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Overland movement in African clawed frogs (*Xenopus laevis*): a systematic review

John Measey

African clawed frogs (*Xenopus laevis*) are often referred to as 'purely aquatic' but there are many publications which suggest extensive overland movements. Previous reviews which considered the topic have not answered the following questions: a) are there differences in overland movement within native and invasive ranges? b) what range of distances are moved overland? c) when does movement overland occur? and d) whether there is evidence of migratory behaviour? Google Scholar was used with the search term "*Xenopus* overland" and the resulting literature was searched for citations on the topic. This resulted with 56 documents reviewed which showed a paucity of empirical studies, with most data on the subject being anecdotal. Both native and invasive populations of *X. laevis* appear to move overland, as well as being well documented in several other members of the genus. Although most reports are of short distances moved, there are suggestions that extensive movements are made of 2km (direct-distance). Overland movements are not confined to wet seasons or conditions, but the literature suggests that moving overland does not occur in the middle of the day. Migrations for breeding have been suggested but without any corroborating data.

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Summary

African clawed frogs (*Xenopus laevis*) are often referred to as 'purely aquatic' but there are many publications which suggest extensive overland movements. Previous reviews which considered the topic have not answered the following questions: a) are there differences in overland movement within native and invasive ranges? b) what range of distances are moved overland? c) when does movement overland occur? and d) whether there is evidence of migratory behaviour? Google Scholar was used with the search term "*Xenopus* overland" and the resulting literature was searched for citations on the topic. This resulted with 56 documents reviewed which showed a paucity of empirical studies, with most data on the subject being anecdotal. Both native and invasive populations of *X. laevis* appear to move overland, as well as being well documented in several other members of the genus. Although most reports are of short distances moved, there are suggestions that extensive movements are made of 2km (direct-distance). Overland movements are not confined to wet seasons or conditions, but the literature suggests that moving overland does not occur in the middle of the day. Migrations for breeding have been suggested but without any corroborating data.

Key Words: aquatic, clawed frogs, dispersal, migration, Pipidae, terrestrial

Introduction

Dispersal is a key trait in the life-history of any organism influencing the distribution, community structure and abundance of populations (Clobert et al 2009). In anthropogenically disturbed environments, dispersal may be interrupted or facilitated by novel landscape features that may hinder the conservation of threatened species or facilitate the spread of invasive species (Carr & Fahrig 2001; Brown et al 2006). For invasive species, dispersal is one of the main variables which determines the success of establishment as well as the rate of spread (Wilson et al 2009). In fact, some aspect of all ecological, evolutionary and conservation problems are affected by dispersal. Amphibians are model organisms for studies in dispersal as they are generally thought to have low dispersal abilities which brings about strong phylogeographical structuring (e.g. Avise 2000).

Despite their reputation for strong site fidelity, amphibians have been shown to have considerable dispersal abilities. Smith & Green (2005) reviewed evidence for maximum dispersal in amphibians and concluded that although most individual anurans move short distances (<1km), small numbers of individuals could be expected to move much further (>10km). Moreover, these dispersal events may well be informed by a multisensory orientation system that enables individuals to locate water-bodies in which to continue their complex life-histories (Sinsch 2006). For most amphibians, this involves laying eggs into water where larvae grow and metamorphose to emerge onto land. But for frogs in the genus *Xenopus*, adults inhabit the same water as their eggs and larvae prompting many workers to refer to them as ‘completely’ or ‘purely’ aquatic (e.g. Elepfandt et al. 2000).

The African clawed frog, *Xenopus laevis*, is one of four model vertebrate species (Travis 2006), and as such has been distributed to laboratories globally (van Sittert & Measey 2016), as well becoming very popular in the pet trade (Measey in review). This has resulted in invasive populations on four continents (Measey et al. 2012), and the suggestion that climate-change may increase invasion success in Europe (Ihlow et al. in press). Surprisingly, the ecology of *X. laevis* is better studied in invasive populations than in their native range, and this lack of ecological data from the native range is problematic as it stymies interpretation of invasive studies. Data on overland movement is particularly important for this principally aquatic amphibian, as it provides insights into dispersal and thus invasion potential.

