Overland movement in African clawed frogs (*Xenopus laevis*): empirical dispersal data from within their native range (#20116)

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Overland movement in African clawed frogs (*Xenopus laevis*): empirical dispersal data from within their native range

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Dispersal forms an important component of the ecology of many animals, and reaches particular importance for predicting ranges of invasive species. African clawed frogs (*Xenopus laevis*) move overland between water-bodies, but all empirical studies are from invasive populations with none from their native southern Africa. Here we report on incidents of overland movement found through a capture-recapture study carried out over a three year period in Overstrand, South Africa. The maximum distance moved was 2.4 km with most of the 91 animals, representing 5% of the population, moving ~150 m. We found no differences in distances moved by males and females, despite the former being smaller. Less males moved overland, but this was no different from the sex bias found in the population. In laboratory performance trials, we found that males out performed females, in both distance moved and time to exhaustion, when corrected for size. Overland movement occurred throughout the year, but reached peaks in spring and early summer when temporary water-bodies were drying. Despite permanent impoundments being located within the study area, we found no evidence for migrations of animals between temporary and permanent water-bodies. Our study provides sufficient data for the first dispersal kernel for *X. laevis*. Our data suggest that *X. laevis* are similar to many non-pipid anurans with respect to dispersal.

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Summary

Dispersal forms an important component of the ecology of many animals, and reaches particular importance for predicting ranges of invasive species. African clawed frogs (*Xenopus laevis*) move overland between water-bodies, but all empirical studies are from invasive populations with none from their native southern Africa. Here we report on incidents of overland movement found through a capture-recapture study carried out over a three year period in Overstrand, South Africa. The maximum distance moved was 2.4 km with most of the 91 animals, representing 5% of the population, moving ~150 m. We found no differences in distances moved by males and females, despite the former being smaller. Less males moved overland, but this was no different from the sex bias found in the population. In laboratory performance trials, we found that males out performed females, in both distance moved and time to exhaustion, when corrected for size. Overland movement occurred throughout the year, but reached peaks in spring and early summer when temporary water-bodies were drying. Despite permanent impoundments being located within the study area, we found no evidence for migrations of animals between temporary and permanent water-bodies. Our study provides sufficient data for the first dispersal kernel for *X. laevis*. Our data suggest that *X. laevis* are similar to many non-pipid anurans with respect to dispersal.

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

Introduction

The ability to disperse is present in most organisms (Clobert et al. 2009), and is one of their most important characteristics (Bonte & Dahirel 2017). Dispersal entails the individual movement between habitat patches, and as such not only affects individual traits, but also population characteristics, such as community structure (Bowler & Benton 2005; Doebeli 1995; Holt 1985; Matthysen 2005). Dispersal is not a static event but differs between as well as within species (Altwegg et al. 2000; Bowler & Benton 2009; Schneider et al. 2003; Stevens et al. 2010). This is because factors, which include mate finding, habitat quality and competition (both intra and interspecific) influence the cost and benefit relationship of dispersal (Bowler & Benton 2009; Clobert et al. 2009). Characterising how acute these differences are is increasing in meaning as models and simulations require accurate character traits to define variables. For dispersal, it is common to produce a dispersal kernel (e.g. Nathan et al. 2008), displaying the different distances that different individuals have dispersed. This is particularly important for invasive species (Travis et al. 2009) where dispersal is a key characteristic, and such models help inform managers of potential invasive spread (e.g. Vimercati et al. 2017).

Locomotion, including dispersal, has been linked to an individual's morphology by studies of laboratory performance (Arnold 1983; Huey & Stevenson 1979). Performance ability represents the animal's maximum exertion, whereas dispersal represents the observed distance dispersed. As such, performance ability may be a good indicator as to the relative dispersal ability of that animal. For example, Leis et al. (2007) have shown that reef fish larva with higher than average swimming speed had more influence on their dispersal and could potentially disperse further. Morphology ultimately determines the performance ability of the animal and consequently the animal's dispersal ability, which is why natural selection acts upon morphology (Hertz et al. 1988; Zug 1972). An interesting example of this was observed with cane toad (*Rhinella marina*) populations, at the invasion front, have increased dispersal abilities (Alford et al. 2009) due to an increase in endurance (Llewelyn et al. 2010) resulting from longer leg length (Phillips et al. 2006), and shifts in behavioural traits (Gruber et al. 2017). This spatial sorting of a population has now been found in an increasing number of invasive species, including the pipid frog, *Xenopus laevis* (Courant et al. 2017a; Louppe et al. 2017).

