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The heritability of lateral banding in *Dolomedes plantarius*

Running title: Heritability of banding in *D. plantarius*

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Abstract

Pale lateral bands that contrast with somatic colouration are common to many semi-aquatic spider species and may contribute to camouflage. *Dolomedes plantarius* is dimorphic for the presence or absence of a broad, pale lateral band on the abdomen and cephalothorax. Here we investigate the heritability of this banding pattern by assessing the proportion of banded progeny in broods of spiderlings for which the phenotype of one or both parents was known. Our results indicate a single-gene system of inheritance with the banded allele dominant to the unbanded. This finding offers a simple way to investigate various aspects of the biology of this rare spider, which is classified as vulnerable to extinction. We consider the implications for further understanding the mating system of *D. plantarius* and for studying the function and maintenance of banding in wild populations.

Introduction

Most invertebrates are, of necessity, masters of subterfuge, whether for escape from predators or access to prey. Although some achieve this through the pattern, colour and behavioural mechanisms constituting different forms of mimicry (Jamie 2017), most use camouflage to make them difficult to distinguish from their background. The latter are generally divided into those that match their background using cryptic patterns and colours that sample it randomly, and others that have disruptive coloration, with highly contrasting patterns breaking up their outline (Endler 1981, Cuthill *et al*. 2005). Although crypsis and disruption are usually presented as alternative mechanisms of camouflage, both may potentially be deployed in the same species (Schaeffer & Stobbe 2006). Spiders present many examples of both strategies, although crypsis is the more common, with species such as the sand-matching *Rhysodromus fallax* (Sundevall, 1833) and leaf-matching *Nigma walckenaeri* (Roewer, 1951) presenting classic examples. Some species have evolved the ability to match a variety of backgrounds by reversible colour changes, such as those in *Misumena vatia* (Clerck, 1757) (Gabritschevsky 1927; Théry & Casas 2009) but in most species colour and pattern are directly genetically determined (Oxford & Gillespie 1998).

The family Pisauridae appears to present examples of both camouflage strategies. Within the genus *Dolomedes* Latreille, 1804, for example, some species are highly cryptic, matching the tree bark or mud surfaces typical of their habitat, while the many semi-aquatic species tend to have a more uniform, dark ground colour often with highly contrasting light lateral bands (Fig. 1A) on the cephalothorax and abdomen (Carico 1973; Dondale & Redner 1990). These bands also feature in the closely allied semi-aquatic genera *Nilus* O. Pickard-Cambridge, 1876 and *Perenethis* L. Koch, 1878. The Lycosid genus *Pirata* Sundevall, 1833, exhibits similar variation, with pale lateral bands a common feature of the semi-aquatic species, such as *Pirata piscatorius* (Clerck, 1757).

Many pisaurid species are polymorphic with respect to their colour and pattern, including lateral banding. These polymorphisms have led to considerable taxonomic confusion, for example with *Pisaura lama* Bösenberg & Strand, 1906, *D. sulfureus* L. Koch, 1878 (Yaginuma 1986), and *D. horishanus* Kishida, 1936 (Tanikawa 2003), formerly being split on the basis of their contrasting morphs. Several *Dolomedes* species are polymorphic for the presence of lateral banding, with certain individuals lacking it altogether. In those investigated to date, these polymorphisms are genetically determined and so offer a potential route for investigating the function of the bands and their maintenance in the population. *Dolomedes raptor* Bösenberg & Strand, 1906, is sexually dimorphic, with broad white lateral stripes present only in the males (Lin *et al*. 2015). *Dolomedes sulfureus*, and *Dolomedes horishanus* both exhibit pattern polymorphisms which are genetically

determined but not sex limited, and include morphs with and without lateral bands (Yaginuma 1986 and Tanikawa 2003 respectively). In *D. sulfureus*, the polymorphism has been bred out through successive generations and comprises three distinct forms, one of which is unbanded (Nakahira 1979). A more complex, sex-limited colour and pattern variation, including lateral banding occurs in *Megadolomedes australianus* L. Koch, 1865 (Davies & Raven 1980).

Although lateral bands may provide disruptive camouflage, there has been little work on their function. *Dolomedes* are ambush hunters. The semi-aquatic species typically use emergent perches where they can sit with their front tarsi in contact with the meniscus to detect approaching prey and predators via their sophisticated mechanosensory system (Bleckmann & Barth 1984). In this situation the lateral band looks very similar to the curved reflection of sunlight on the meniscus around emerging plant stems, as well as to dead leaves of aquatic plants (Fig. 2). In the nocturnally active *D. raptor* there is evidence that the contrasting bands attract flying insects (Lin *et al*. 2015), but the position of the lateral bands makes it unlikely that this is an important function in *Dolomedes* species that prey predominantly on aquatic invertebrates. Although *Dolomedes* species have very poor eyesight, and can hunt effectively when blinded (Williams 1979), Lin *et al*. (2015) further show that the male's white bands have a role in courtship recognition in this sexually dimorphic species.