There is no doubt that *Xenopus laevis*, like other species in the genus *Xenopus* and the family Pipidae, are secondarily aquatic (Gans & Parsons 1966; Trueb 1996), spending the majority of their active time within water-bodies. They have a number of morphological and anatomical adaptations to an aquatic lifestyle including an extensive lateral line system in adults (Elepfandt 1996), aquatic olfactory receptors (Freitag et al. 1995), type I ilio-sacral articulation for more efficient swimming locomotion (Emerson 1979), aquatic auditory apparatus (Elepfandt et al. 2000) and suction feeding (Carreño & Nishikawa 2010). However, referring to the species as 'purely aquatic' appears to exclude the possibility of individuals leaving a water-body. It is noteworthy therefore that *X. laevis* retains many traits which have terrestrial functionality, including the auditory apparatus (Katbamna et al. 2006; Mason et al. 2009), the olfactory apparatus (Freitag et al. 1995), terrestrial jumping and feeding (Measey 1998b). This indicates that terrestrial activities in *X. laevis* are sufficiently important that these animals retain terrestrial functions in addition to aquatic specialisations.

Existing literature on overland movement in *Xenopus laevis* dates back to anecdotal observations at the beginning of the twentieth century (Hewitt & Power 1913). However, such records do not appear to agree on whether movements are migrations (Hey 1949), or animals moving out of drying ponds *en masse* (Loveridge 1953). On the other hand, there appears to be a paucity of empirical studies with some authors inferring overland movement between isolated ponds. Therefore, I conducted a systematic review of the literature on overland movements in in African clawed frogs (*Xenopus laevis*) in order to answer the following questions: 1) What is the evidence in the literature for overland dispersal in native and invasive ranges? 2) What distances are moved overland? 3) When it occurs, is there evidence that overland movement is seasonal or associated with rain or drying habitats? 4) Is there evidence of overland movement being migratory in nature?

Materials & Methods

Study species

The African clawed frog, *Xenopus laevis*, has undergone significant taxonomic revision following comprehensive molecular study by Furman et al. (2015). The results of this revision mean that what was previously known as *X. l. laevis* by a number of authors (e.g. Kobel et al. 1996; Poynton 1964) is now known as *X. laevis* with all other subspecies being recognised as full species, as well as some newly described species (e.g. Evans et al. 2015). The full range of *X. laevis* is now known to cover much of southern Africa: South Africa, Lesotho, Swaziland, Namibia, parts of Botswana, Zimbabwe, parts of Mozambique and protruding north into Malawi. While *X. laevis* was the focus of this review, publications that mentioned other species were not ignored, especially as many formed an integral part of the citation matrix.

Literature review

A searched for “*Xenopus* overland” (anywhere within a document and for all years) in Google Scholar was conducted on 8th April 2016. Other potential terms (“*Xenopus* terrestrial” and “*Xenopus* dispersal”) were rejected as they produced too many results that were not relevant; Specifically, “terrestrial” was generally used to contrast *Xenopus* with other Anura, while “dispersal” was used as a description for intercellular ion movement. Google Scholar has the advantage over other literature databases that the search term may occur anywhere in the text, instead of just in the title, abstract and keywords. This produced 322 results; while similar searches in Web of Science and Scopus using “*Xenopus* AND overland” returned 6 and 5 results, respectively, all of which had already been found in Google Scholar. Each result was inspected to determine whether or not it contained information on the subject matter. Articles that had no relevance (e.g. author was called Overland or subject was not a pipid) were excluded. The remaining articles (n=40) were scrutinised for mention of *Xenopus* moving overland. Similarly, publications where the given the subjects *Xenopus* and overland were disassociated were removed (n=5). If no evidence was provided but a citation given, the paper was retained and any citation accessed. Articles that had been cited as giving evidence that *Xenopus* move overland were retained whether or not they actually contained any pertinent information. Citations provided 16 more documents. Lastly, expert knowledge was used to access a further five documents that did not appear in Google Scholar or in citation. This gave a total of 56 documents (Appendix 1). This collection was biased for literature that had electronic full texts that could be crawled by Google Scholar. The additional documents added through citations and by expert knowledge only partially alleviated this bias. Each document was read critically for the information that it contained on *Xenopus* moving overland, the species concerned, and with special reference to answering the four study questions. Figure 1 shows a flow diagram for the systematic review following Prisma guidelines.

Network visualisation

A network visualisation was constructed using Gephi (v 0.8.2) with the aim of showing how citations follow different data types. Literature in the final dataset were classified into five data types: anecdotal (n=18), inferred (n=4), empirical (n=3), reviews (n=4) and publications without any relevant data, but that typically cited other papers (n=27). Anecdotal and inferred papers did not always refer to *X. laevis*, despite citations to the contrary. This was in part because of taxonomic adjustments that have only been resolved recently (see above), and partly as citations often referred to overland movements in *Xenopus*, without specifying the species. Lastly, documents were classified according to whether they were reporting on invasive (n=16) or indigenous (n=40) populations. The network visualisation discriminated between citing and cited publications.