Xenopus laevis occurs throughout southern Africa (Furman et al 2015), occupying almost every aquatic habitat found within this range (Furman et al. 2015; Measey 2004). The frogs in this genus are highly adapted for an aquatic lifestyle (Trueb 1996), as most of their life is spent in the water. It has been suggested dispersal is facilitated through aquatic corridors (i.e. rivers, streams, irrigation ditches, etc.), leading to the classical view that these frogs are fully aquatic (Fouquet & Measey 2006; Lobos & Measey 2002; Measey & Channing 2003; Van Dijk 1977). However this view has been challenged by many observations of overland migrations (reviewed by Measey 2016), which suggest that these frogs are capable of dispersing overland, and that they might better be termed “principally aquatic”. However, the majority of the literature represents anecdotal or inferred movements with little or no information on what proportion of the population disperses, what time of year they disperse and the function of the dispersal kernel.

Literature on the ecology of *X. laevis* is growing at an important rate, due to increasing numbers of studies of invasive populations (e.g. Amaral & Rebelo 2012; Courant et al. 2017b; Lillo et al. 2011). However, there have been very few empirical studies conducted within its native range, despite the species being almost ubiquitous in southern Africa. Here *X. laevis* is associated with artificial impoundments, such as farm dams, sewage works, fish hatcheries, etc. (Schoonbee et al. 1992; Van Dijk 1977) while the instances of occurrence in natural water-bodies go almost unnoticed. Intriguingly, this species appears to occur in impoundments in desert areas where it is unlikely to have had anything but a transient presence, making them the most widespread species in South Africa (Measey 2004). This might be because there is a tendency for human mediated dispersal of *X. laevis* for fishing bait and via universities (Measey et al. 2017; Van Sittert & Measey 2016; Weldon et al. 2007). Poynton was of the opinion that *X. laevis* made use of artificial water-bodies to expand their range and become an extra-limital species (quoted in De Moor & Bruton 1988), and it has been suggested that there is leading edge dispersal in *X. laevis* which could explain the near ubiquitous distribution (Measey et al. 2017; Van Dijk 1977). However, the extent to which populations disperse between natural and artificial impoundments in their native southern Africa is largely unknown (Measey 2016).

To redress the dearth in data on overland movement from native populations, we conducted a capture-mark-recapture exercise with *X. laevis* in seven water-bodies in the Overstrand region, southwestern South Africa. We conducted a study over 33 months asking the same four questions posed by Measey (2016) of our data: (1) Is there evidence for overland dispersal in a native population of *X. laevis*; (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 with respect to breeding? Lastly, we use a small dataset of individuals in a laboratory maximum performance experiment to ask whether differences in sex and size seen there match population movement data from the field.

Materials & Methods

Study site

Water-bodies 8km east of Kleinmond (hereafter referred to as Kleinmond) are divided between temporary water-bodies (vleis: typically full between July and November) and permanent impoundments (dams) which contain water all year, but may vary in depth. *Xenopus laevis* is known to occur in all sites, but *X. gilli* only occurs in the temporary vleis (see De Villiers et al. 2016; Fogell et al. 2013; Furman et al. 2017; Vogt et al. 2017). In each case, the permanent impoundments are artificial, while the vleis are natural.

The study area falls within a single catchment and is relatively homogenous with a very gentle slope running approximately north-south with a change of less than 10 m altitude. Vegetation is lowland sand-stone fynbos (Mucina & Rutherford 2006), with areas particularly heavily invaded by *Acacia saligna* (Port Jackson Willow), *Hakea sericea* (Silky Hakia) and *Acacia mearnsii* (Black Wattle). Three temporary streams run north-south through the study area, but ran only part of the year. None link any of the water-bodies. A tarred road and several dirt roads run throughout the area.

It is noteworthy that the southwestern Cape of South Africa was undergoing a drought at the time of this study and periodicity of temporary water was affected. The temporary pools held water for 6 and 7 months in the first and second years of the study, and these times did not coincide with seasonal changes due to a lag between the onset of rains and the filling (and emptying) of pools. In contrast, the permanent dams contained water throughout the study, although the levels changed considerably.

Capture-mark-recapture

Frogs were collected from January 2014 to June 2016 by using baited traps (bucket or fyke traps; see (Lobos & Measey 2002; Vogt et al. 2017). Three to five traps were set in five temporary and three permanent ponds (Figure 1.1). Each trapping session was conducted over one to four consecutive nights, each night the traps were set and collected again the following morning. All animals were processed at the edge of each site and returned to the site in which they were trapped. In addition to the eight regular trapping sites, in June 2016 we placed traps for three nights in three water-bodies immediately outside of the area, but none were found to contain *X. laevis* leading us to believe that we were covering a discreet population. Ethical clearance was obtained from Stellenbosch University (SU-ACUD14-00028) and permits were issued from CapeNature (AAA007-00092-0056).