In the semi-aquatic *Dolomedes plantarius* Clerck, 1757, one of only two *Dolomede*s species in western Europe, both sexes are dimorphic for the presence of conspicuous pale lateral bands. An unbanded morph (Fig. 1B) is widely reported (e.g. from: the Netherlands, Helsdingen 1993; Germany, Harms *et al*. 2009 and Unruh 2008; France, Bonnet 1930 and Lecigne 2006; Sweden, Sollfors 2019; Spain, Bellvert *et al*. 2013; Italy, M. Paschetta pers. comm.), including in the three remnant British populations. At one of these (Redgrave and Lopham Fen, East Anglia) it occurs at frequencies of up to 28% (Smith, unpublished data) and has been recorded for over 60 years. Indeed, the species was first definitively described from Britain at this site in 1956 as a fortuitous result of the polymorphism. Dr Eric Duffey encountered an unbanded female, alerting him to the possibility that this was *D. plantarius* rather than the much commoner *D. fimbriatus* (Duffey 1958), in which entirely unbanded morphs have not been described.

Although clearly dimorphic for the presence of lateral bands, many other aspects of colour and pattern in *D. plantarius* are highly variable. This includes the width and colour of the lateral band (from white through creamy-yellow, infrequently to a pale brown that contrasts poorly with the body colour) and the extent to which it is solid or broken. It also includes the ground colour of the body (from black to pale brown), and presence of white dorsal spots on the abdomen. The lateral bands can differ in colour between moults (e.g. Fig. 3), and between the carapace and abdomen, and

are often more muted in adult females. Much of this variation in colour and pattern is likely to be determined by multiple genes (Oxford & Gillespie 1998). However, the long-term persistence of the banding dimorphism at fairly constant frequencies in wild populations, suggests that it may be under simple genetic control maintained by balancing selection.

Here we use the ratios of banded to unbanded progeny in broods of both captive and wild mated *D. plantarius* to determine whether their frequencies conform to expectations of a genetically determined trait. We discuss the potential of our results for furthering understanding of both the maintenance of the dimorphism in *D. plantarius* populations, and the function of the lateral band. The implications of our results for sexual strategy in *D. plantarius*, and the relevance of this to the conservation of this species, which is currently classed as Vulnerable to extinction both in Britain and internationally (World Conservation Monitoring Centre 1996; Harvey *et al.* 2017), are considered.

Methods

Provenance of the spiders

All of the spiders assessed originated from one or other of the two populations known from England: at Redgrave and Lopham Fen in East Anglia (52°20'N 1°70'E), and on the Pevensey Levels in East Sussex (50°51'N 0°20'E).

In Britain *Dolomedes plantarius* is fully protected under Schedule 5 of the Wildlife and the Countryside Act 1981 (as amended). Our assessments were made under licenses issued by Natural England, mostly using animals that were being used to evaluate and deliver a conservation translocation programme to reduce the extinction risk (Smith 2018). This inevitably limited the pairings that were possible, and particularly restricted the availability of unbanded individuals, which occur at relatively low frequency.

The broods assessed

Data on 47 broods were collected over five years, between 2009 and 2013. In 2009 most of the data came from animals used to assess captive rearing methodologies at the John Innes Centre, Norwich. These were third generation descendants of a single banded female collected from the Pevensey Levels in 2005. No unbanded males were available so a single individual was collected from Redgrave and Lopham Fen to increase the number of possible band-morph combinations. Seven crosses were made under standardised conditions in a laboratory arena (Table 1). Each female was

presented sequentially with different males, which were removed if there was a clear behavioural rejection, until a successful copulation was observed. No further mating opportunities were presented to ensure single paternity and to reduce the chance of losing males to the rare but present risk of post-copulatory cannibalism.

In subsequent years (2010 and 2012) a further 16 laboratory-mated broods were evaluated for banding ratios. These resulted from reciprocal crosses, made in preparation for a translocation programme, between spiders caught as sub-adults from the two English populations. As in 2009, the numbers of crosses and the band morph combinations were determined by the availability of mature spiders and their willingness to mate (Table 1).