Results & Discussion

Literature use

Analysis of the use of literature allows an overview into the importance of this topic. The majority of studies which were found in the literature search did not have data on *Xenopus* overland movement (circles on right in Figure 2). Those with original observations were mostly anecdotal in nature (squares on right), relaying information on instances where *Xenopus* have been observed moving overland. There was a clear trend over time for observations to move from anecdotes to inferences or empirical data (triangles and stars, respectively), with interest in the topic clearly increasing as 60% of publications were published after 1995. The majority of citations referred to publications with observations (curves above a direct connecting line between columns), or to reviews. However, there were several instances where curves below the line suggest that authors were citing publications without any data or observations. It is hoped that this review will help alleviate any past misunderstanding in this respect. The network also showed that many of the citations refer to work that was conducted on invasive populations; to date, no empirical data exists on indigenous *X. laevis* moving overland, although both anecdotes and inferences have been made. There is a clear need for empirical work in general, but in particular to fill the deficit identified here regarding indigenous populations of *X. laevis*. Limitations in the literature search were partially alleviated by adding expert knowledge of the literature, as well as using citations to publications from all articles identified. The existence of uncited literature, however, suggests that this may not have been exhaustive and that other information on overland movement, particularly in other *Xenopus* species may shed further insight into this behaviour. Despite the limitations of this study, there is surely potential for new empirical studies on movements of *Xenopus* species within their native range.

The most cited paper refers to one of only three empirical observations with capture-mark-recapture data of an invasive population of *X. laevis* in South Wales (Measey & Tinsley 1998; Figure 2). The other empirical observations involved radio-telemetry of another invasive population in France (Eggert & Fouquet 2005), and a thesis which expanded data reported on the Welsh study (Measey 1997). Anecdotal observations, those that report chance findings of *Xenopus* moving overland, were the most numerous of publications that reported overland movements. Often these reported observations by third parties (e.g. Crayon 2005; Loveridge 1953) and not those of the authors. This can be taken as indicative of the unusual nature of these observations, also commented on by many authors (Fouquet & Measey 2006; Loveridge 1953). Although anecdotal observations were cited more often, probably as a result of their older publishing date, an interesting and extensive account (Wager 1986) was not cited at all, despite original observations contradicting others (see below).

Several anecdotes refer to spectacular mass overland movements of *Xenopus*, observed both in native and invasive populations (reported by Channing 2001; Crayon 2005; Hewitt & Power 1913; Lobos & Jaksic 2005), and other congeners (Loveridge 1953; Thurston 1967; Weisenberger 2011). These examples all have dam drying in common, where animals appear motivated to move by reduction in water level, but notably do not wait until there is no water, instead leaving when levels are very low. There is a single account which suggests that such mass movements do not occur only as dams dry: Wager (1986) comments on large numbers of animals moving overland after heavy rains. The best documented account of mass overland movement comes from the observations of Gabriel Lobos who reported on movement in an invasive population of *X. laevis* in Chile. He noted that water levels had dropped to 5-15 cm (from several metres deep when the dam was full: Lobos & Jaksic 2005). The animals that moved were in good condition, with no apparent sex bias (although no juveniles were seen moving) and estimated to be in their 1000s. A previous estimate of population for the same dam suggested that numbers two years earlier may have been as high as 20 000 (Lobos & Measey 2002). Mass movements when water-bodies dry are also reported in South Africa, resulting in large amounts of associated road-kill (N. Passmore pers. comm.). One noteworthy observation is that when moving *en masse*, the animals form an unbroken chain (Lobos & Jaksic 2005; Weisenberger 2011). This might reflect the lead animals being stimulated by olfaction (Savage 1961), while those following cannot see their leaders (see Elepfandt 1996), and may not obtain olfactory cues, therefore trying to remain in physical contact with them. Perhaps unsurprisingly, anecdotes of smaller numbers of *Xenopus* moving have also been recorded when dams are drying (e.g. Loveridge 1976).