Each frog was photographed dorsally on a 10×10 mm grid. Frogs were sexed externally by the presence of labial lobes in females and nuptial pads on the forearms of males (see Measey 2001). Generally, it was possible to sex individuals greater than 45 mm snout-vent length (SVL), and smaller animals were classified as juveniles if sex could not be unambiguously determined. Individuals below 30 mm SVL were too small to be tagged. Sex ratio (m/f*100 with juveniles ignored) was calculated per capture session. Frogs were then tagged using 8mm PIT tags, which are small glass capsules with an electromagnetic coil (Guimaraes et al. 2014). The tag was placed in 15-gauge hypodermic needle and injected underneath the skin above the dorsal lymph sac (Donnelly et al. 1994). Each individual was scanned with a hand held scanner (APR 350, Agrident, Barsinghausen Germany) and the unique number recorded together with the locality of the individual. Image numbers were recorded together with tag numbers, and the scaled images used to calculate (SVL) using ImageJ (Rasband 2012).

The distance between the pond of origin (i.e. the pond where the frog was tagged) and the destination pond were measured (to the closest meter) using ArcGIS (ESRI, 2014). As such this represented the Euclidian distances between sites. Dispersal distances were log transformed to meet assumptions of homoscedasticity. Normality of data was determined by using pp-plots and the homogeneity of the variances were determined by using Levene’s test.

Performance measures

Twenty (10 male and 10 female) *X. laevis* were collected from Kleinmond, and transported to and housed at Stellenbosch University’s Department of Botany and Zoology. Each frog was PIT tagged and housed separately in its own aquarium at a constant temperature of 20˚ C (Careau et al. 2014; Herrel et al. 2012; Louppe et al. 2017). Animals were fed every second day with sheep’s heart, *ad libitum*, and each was weighed once a week to monitor their well-being.

Prior to performance trials, each animal was measured using digital callipers (to the nearest 0.01 mm). Measurements were taken as follows: head length and width, jaw length radius length, humerus length, hand length, longest finger length; longest toe-length; foot-length; tibia-length; femur-length; ilium length and width; SVL and inter axial distance (i.e. a lateral measurement of the vertebral and ilium length: (Herrel et al. 2012; Louppe et al. 2017). SVL was quantified as the length from the tip of the snout to the cloacae (Herrel et al. 2012). Where appropriate, all measurements were size (SVL) corrected for comparison.

All performance trials were conducted in a controlled environment with a constant temperature of 20˚ C (±2˚ C), as this is the optimal performance temperature for *Xenopus laevis* (Miller 1982). All animals were rested for at least 24 hours between trials, with each animal undergoing three trials where the longest distance in the shortest time was retained for analysis. The performance trials were conducted within three weeks of the capture of the frogs. Dry endurance was determined on a 4m circular track with a rubber grip mat as substrate. Each trial was timed and the distance moved was calculated from the number of laps with continuous movement insured by tapping the frog between the hind legs. The trial was considered finished if the frog refused to move after multiple taps, and was unable to right itself (Herrel & Bonneaud 2012).

Data analysis

In order to assess potential bias in capture rates in our dataset, we first compared sex-ratios and sizes of animals that were captured once (26.7%) with those that were captured more than once. A chi-squared test (χ^2) showed that sex ratios were the same for animals that were captured once, or more than once (χ^2 = 0.012488, p-value = 0.9123), but an ANOVA shows that there was a significant difference in size ($F_{1,1750}$=5.327, p = 0.0211) with larger animals being captured more than once. This means that to test for sex bias in dispersal, we use the entire dataset, but that for size, we use only those animals which were captured more than once. In each case, a χ^2 test was used in R (R Core Team 2017) with a P-value based on 10 000 000 bootstraps.

Movement events (events where an animal was tagged in one location, but recaptured in another) were coded according to whether or not they occurred within one season (dry: December to May; wet: June to November), the sex and size of the individual. The dataset for comparison was made up of individuals that were marked and recaptured during the same period within one of the ponds.

The dispersal kernel was fitted using all dispersal distances (including instances where individuals moved more than once). We used the fitdistrplus package (Delignette-Muller & Dutang 2015) in R (R Core Team

2017) to test the fit of the data against three distribution types: exponential, lognormal and gamma. We then inferred the best fit through minimum AIC.