A second set of 24 broods, in which only the maternal parent was known were also evaluated for banding ratios. Twenty-one of these came from females caught at Redgrave and Lopham Fen when either gravid or already carrying an egg sac, and so both the paternal morph and the number of matings was unknown (Table 2). The spiderlings from these broods were captive-reared for approximately three months before being used to stock new populations established in East Anglia as part of the translocation programme (Smith 2018). The remaining three broods (Table 2: brood numbers 24-26) where only the maternal parent was definitely known came from spiders caught for the reciprocal crosses made in 2010 (above). These were caught as newly-emerged adults, rather than sub-adults, and so we could not be certain that they were previously unmated.

All of the brood parents were photographed to provide a detailed record of their banding morphology.

Assessing banding ratios in spiderling broods

The numbers of banded and unbanded spiderlings were assessed in randomly selected sub-samples of each brood. A maximum of 80 spiderlings per brood was assessed in 2009. In subsequent years subsamples of 100 were assessed from larger broods (mean brood size is >500) while all spiderlings were assessed from smaller broods (Tables 1 & 2). Spiderlings were reared in captivity until the banding morph was distinguishable. When they first emerge from the egg sac, spiderlings are guarded by their mother in a nursery web for approximately five days before dispersing. At this stage they all look very similar, with a dorsal band, and often an impression of lateral bands created by the translucency of the integument and by a scattering of white hairs (Fig. 4A). Dispersal stage

spiderlings were reared individually in ventilated 15mm test tubes lined with damp cotton wool, and fed with small Diptera every two to three days; this rearing method prevented cannibalism and usually delivered survival rates between 80 and 95% over the first three months of life. It was first possible to assess whether or not they had lateral bands by the third post-emergence instar, when they were around three weeks old (Fig. 4B & C).

In 2009, the first year in which we made assessments, all observations were made by two, independent observers (AB and HS) and re-checked after at least one further moult. Growth rates varied considerably between spiderlings within each brood and microscopical examination was used to assess banding in the smallest individuals. Assessments were consistent between observers. Whether or not the spiders were banded was entirely consistent between instars, although band colour was less so; band morph also remained constant in a sample of spiders from each of the 2010 broods that was reared through to maturity and checked after each moult. In 2010, 2011 and 2013 all assessments were made by the same observer (HS). In 2012 the broods were shared between different institutions for captive rearing. The original observer (HS) assessed a small sub-sample of each brood but remaining subsamples were assessed by other, inevitably less experienced, observers. A very small number of assessment errors arose from the difficulty of evaluating the smallest individuals.

Analyses

Ninety five percent binomial confidence limits for the proportion banded were calculated for each brood. Based on our initial finding in 2009 that the banding ratios in the broods appeared to conform with simple Mendelian ratios consistent with the parental phenotypes and with banded dominant to unbanded, we tested against the expectation that our population contained genotypes BB (homozygous banded), BU (heterozygous banded) and UU (homozygous unbanded). Thus we expect broods to be binomial samples from populations determined by parental genotypes as follows:

Both parents banded	BB x BB	100% banded
	BB x BU	100% banded
	BU x BU	75% banded
One parent banded	BB x UU	100% banded
	BU x UU	50% banded

Both parents unbanded   UU x UU   0% banded

Broods were classified as having an expectation of 0%, 50%, 75% or 100% banded based on the nearest of these values to the observed banding proportion consistent with parent phenotypes. We fitted binomial Generalized Linear Models (Nelder & Wedderburn 1972) to test for differences in banding frequencies between groups and to obtain mean banding frequencies with confidence intervals for each group. We present means and confidence intervals back transformed to the linear scale. Analyses are presented separately for broods where both parent phenotypes were known and for broods where only the maternal phenotype was known.

For broods that had values around 50% or 75% we also tested against the relevant expectation using chi-square tests (Zar 1999). We first tested for differences between broods within one category using a heterogeneity chi-square test. Assuming the result was non-significant we then combined the data across broods and tested against the expected proportion banded. In cases where we expect 100% or 0% banding there should be no variation in the results so statistical testing is unnecessary. All analyses were carried out in R version 3.6.0 (R Development Core Team 2018).

Results

In 2009, the results of the nine crosses made in a laboratory arena between and within the two banding morphs of *D. plantarius* very clearly conformed to Mendelian ratios, with the proportion of banded individuals at either zero or 1.0, or close to 0.5 or 0.75 (Table 1). The pairing with two unbanded parents (brood 5) produced only unbanded progeny, pairs with two banded parents produced either all banded or *ca* 75% banded progeny: results consistent with a simple single-gene system of inheritance in which the banded allele is dominant. We therefore tested these broods, and those from subsequent years, for departure from the expectations of this system.