Records of mass movements suggest that entire populations move, but no reports have specifically tested this idea. In the cases where impoundments have dried, it may be safe to assume that all individuals were forced to make overland movements (especially when burrowing into the substrate is not an option). The only other study that estimated the number of animals moving overland suggests a surprisingly high proportion of the population. Measey & Tinsley (1998) report movements between capture sites (which necessitated overland movements) for 21% of individuals captured more than once at one locality in and around the Afon Alun, South Wales. At their other locality (Dunraven) this was as high as 36% of animals: although here is not clear whether animals had to move overland due to the existence of subterranean aquifers. Some authors mention movements between flowing and still water-bodies (McCoid & Fritts 1980; Measey & Tinsley 1998). Measey (1997) gives a full account of recaptures from invasive Welsh populations, stating that trapping in ponds very close to a river were most common (69% of all captures) when the river was not flowing (see also Measey & Tinsley 1998; Tinsley et al. 2015). This appears to suggest that these individuals were using permanent ponds mostly when the river dried. Interestingly, subsequent studies in the same area suggest that these movements became less substantial over time as the population waned (Tinsley et al. 2015). This may indicate that movements are driven, at least in part, by the existence of populations with high densities (see also McCoid & Fritts 1980). Measey (1997) further notes that movements from river to ponds "...would have to be overland, and in the cases of FP and TFP [abbreviations of pond names], obstacles including vertical walls (up to 0.5 m) and dense hedgerows would have had to be traversed. Some of the animals caught were noted to have heavy scarring of dorsum and ventrum, consistent with movement over such terrain." This suggests that *X. laevis* are able to overcome modest obstacles in their path, in order to gain access to water-bodies. This concurs with my observations in South Africa where walls and thick vegetation are regularly traversed (also see Schramm 1987). Similar observations have been made in other invasive populations where it is inferred that individuals are able to move steep walls and slippery slopes (R. Rebelo pers. comm.). To build barriers to prevent dispersal in invasive populations, it would be of interest to determine whether these inferences are accurate.

Observations also suggest that *X. laevis* (and *X. gilli*) move into ponds at the onset of rains, not only from areas that might have dried up, but also as normal/regular movement between ponds (e.g. Hey 1949; Picker 1985). Clearly, if animals are aestivating out of water, such movements do not need a great deal of explanation, but Hey (1949) and Picker (1985 – although it is not clear whether he refers to *X. laevis*, *X. gilli* or both) appear to describe the movement of animals from one pool to another. Hey (1949) specifically interprets these movements as a migration to breed in temporary waters, and this is repeated in correspondence reported by Mahrdt & Knefler (1973). This record is of interest as Hey extends his observation to include “defined migration routes” for mass movements that occur at night in damp or cold weather. In addition, Hey notes that these routes result in mass mortalities when interrupted (the example given is the construction of a new barn; Mahrdt & Knefler 1973), a similar observation having been made by Loveridge (1953).

Does <u>X. laevis</u> migrate?

Migration from permanent to temporary water-bodies for spawning is certainly logical, given the impressive potential for cannibalism of this species (e.g. Measey 1998a; Measey et al. 2015; Schoonbee et al. 1992), and as temporary waters are likely to have reduced densities of occupants. Similarly, temporary waters are likely to be high in nutrients, sometimes experiencing algal blooms and having reduced predator pressure, making them ideal habitats for developing larvae. Such observations and inferences are available from other species (Rödel 2000; Thurston 1967), but for *X. laevis*, Du Plessis (1966) noted that ponds that were fertilised attracted frogs to move into them before any algae had time to grow. In accordance with many observations, the stimulus to move into temporary waters comes with initial rains that fill them, and this is often combined with immediate egg laying (e.g. Balinsky 1969). A movement into a temporary water-body suggests a reciprocal movement upon drying conditions (see above), except that in many anecdotes it is not clear whether individuals have moved from other (presumably permanent) water-bodies, or simply appeared from the substrate.

