both non-cannibals, their offspring had a high frequency of non-cannibals (see Appendix I, available as Supplementary Material online). Thus, what is inherited is kin recognition which results in a high frequency of non-cannibalism. This possibility was the basis of our further search for more specific information on inheritance.

Table 1 shows the frequency of non-cannibals in all sibships, matched with the behaviour of their parents and according to the inbreeding coefficient. The main reason to do this was to detect a possible effect of genes for recognition linked to the sex chromosomes. The results are clear, however, showing a very homogeneous set of values within each value of F. There is no significant difference among the values for each inbreeding coefficient. Moreover, the frequency of non-cannibalism is always greater among the crosses with F = 0.25 \((P < 0.001)\), suggesting that this behaviour, at least in part, has a heritable component.

The pattern of inheritance for kin recognition was consistent with polygenes with a threshold; above this threshold the phenotype would be non-cannibal, and below,
We then decided to estimate the heritability for threshold characters by four different methods available in the literature (Material and methods). The results are shown in Table 2.

**DISCUSSION**

The results presented here show that the inheritance of non-cannibalism is probably associated with caterpillar-egg kin recognition. Further, the results can also be understood as an example of quantitative inheritance with a threshold to show kin recognition. Regrettably, the number of genes involved is still unknown, although an effort is being made presently to solve this. The system works as if the non-cannibal phenotype is expressed as soon as a minimum number of genes are present; otherwise, the cannibal phenotype is expressed.

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**Table 1.**

Frequency of non-cannibals in sibships matched by parental behaviour and inbreeding coefficient.

| Inbreeding coefficient | Parental behaviour |  |
|------------------------|--------------------|--|
|                        | Cannibal | Non-cannibal | Cannibal | Non-cannibal |
| F = 0                  | 0.3878\textsuperscript{a} | 0.3770\textsuperscript{a} | 0.3889\textsuperscript{a} | 0.3768\textsuperscript{a} |
| F = 0.25               | 0.6512\textsuperscript{b} | 0.6105\textsuperscript{b} | 0.6147\textsuperscript{b} | 0.6528\textsuperscript{b} |
| Two-tailed t-test      | −11.128   | −10.011      | −9.783   | −12.222      |
| P                      | < 0.001   | < 0.001      | < 0.001  | < 0.001      |
| df                     | 140       | 284          | 231      | 277          |

\textsuperscript{a,b}Means with the same letter are not significantly different.

**Table 2.**

Estimates of heritabilities (± SE) on the underlying scale, by the four methods used in this study. The heritability for inbreds was corrected, as described in Material and methods.

| Method                    | F = 0               | F = 0.25           |
|---------------------------|---------------------|--------------------|
| ANOVA                     | 0.248 ± 0.122       | 0.208 ± 0.175      |
| \(\chi^2\)                | 0.242 ± 0.120       | 0.199 ± 0.172      |
| Maximum likelihood        | 0.135 ± 0.097       | 0.191 ± 0.170      |
| Bull et al. (1982)*       | 0.476 ± 0.165       | 0.199 ± 0.172      |

ANOVA: analysis of variance.

*Bull et al. (1982) do not provide expressions for standard error. We used that suggested by Roff (1997).
Before going on to the heritability estimates, we must discuss, briefly, the possibility of sex chromosomal inheritance. Our data do not support this hypothesis, which is different from what occurs in Papilio glaucus, where a strong case for sex inheritance was shown by Scriber and Evans (1986). They have found that melanic females generally only have female melanic offspring, while yellow females produce only yellow female offspring, suggesting that colour depends on the W chromosome. Turner and Sheppard (1975) suggested the absence of crossing-over in females of Heliconius erato. These results were expanded to include all Lepidoptera (e.g. Jiggins et al. 2005; Marec et al. 2010). Thus, if in our results there was a relation in the proportion between non-cannibal mothers and a non-cannibal offspring, the lack of crossing-over would support the correlation between a female and her offspring as far as any gene present in the sex chromosomes.