In subsequent years, among broods where both parental phenotypes were known, around 0.2% of spiderlings appear to have been misclassified (5 of 2216 spiderlings recorded). Eleven broods had banding ratios of exactly 1.0 or zero, while a single brood (Table 1: brood 21) was recorded as having 90 banded and two unbanded individuals. Among broods where only the maternal phenotype was known, 10 had banding proportions of either 1.0 or zero, while two broods had ratios of one unbanded to 168 banded and two unbanded to 142 banded respectively (Table 2: broods 38 and 40). Given the difficulties of classifying some small spiderlings we consider that the five records of

unbanded spiderlings within these broods are the result of misclassification. This gives a proportion misclassified as 0.0021 (2/959) for broods with both parents known, and 0.0024 (3/1257) for broods with one parent known. In reporting and interpreting the subsequent analyses we assume a very small error rate in the classification of spiderlings and do not reject our hypothesis of simple Mendelian inheritance based on these five records.

All of the 23 broods for which both parental phenotypes were known had banding ratios consistent with a simple Mendelian model of inheritance. Ten had banding ratios at or close to 1.0, three had banding ratios close to 0.75, eight had banding ratios close to 0.5 and two broods had a banding ratio of 0.0 (Fig. 5). A generalized linear model gave estimated proportions banded, and confidence intervals, that were consistent with this classification (Table 3), while Chi-squared tests indicated no significant deviations from our expected ratios of 0.75 (test for heterogeneity between broods $\chi^2=1.920$, df=2, p=0.383; test against proportion banded=0.75 $\chi^2=0.751$, df=1, p=0.386) and 0.5 (test for heterogeneity between broods $\chi^2=5.401$, df=7, p=0.611; test against proportion banded=0.50 $\chi^2=0.583$, df=1, p=0.445). Of the ten broods with banding proportions at or close to 1.0, nine had two banded parents and one had one banded and one unbanded parent. The parents of all three broods close to 0.75 were both banded while those of the eight broods close to 0.5 had one banded and one unbanded parent. Both parents of the two broods with a banding ratio of 0.0 were unbanded (Table 1).

One of the broods with a banding ratio of 0.0 (Table 1: brood 17) was initially assessed as having unbanded maternal and banded paternal phenotypes. However, close examination of the father's pattern shows only a very narrow white line fringing the lower margin of the carapace (Fig. 6B). All other males assessed as banded had a broader white line slightly higher on the flank of the cephalothorax (Fig. 6A). It therefore appears to be the inheritance only of the latter band that is controlled by the simple Mendelian system identified here.

Most of the 24 broods from wild-caught females which mated prior to capture, for which only the maternal phenotype was known, showed a similar pattern to those for which both parental phenotypes were known (Table 2, Fig. 7), although there are indications of some multiple paternity. Eleven broods had banded to unbanded morph ratios at or close to 1.0 (see above on misclassifications), seven broods had banding ratios close to 0.75 (but see further details below), four broods had ratios close to 0.5 and one brood had a ratio of 0.0. One of the 2013 broods (Table 2: brood 45), with a banded maternal phenotype, had a ratio of banded to unbanded spiderlings of 0.880 (95% confidence interval 0.800-0.936) which differs significantly from the Mendelian

expectations and is not consistent with a single pairing, suggesting that this individual was multiply mated.

Again, a generalized linear model provides estimates consistent with Mendelian outcomes (Table 3). Of the 11 broods with banding proportions at or close to 1.0, ten were produced by banded females and one by an unbanded female. Seven broods with banding ratios close to 0.75 (Table 2: Broods 30, 31, 34, 37, 41, 44 and 46) were all produced by banded females. Although there was no significant difference in proportion banded across these seven broods (χ^2=3.156, df=6, p=0.789), the overall banding ratio of 0.71 differed significantly from 0.75 (χ^2=10.275, df=1, p=0.001). The three of these broods with the lowest proportions banded (0.680, 0.681 and 0.692) may have involved multiple paternity. The remaining four broods showed no significant difference in the proportion banded (χ^2=0.764, df=3, p=0.858) and their combined banding ratio did not differ from a predicted value of 0.75 (χ^2=2.2081, df=1, p=0.137).

The four broods with banding ratios close to 0.5 (Table 2: broods 24, 35, 43 and 47) did not differ significantly in the proportion banded (χ^2=2.087, df=3, p=0.555) and their overall banding ratio did not differ from 0.5 (χ^2=1.574, df=1, p=0.210). Finally one brood from an unbanded female had all unbanded offspring.

Overall these results from broods where mating took place in the wild, and only the maternal phenotype is known, are consistent with our analysis for broods where both parental phenotypes were known. However it seems likely that at least four of these 25 broods involved multiple paternity.