Hewitt & Power (1913) recount an anecdote indicating that *X. laevis* were aestivating in the mud of a pond, and that when this mud was moved to a new location the frogs continued to aestivate, only re-emerging from this new location following rains. Such particular observations have also been made elsewhere (A. Channing pers. comm.). This suggests that animals do burrow into the mud of some temporary waterbodies, but this does not seem to be consistent, as Hewitt & Power (1913) also note. It is worth noting that Crayon (2005) suggested that Tinsley & McCoid (1996) reported migration of “0.2km in late spring to a spawning site”, but the idea that this was a migration to a spawning site was an embellishment. Fuller accounts of the same movement (Measey 1997; Measey & Tinsley 1998), simply refer to a movement from a permanent pond to a temporary one within 48 hours. Other data suggesting migration in the Welsh studies implies that animals moved from the river into ponds (see above), although this could be interpreted as movement due to drying of habitat. Of all citations given by Crayon (2005) suggesting breeding migrations, only Hey (1949) and Hey's comments in Mahrdt & Knefler (1973) actually state this. Although there is no reason to dismiss Hey's statements, since he clearly was very familiar with the biology of this species after raising animals at Jonkershoek for export (see van Sittert & Measey 2016), he offered no evidence of migration, be it anecdotal or empirical. Thus the literature provides a clear hypothesis that *X. laevis* may migrate to spawn, as many other anurans are known to (e.g. Lizana et al. 1994), but it seems likely that this behaviour would be context dependent; in areas with temporary waters forming within migrating distance, but where all water-bodies are temporary there would appear to be no advantage to migratory behaviour. In the majority of its indigenous and invasive ranges, water-bodies inhabited by *X. laevis* are anthropogenically created impoundments. Testing a hypothesis on migration in *X. laevis* would require a set of relevant natural water-bodies.

Is overland movement seasonal or weather dependant?

Many authors note that overland movements occur during or shortly after rain (e.g. Du Plessis 1966; Fouquet & Measey 2006; Hewitt & Power 1913; Loveridge 1976; McCoid & Fritts 1980; Wager 1986). However, movement does not appear to be confined to wet periods, or during rain-showers, for mass migrations. In addition, I have both observed *X. laevis* moving overland in the middle of austral summer without any apparent motivation from rainfall or drying habitats (19h00, 28 January 2016, at Jonkershoek). Other authors have suggested that overland movements take place at night (Crayon 2005; Yager 1996), or during the evening (Hewitt & Power 1913; Lobos & Jaksic 2005). The only paper that states this is not so is that of Loveridge (1976) who recorded all overland movements of *X. laevis* early in the morning. That *X. laevis* would not move overland during the middle of the day (or at least not start a movement during the day) does not sound unreasonable for a species which is prone to desiccation away from water. Therefore, the literature suggests that overland movements may peak during wet periods, but are by no means confined to rain or wet seasons.

Distances moved

Distances of inferred movements are in general accordance with those measured by empirical studies (Table 1), but both suffer from a lack of information about movements under extreme rainfall. For example, McCoid & Fritts (1980) refer to sheet flooding facilitating the movement of juvenile *X. laevis* in San Diego County. Thus, it is hard to treat distances reported in the literature comparatively, as they may relate to quite different scenarios, with respective distances estimated in different ways. For example, Measey & Tinsley (1998) report distances up to 2km travelled, but these refer to straight line distances, whereas distances actually travelled could have been much higher. However, this total distance could have included use of a river, making the total distance moved overland not 2km but around 200m, if dispersal events occurred when the river was flowing. In fact, most distances reported in the literature do not provide any indication of how they were estimated. Despite these issues, it is clear that *X. laevis* is able to move substantial distances overland, and that these appear to be comparable to distances travelled by other terrestrial amphibians (Smith & Green 2005). Indeed, when considering the distances reported, there is little to suggest that *Xenopus* species are constrained in their overland dispersal abilities.

Movement in other Xenopus species

This review of the literature presents anecdotal and inferred data from overland movement of other species of *Xenopus*, which although not as comprehensive as those on *X. laevis*, and lacking any quantitative element, are here compared (Table 1). There is data that indicates movement during dry periods in *X. borealis*, which suggests that mass movements also occur in other species (Weisenberger 2011). Perhaps unsurprisingly, other anecdotal observations of mass movements for *X. borealis* (Loveridge 1953), as well as *X. muelleri* (Loveridge 1953; Thurston 1967). Movements overland outside of rainy periods also exist for *X. tropicalis* (Rödel 2000 and references therein) and suggest that, like *X. laevis*, other *Xenopus* species move throughout the year irrespective of rains. To date, there is no reason to suspect that *X. laevis* moves any further overland than any of its congeners (see Table 1), despite its larger size. However, there are no suggestions that any congeners move for migration purposes, which is perhaps not surprising, given that there is only a single suggestion of this happening for *X. laevis* (Hey 1949). Thus, none of the movement data existing for other *Xenopus* species appear to contradict the findings here for *X. laevis*, prompting the question of whether any *Xenopus* species might be expected to be substantially different in their overland movement patterns? One species, *X. longipes*, stands out in that, within the genus, it appears to be aquatically adapted to an extreme. Moreover, it is known from a single hydrologically closed locality, Lake Oku, and no specimens have ever been found outside this lake, despite a recent increase in research interest in this species. As residents of a volcanic lake in the Cameroon highlands, it seems unlikely that this species would ever have experienced a drying habitat that might have prompted overland dispersal. Similarly, a lack of food and conditions prompting mass mortality events appear not to have been averted by individuals leaving the lake (Blackburn et al. 2010; Loumont & Kobel 1991).