Systems of kin recognition usually are specific and regulated by one or more polymorphic loci (Crozier 1986; Grosberg 1988). According to Grafen (1990), the evolution of a true kin recognition system relies on three categories of loci: matching, detecting and using. The matching locus would be essential to detect relatives because of the matching between the phenotypes of parents and offspring. Given this, the ability to detect it would be done by the second kind of loci. Finally, the using locus would control how the information over the match is used.

Lacy and Sherman (1983) developed models to explore possible mechanisms individuals use to classify conspecifics as full-sibs, half-sibs or non-relatives, assuming that kinship is evaluated by comparing to the conspecific phenotype with a learned cue, which can be the cue itself (phenotype matching). One of the methods is based on the comparison of discrete traits, whose expression is determined by alleles in a single locus, while the other method considers traits changing continuously, and assumes a polygenic inheritance. They stressed that if the metric traits are mostly determined by additive genetic effects, then each polygenic trait would provide more information than would a discrete trait with several variants. This suggests, for example, that the amount of each component in a smell might be better as a recognition trait than the presence or absence of each component. However, if environmental and non-additive genetic factors reduce the reliability which reflects a genetic similarity, the value of metric traits to the phenotype matching is also reduced.

Several research papers deal with several animal behaviours and their heritabilities, as in insects (Hadler 1964; Gromko 1987; Brandes 1988; Shuker et al. 2007; among others). For instance, Brandes (1988) estimated the heritability of learning behaviour in honeybees (Apis mellifera capensis); estimates for other animals were made for crustaceans (Stirling & Roff 2000), fishes (Dodson et al. 2013), amphibians (Relyea 2005) and birds (Pulido & Berthold 1998; Dingemanse et al. 2002; Charmantier et al. 2007). The latter showed the first evidence that the cooperative behaviour in natural populations of Sialia mexicana (Western bluebirds) has a heritable component. There are also papers dealing with mammals (Ruefenacht et al. 2002; Gade et al. 2008; Sartori & Mantovani 2013; among others). Some of these papers estimated heritability in a continuous observable scale, while others estimated heritability in an observable binary scale, with the results expressed as a continuous underlying scale, as we have done.

Robertson (1951) discusses the methods of $\chi^2$ and maximum likelihood to analyse variables distributed binomially within groups. The $\chi^2$ method has the advantage of not being restricted to a constant sample size, even though this method becomes more inefficient as the variation on the sample size increases. For small samples, the estimate by maximum likelihood might have more bias than the $\chi^2$ method; however, although more biased, the maximum likelihood might be more
efficient. Moreover, when the variable of interest $p$ is estimated from data, the $\chi^2$ method is less biased than maximum likelihood. Therefore, differences found by maximum likelihood might be due to differences in the number of offspring. According to Roff (1997), for the full-sib design, as for the offspring mean on the mid-parent regression (which we did not use), a family size between six and 10 is desirable, unless it can be assured to keep a family size of four or more individuals. This is what we have done; all the offspring with family sizes smaller than four were discarded. Doing this, we might incur some error in the estimates due to a variation on $n$, though this would be better than discarding more offspring, which would involve losing information about the families. The method of Bull et al. (1982), with the conversion to the subjacent scale according to Lynch and Walsh (1998), resulted in estimates also a little different for the heritability of $F = 0$, which could be due, again, to a variation in the sizes of the offspring families.