Discussion

Our results from 47 broods of spiderlings show that the lateral banding dimorphism in both male and female *Dolomedes plantarius* is controlled by a simple Mendelian system of inheritance in which the banded allele is dominant. This system controls the presence or absence of pale bands on the side of the carapace and abdomen. It does not appear to control the presence of a very narrow white band at the lower edge of the carapace in many males. Further work is needed to determine the frequency of this band and its pattern of inheritance.

The lateral bands were usually first identifiable in the third post-emergence instar. They appeared consistently thereafter although they varied in their colour, intensity/solidity and width between moults, and between individuals. Our results are not consistent with those of Helsdingen (1995),

who reported loss of banding in some captive-reared *D. plantarius* at ecdysis, with some but not other individuals regaining it after a few days. Duffey (1995) did not observe any unbanded morphs among small juveniles he saw at Redgrave and Lopham Fen and speculated that banding is lost in some individuals as they mature. However, later more intensive field studies at the same site found unbanded morphs at similar frequencies in small juveniles and in adults (HS unpublished data).

The simple Mendelian inheritance of the lateral band in *D. plantarius* offers potential for better understanding of this species' mating system. Although each of our broods where the female mated only once and the paternal phenotype was known conformed to the Mendelian model, we found four of the broods from wild-caught adult females, that were potentially multiply mated, differed significantly in their banding proportion from our Mendelian expectation. Vugdelic (2006) found evidence of multiple paternity in a single female *D. plantarius* caught with an egg sac from one of the sites from which we obtained our stock (the Pevensey Levels). The female subsequently produced two more fertile sacs; sperm storage to fertilize later broods is the norm in this species in Britain, where male numbers decline rapidly by early August but fertile egg sacs can be produced as late as October. Using some progeny from each sac, analysis of six microsatellite loci in 30 individuals inferred a minimum of two fathers, with one male genotype having more offspring than the other in the first two but not the third brood. Vugdelic analysed only one other brood, which resulted from a mating of laboratory-reared virgin parents. In this case genotype frequencies were consistent with single paternity.

A combination of further laboratory and field work is needed to establish the frequency of polyandry, and the resulting extent of multiple paternity. The possibility of polyandry in a species of such high conservation concern is of more than academic interest because of its potential for increasing effective population size and maintaining genetic diversity through inbreeding avoidance (Sugg & Chesser 1994; Maklakov & Lubin 2006; Cornell & Tregenza 2007). In common with many spider species, *D. plantarius* males are promiscuous, showing courtship behaviour towards multiple females at once and to unreceptive females, including sub-adults, those already carrying egg sacs, and even to recently dead individuals (HS, unpublished data). It is much more difficult to assess the extent to which females mate multiple times; they are usually hidden under emergent vegetation and courtship can be protracted over several hours. Multiple matings do not guarantee multiple paternity because of the possibilities of post-copulatory sperm competition and cryptic female choice (e.g. Toft & Drengsgaard 1999, Eberhard 2004). Although our laboratory-mated females did not have an opportunity to mate more than once, they exhibited choice, often rejecting several

potential partners before mating successfully. In only one case was the potential for further mating clearly diminished by the male embolus breaking in the epigyne.

Our new findings concerning the inheritance of the banding dimorphism in *D. plantarius* offer possibilities for advancing our understanding of its maintenance in the population and the adaptive significance of lateral bands in this and other semi-aquatic pisaurids. With frequencies of the recessive, unbanded morph below 30% in all three British populations, and consistently so over a 28 year period at Redgrave & Lopham Fen (unpublished data), the dimorphism appears to be atypical of others described in spiders, where the recessive morph is usually the more frequent in natural populations (Oxford & Gillespie 1998). Both courtship and hunting in *D. plantarius* are diurnal activities although, apart from egg sac and nursery construction, the extent of nocturnal activity is unclear. It hunts on, above and below water, and is itself a potential target for both vertebrate predators and invertebrate parasitoids. These traits suggest many possible elements of spatial and temporal environmental heterogeneity that might differentially favour either the banded morph through disruptive camouflage or the unbanded morph through crypsis. Factors other than camouflage may also be at play. Tso *et al*. (2002) found that a persistent, genetically determined melanic morph in *Nephila maculata* had significantly reduced body surface UV reflectance and foraging success, although there was no direct evidence of causation. They suggested that melanic individuals may have advantages in thermal properties or in reduced visibility to predators and parasitoid hymenopterans, including those with UV perception. The unbanded morphs may also benefit from their low frequency in the population because of frequency dependent foraging by predators (Bond 2007), or dietary wariness (Franks & Oxford 2009).

Finally, our understanding of the inheritance of lateral bands in *D. plantarius* offers the possibility of using significant changes in banding ratios in the wild to identify critical population changes in this threatened species. These could include founder effects during colonisation of new habitat, and genetic drift and bottlenecks in small, isolated and declining populations.