Conclusion

A review of the literature has shown that overland movements of *Xenopus laevis* have been found in both its native and invasive ranges. Although no empirical data exists for their native range, there is nothing to suggest that overland movements will be found to be less substantial or frequent than in their invasive range. Given the paucity of empirical studies, distances moved appear to conform to those typical for other anurans, with large numbers of animals moving short distances and some individuals moving up to 2km (direct distance). The literature does not appear to agree on whether overland movements are seasonal, although the majority of studies suggest that movements are more frequent when conditions are wet and they tend not to happen during the middle of the day. Lastly, although this has been suggested, there is currently no evidence in the literature to support the notion that overland movements are migrations to and from water-bodies for individuals to spawn.

In addition to providing an overview on overland movements in *X. laevis*, this review also suggests that the situation for *X. laevis* may be similar to other members of the genus *Xenopus*. Although this review only mentions overland movement in six of 29 currently described species (Frost 2016), lack of reports for the other species probably relates to a reduced number of studies.

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Table 1(on next page)

Table showing distances moved by *Xenopus* species recroded in the literature

Distances moved by *Xenopus* species recorded in the literature.

Table 1: Distances moved by *Xenopus* species recorded in the literature.

Reference	Species	Number of individuals	Distance reported (km)	Population
Loveridge (1953)	*X. borealis*	Unspecified	0.45	indigenous
	X. muelleri	>14	0.9	indigenous
Inger (1968)	*X. muelleri*	1	0.02	indigenous
McCoid & Fritts (1980)	*X. laevis*	Unspecified	0.8	invasive
Picker (1985)	*X. gilli*	11	0.9	indigenous
	X. laevis	Unspecified	1.5	
Wager (1986)	*X. laevis*	Unspecified	1.0	indigenous
Measey & Tinsley (1998) (Measey 1997*)	*X. laevis*	55 (21%)	0.2 (within 48 hrs) 0.75, 1.5 & 2.0 (direct distance)	invasive
Lobos & Garín (2002)	*X. laevis*	1	0.04	invasive
Lobos & Jaksic (2005)	*X. laevis*	Unspecified	0.1	invasive
Eggert & Fouquet (2005)	*X. laevis*	1	0.08	invasive
Faraone et al. (2008)	*X. laevis*	Unspecified	0.48	invasive