Theory predicts that traits related to fitness should have low heritability (traits related to life history, as fecundity and development rate), while traits less related to fitness might have higher heritability (as morphologic traits) (e.g. Mousseau & Roff 1987; Falconer 1989). Furthermore, the authors showed that the heritabilities of behavioural and physiological traits are more similar to the traits related to life history than those of morphologic traits. An interpretation for these finding might be that physiological and behavioural traits are subject to similar restrictions to those that influence fitness. Additionally, the heritability of morphologic traits tends to be higher in favourable environments; heritability can also differ among sexes and life stages (Visscher et al. 2008). Glazier (2002) proposed an evolutionary explanation for this: the resource allocation priority hypothesis. Traits with low priority are more sensitive to environmental effects, reducing the genetic effects and consequently having low heritabilities. On the other hand, morphological or physiological traits are of high priority, resulting in higher values of heritability. Our findings on heritability showed values closer to those traits related to life history and fitness. The main variable in this study was non-cannibalism, and given that non-cannibals allow their sibs to survive, they increase their inclusive fitness (Hamilton 1964). So we would expect to find low values for the heritability of kin recognition. Although large sample sizes are required to give small sampling errors in estimates of heritability, and additionally comparisons of different heritability estimates often have low statistical power (Keller et al. 2001), at least some quantification of heritability is desirable, when one is interested in the potential for evolutionary change of a trait, as well as the rate at which it responds to selection (Falconer 1989). This is exactly what we have done, by showing that the non-cannibal phenotype is heritable and so may be under selection scrutiny (and further supported by unpublished work).

The results shown here were obtained from butterflies captured in the field; their offspring was grown and bred in insectaries, or formed a second generation used in the different crosses. As the environment is very similar in the insectaries used, and also in the laboratory where caterpillars were grown, our heritability estimates could be biased. These estimates would be impossible to do in nature, regrettably. Weigensberg and Roff (1996) evaluated whether the estimates of heritability in the laboratory are reliable. They compared several estimates made in the field and in the laboratory, and found a high correlation between them. They suggested that heritabilities calculated in the laboratory are reasonable estimators not only in meaning but also in magnitude to those obtained in nature.

Theory predicts that for a given population, and a given trait, estimates generated using full-sib design are usually larger than or equal to those obtained by the method of parent-offspring regression. As Falconer (1989) pointed out, the heritability resulting of the phenotypic similarity between full siblings includes dominance and environmental
variance. Mousseau and Roff (1987) tested whether the heritabilities estimated by parent-offspring regression and full-sib design had different results. They used paired samples for 11 independent studies, with nine species, in outbred natural populations. Although their findings were in general larger than those estimated by the method of parent-offspring regression, there were no statistical significance between these two methods.

Roff (1998b) analysed the effects of inbreeding in morphological and life-history traits in the cricket Gryllus firmus. The heritabilities found in the outbred crosses were greater than those for inbred when a correction was used. The heritability values found in this paper are low and a little greater for outbreds than for inbreds. This can be explained, since inbred are mainly homozygotes and consequently the genetic variance within crosses is less, as compared to outbred. As inbred crosses may have a greater variance between them, that effect could be reduced. Falconer (1985) raises objections to the use of non-random crosses in estimates of heritability in the restricted sense; according to him there is “no useful meaning when the crossings are not random” (p. 337, cited in Moorad & Wade 2005). The values found for the maximum likelihood are still low, although numerically inbreds showed greater values. We are not able to explain this, but perhaps this difference may be irrelevant. Bull et al.’s (1982) method follows the results for ANOVA and $\chi^2$ with values for outbreds greater than the values for inbreds.

Although we have focused our analysis on the genetic component of kin recognition, which ends in non-cannibalism, the possibility of inheritance of the cannibalistic behaviour cannot be discarded. Starvation is an environmental trigger for cannibalism, but it is not essential for starting such behaviour (Fox 1975). Richter (1986), working with Noctuidae larvae, suggested that the cannibalism is started by starvation, but nevertheless is influenced by many genes that could act in different targets, as in the development of body fat and enzymatic activity, and that this behaviour could be under the control of a single gene, with other genes playing a secondary role. The situation for Heliconius erato phyllis is as yet unknown, however.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.
SUPPLEMENTARY MATERIAL

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