Acknowledgements

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Table 1: Results of crosses for broods where the phenotype of both parents was known (U, unbanded: B, banded)

Year	Brood ref.	Parental phenotypes	Progeny phenotyes		Proportion banded
		♀x♂	B	U	
2009	1	UxB	37	38	0.493
2009	2	UxB	46	33	0.582
2009	3	BxB	46	16	0.742
2009	4	BxB	80	0	1.000
2009	5	UxU	0	79	0.000
2009	6	BxB	36	0	1.000
2009	7	UxB	47	32	0.595
2010	8	BxB	83	0	1.000
2010	9	BxB	91	0	1.000
2010	10	UxB	5	6	0.455
2010	11	BxB	96	0	1.000
2010	12	BxB	95	0	1.000
2010	13	UxB	63	0	1.000
2010	14	BxB	55	27	0.671
2010	15	UxB	47	48	0.495
2010	16	UxB	28	28	0.500
2010	17	UxU	0	94	0.000
2010	18	UxB	44	43	0.506
2010	19	BxB	77	0	1.000
2010	20	BxU	33	41	0.466
2010	21	BxB	90	2[1]	0.978
2010	22	BxB	73	0	1.000
2012	23	BxB	153	51	0.750

1. These individuals are thought to have been misclassified. For further details see text.

Table 2: Results of crosses for broods where only the maternal phenotype was known

Year	Brood ref.	Maternal phenotype	Progeny phenotypes		Proportion banded
			B	U	
2010	24	B	48	41	0.539
2010	25	B	85	0	1.000
2010	26	B	67	0	1.000
2011	27	B	69	0	1.000
2011	28	B	86	0	1.000
2011	29	B	78	0	1.000
2011	30	B	206	84	0.710
2011	31	B	180	80	0.692
2011	32	B	100	0	1.000
2011	33	B	100	0	1.000
2011	34	B	108	37	0.745
2011	35	B	44	55	0.444
2011	36	U	0	100	0.000
2012	37	B	94	44	0.681
2012	38	U	168	1[1]	0.994
2012	39	B	137	0	1.000
2012	40	B	142	2[1]	0.986
2012	41	B	164	61	0.729
2012	42	B	122	0	1.000
2013	43	B	86	99	0.465
2013	44	B	68	32	0.680
2013	45	B	88	12	0.880
2013	46	B	75	26	0.743
2013	47	U	57	68	0.456

1. These individuals are thought to have been misclassified. For further details see text.

Table 3: Comparison against Mendelian expectations of the mean proportions of banded individuals in broods where both parental phenotypes were known and those where only one phenotype was known

Parental type	No. broods	Proportion banded	95% confidence interval
Both phenotypes known			
0.00	2	0.000	Not estimable[1]
0.50	8	0.516	0.475 – 0.558
0.75	3	0.730	0.681 – 0.774
1.00	10	0.990	0.999 – 0.999[2]
One phenotype known			
0.00	1	0.000	Not estimable[1]
0.50	4	0.472	0.428 – 0.516
0.75	4	0.727	0.694 – 0.757
1.00	11	0.997	0.992 – 0.999[2]
Multiple paternity 1[3]	3	0.687	0.645 – 0.726
Multiple paternity 2[3]	1	0.880	0.800 – 0.930

Notes

1. Confidence intervals cannot be estimated where all individuals in a category have the same phenotype.

2. The model is bounded 0-1 so one or two offspring with a recorded phenotype that is inconsistent with our predictions give rise to a confidence interval that does not quite overlap the expected value.