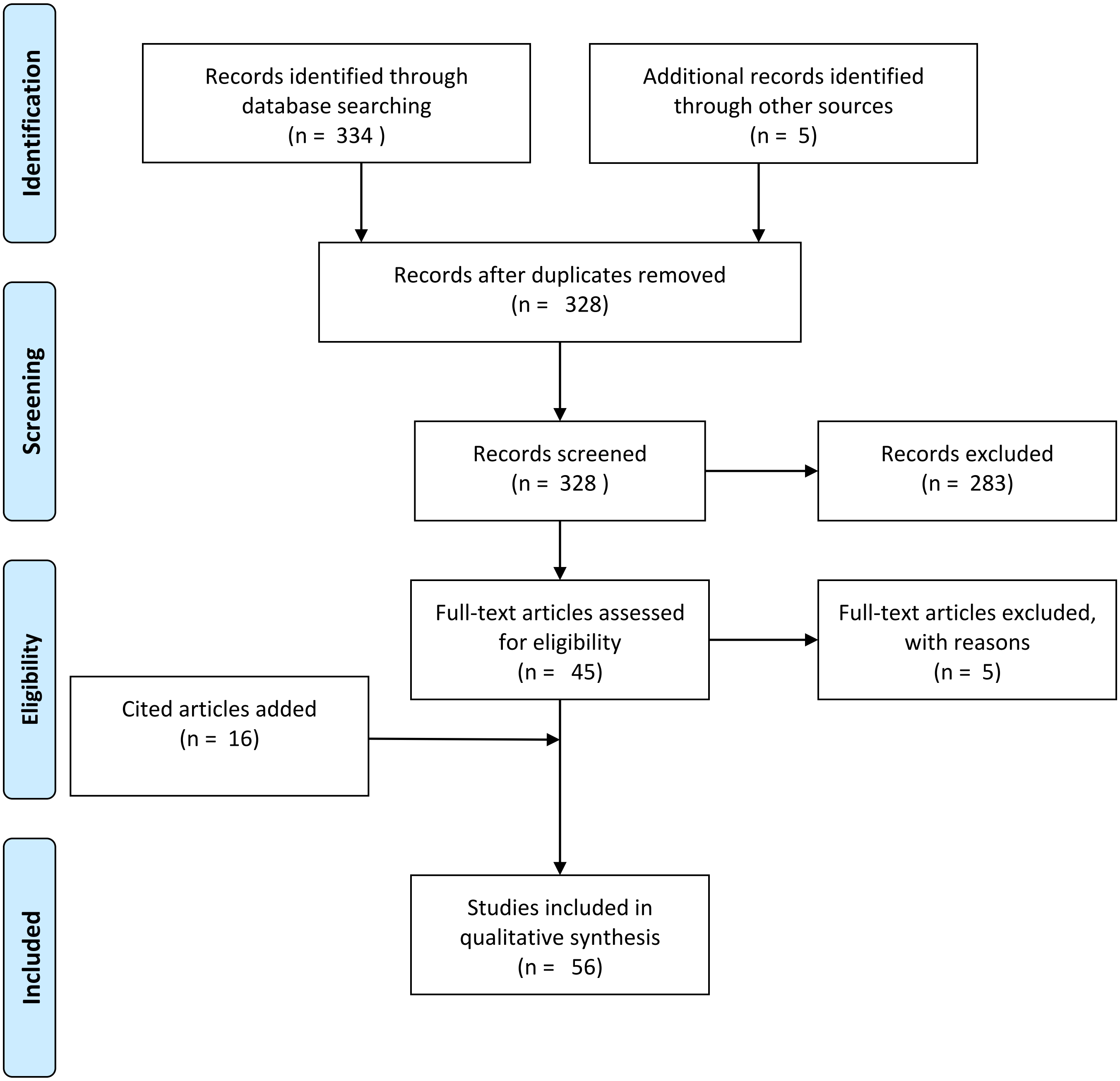
*Literature which report the same data

Figure 1(on next page)

Prisma flow-diagram for literature included in this study.

Flow-diagram for literature on *Xenopus* overland movement included in this study.

PRISMA 2009 Flow Diagram



From: Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group (2009). *P*referred *R*eporting *I*tems for *S*ystematic Reviews and *M*eta-*A*nalyses: The PRISMA Statement. PLoS Med 6(7): e1000097. doi:10.1371/journal.pmed1000097