3. For explanation of multiple paternity categories see text.

Fig.1: *Dolomedes plantarius* with (A) and without (B) a lateral band

Fig. 2: Cryptic nature of banded *Dolomedes plantarius* with sunlight on the meniscus
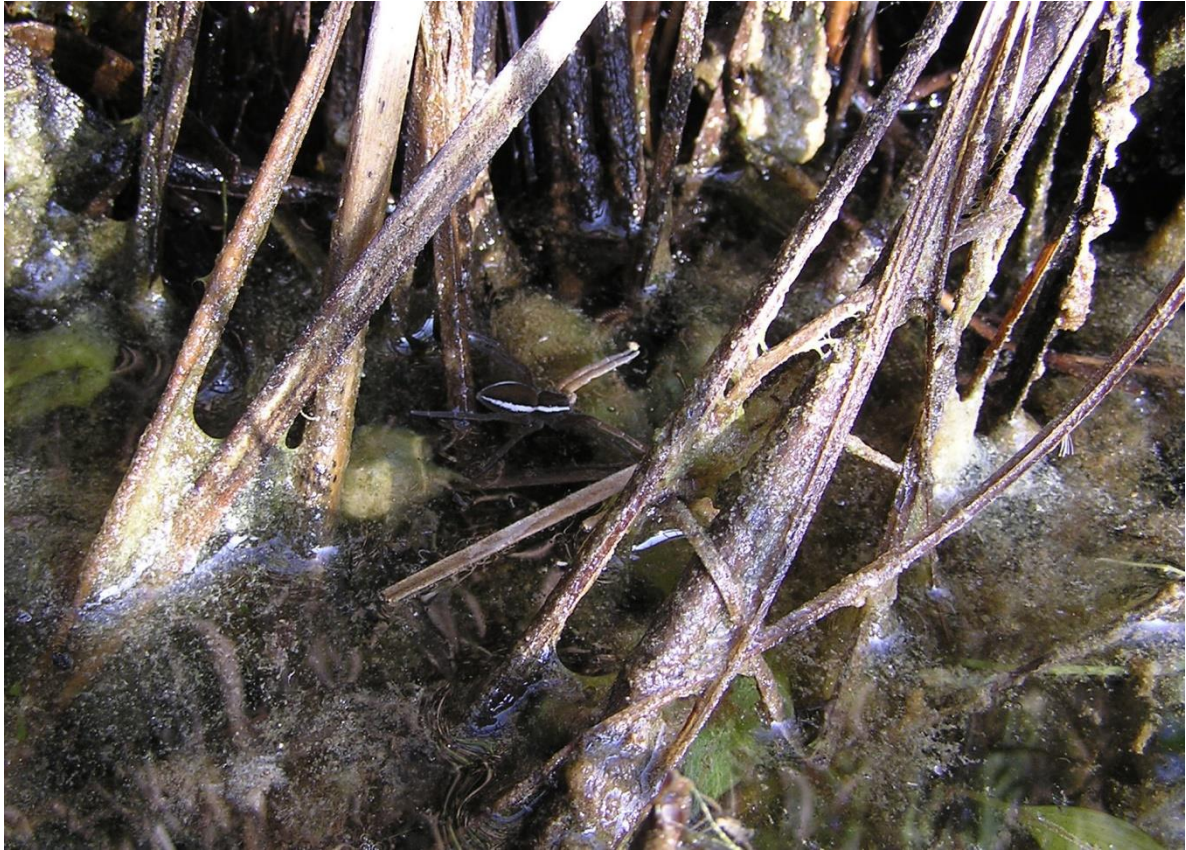
Fig. 3: *Dolomedes plantarius* showing a change from white to cream banding upon moulting

Fig. 4: *Dolomedes plantarius* spiderlings at *ca* 10 days old (A), and at *ca* 20 days old showing the banded (B) and unbanded (C) morph. Scale bars = 1 mm.
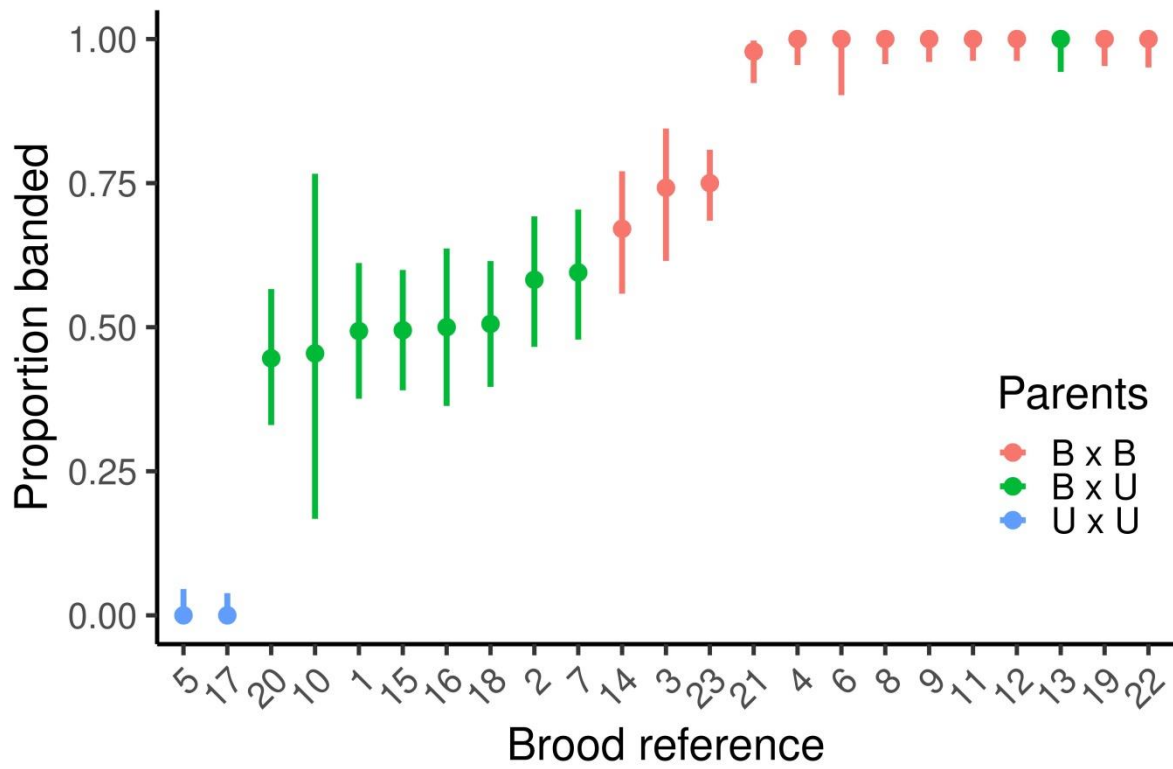
Fig. 5: Proportion banded spiderlings for each brood where both parental phenotypes were known, with broods ordered according to proportion banded. Error bars show 95% binomial confidence limits and colours indicate parent phenotypes (B, banded: U, unbanded).