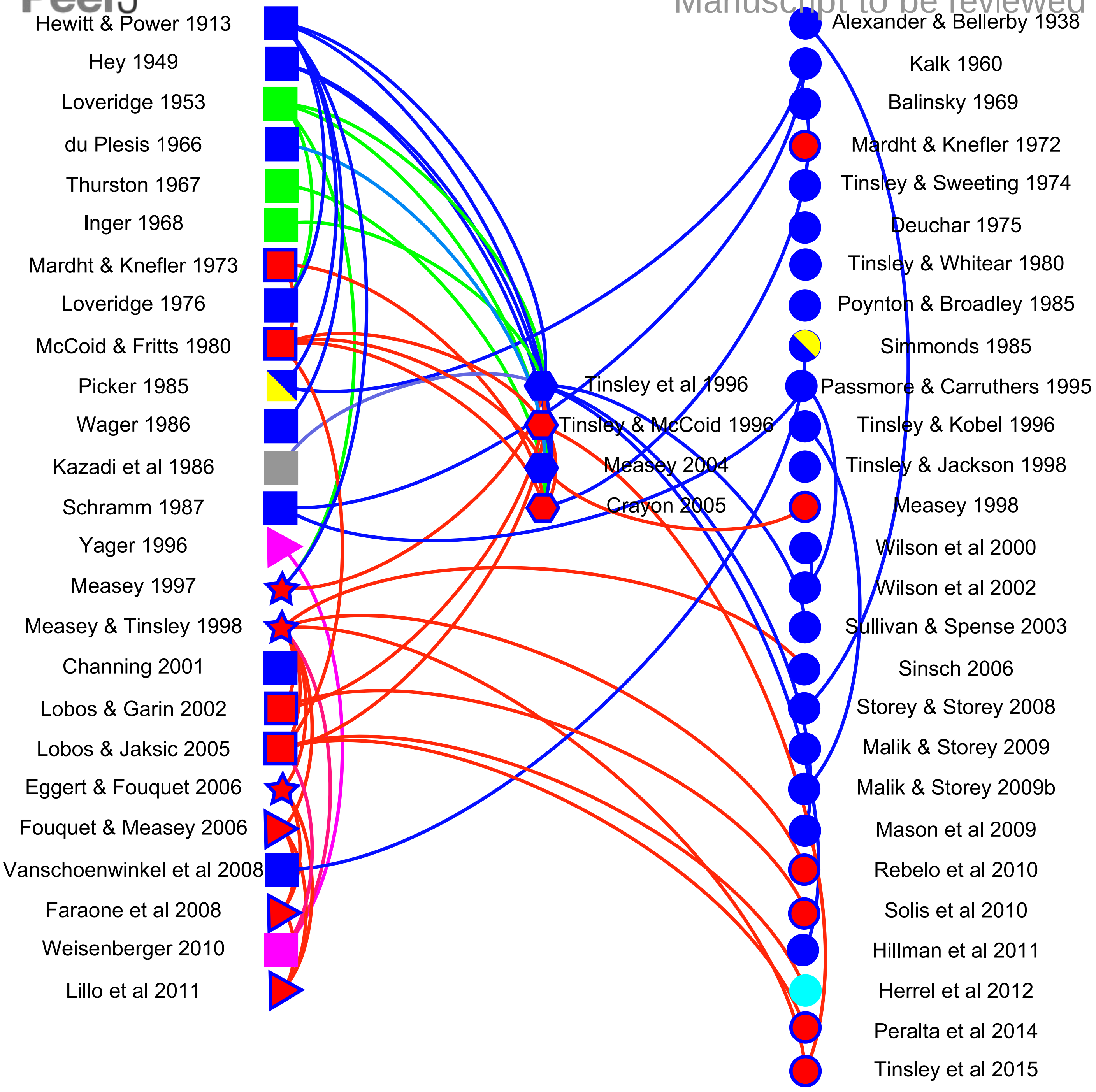
For more information, visit www.prisma-statement.org.

Figure 2(on next page)

Network visualisation for *Xenopus* overland movement literature

A network visualisation of literature mentioning overland movement in *Xenopus* using Gephi. Literature is sorted into that with data (left): anecdotal (squares), inferred (triangles), and empirical (stars); literature reviews (middle: hexagons); and literature which does not have original data on overland movement in *Xenopus* (circles: right). Different species of *Xenopus* are denoted by different colours, and indigenous *X. laevis* (blue filled symbol) are differentiated from invasive populations (red filled blue symbol). Other species are coded as other colours: *X. muelleri* (green), *X. borealis* (pink), *X. gilli* (yellow), *X. fraseri* (grey) and *X. tropicalis* (cyan). Curves connecting nodes denote the direction of the citation: above the line (right to left) or below the line (left to right). Nodes which are not connected represent literature which does not cite and has not been cited in relation to *Xenopus* movement overland. For complete references to the citations, please refer to Appendix 1.

Figure 2


Hewitt & Power 1913
Hey 1949
Loveridge 1953
du Plesis 1966
Thurston 1967
Inger 1968
Mardht & Knefler 1973
Loveridge 1976
McCoid & Fritts 1980
Picker 1985
Wager 1986
Kazadi et al 1986
Schramm 1987
Yager 1996
Measey 1997
Measey & Tinsley 1998
Channing 2001
Lobos & Garin 2002
Lobos & Jaksic 2005
Eggert & Fouquet 2006
Fouquet & Measey 2006
Vanschoenwinkel et al 2008
Faraone et al 2008
Weisenberger 2010
Lillo et al 2011
Tinsley et al 1996
Tinsley & McCoid 1996
Measey 2004
Crayon 2005
Alexander & Bellerby 1938
Kalk 1960
Balinsky 1969
Mardht & Knefler 1972
Tinsley & Sweeting 1974
Deuchar 1975
Tinsley & Whitear 1980
Poynton & Broadley 1985
Simmonds 1985
Passmore & Carruthers 1995
Tinsley & Kobel 1996
Tinsley & Jackson 1998
Measey 1998
Wilson et al 2000
Wilson et al 2002
Sullivan & Spense 2003
Sinsch 2006
Storey & Storey 2008
Malik & Storey 2009
Malik & Storey 2009b
Mason et al 2009
Rebelo et al 2010
Solis et al 2010
Hillman et al 2011
Herrel et al 2012
Peralta et al 2014
Tinsley et al 2015