Fig. 6: Male *Dolomedes plantarius* with lateral band on the carapace and its lower margin (A), and with carapace margin band only (B)
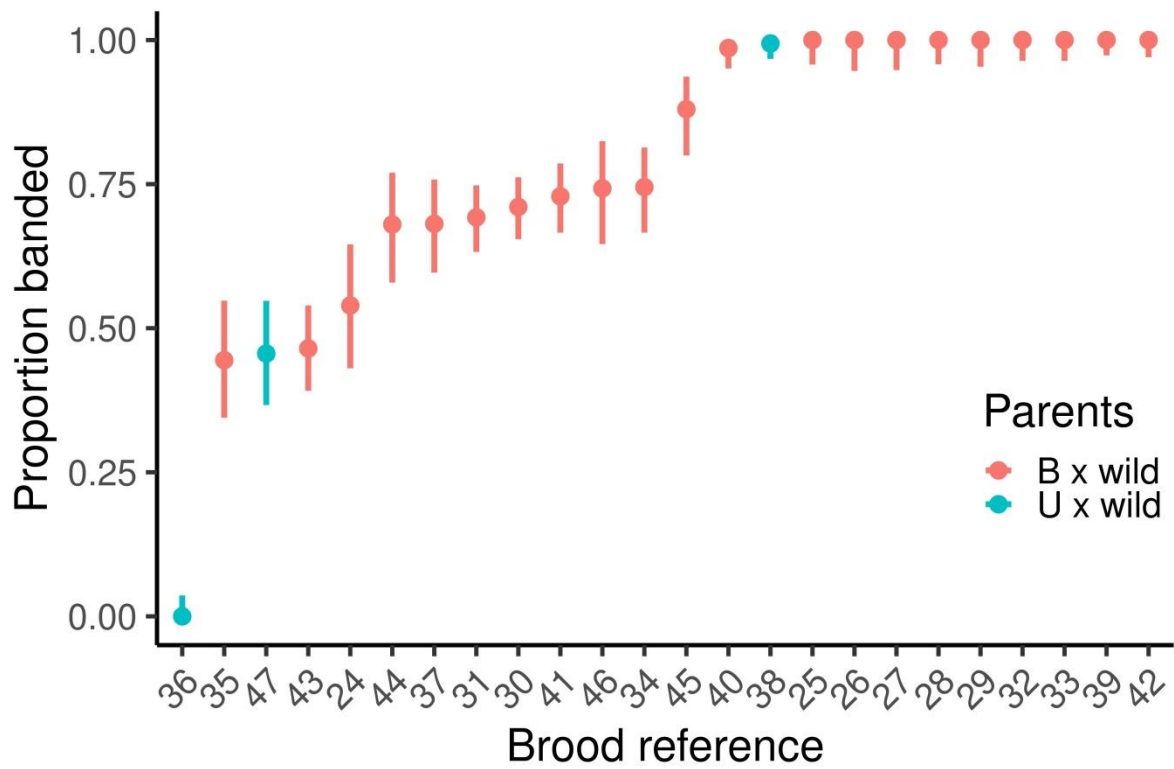
Fig. 7: Proportion banded spiderlings for each brood where only the maternal phenotype was known, with broods ordered according to proportion banded. Error bars show 95% binomial confidence limits and colours indicate maternal phenotypes (B, banded: U, unbanded).