For the performance data, we logged all linear measurement data to to fulfill assumptions of normality and homoscedasticity. We conducted a MANCOVA (R Core Team 2017) with ilia, limb and hand/foot measurements as determinate variables, between sexes with size (SVL) as a covariate with the Pillai test statistic. Next, we conducted another MANCOVA using the (log of) maximum distance moved and time to exhaustion as determinate variables, between sexes with size (SVL) as a covariate.

Results

Capture-mark-recapture

We made 9401 captures of 1755 individual *Xenopus laevis* in 80 capture events over 28 sessions in 3 years. The mean number of animals captured per session was 354 (± 51.21), and the sex ratio was always female biased, varying from 74 to 32. The majority of individuals were recaptured at least once (n = 1298), with only 26% of individuals (n = 457) that were only captured once. We found significant differences between the sizes of males (SVL mean 58.54 mm ± 0.418; max 93.0 mm n = 852) and females (SVL mean 63.06 mm ± 0.447; max 129.6 mm n = 1312: $F_{1,2162} = 42.599$; $P < 0.0001$). Juveniles (<45 mm) made up a significant part of some capture sessions, averaging 9.8% (± 1.3), we noted large numbers of metamorphs at one of the sites (Ysterklip), but animals <30 mm SVL rarely entered our traps.

Ninety-one individuals (5.2%) moved between one and four times (mean 1.19 ± 0.060) over the entire period. Of the 11 animals that moved two or more times, only five returned to their original site of capture. The modal overland distance moved was 147 m, with the frequency of small movements far exceeding long ones (Figure 1), as is usual in amphibian dispersal, with the maximum distance moved 2.42 km (Figure 2). A lognormal distribution fitted the highest dispersal values best (equation 1) as well as performing well on the mid-range values. However, all three distributions fitted the data well, differing by less than 60 δAIC values (Table 1).

$$X = e^{0.75 - 15.5Z} \qquad (1)$$

The nature of capture-recapture does not allow for the precise timing of the majority of movements that occurred between capture sites. Thus, only 69 of 108 movements occurred within a season. When seasons were divided into wet and dry, we found no difference in the numbers of animals moving between sites between seasons (χ^2 = 0.5526, p = 0.5192), nor was there any difference in the proportions of sexes moving over each season (χ^2 = 0.5526, p = 0.519). However, we did find that individuals moved significantly further during the wet period (mean = 245.4m ± 36.75) than during the dry (142.1m ± 54.36: $F_{1,101}$=6.833, p = 0.0103). The maximum dispersal distance observed was a *X. laevis* female, which travelled 2 420 m in less than six weeks, and another *X. laevis* female dispersed 1 360m in less than three weeks. Neither of these movements was downhill or through any form of stream or movement of water overland. In addition, we have a record of a single male animal that was caught in one temporary water site on one night and in another 147 m away on the next night. We also found some examples of synchronous movements. For example, in October 2015 we captured five animals in Arabella that were all captured two nights later 91 meters away, and in February 2015 we captured six animals at Rondegat that were all captured two months later in another water-body 147 meters away.

Many of the movements during the dry season happened between adjacent temporary sites (Figure 2c). However, during the wet season many movements happened between temporary and permanent sites, as well as between temporary sites (Figure 2d). The timing of these movement events were related to drying of temporary water sites in December 2014, and in October 2015 which also coincided with drying events after very poor winter rains (Figure 3). These two events encompassed the majority of movement events (58.6%), but we recorded movements during almost every capture session (83%; Figure 3).

Even though we had twice the number of females (n = 63) moving as males (n = 28), this was not significantly different to the sex ratio of animals that did not move (females 988; males 672; χ^2 = 3.6678, P = 0.06298). No significant bias was found in the size of animals that were moving compared to those that were recaptured within the same water-body ($F_{1,1282}$ = 3.565, p = 0.0593).

Performance

We found significant differences between the sizes of male and female *X. laevis* within the small subset (n = 20) which we used for performance work ($F_{1,18}$ = 10.4; P = 0.0047). In this subsample, all size-corrected forelimb measures of males were significantly longer than females, except the size-corrected length of the longest toe longer in females (Table 2). We found a difference in the size-corrected distance moved by the two sexes before exhaustion, with males moving significantly further ($F_{1,18}$ = 10.4; P = 0.0047). Time to exhaustion, when both sex and corrected size were included, was significant ($F_{2,17}$ = 5.113; P = 0.0182), with smaller males moving for longer than larger females. The mean distance moved was 24.9 m (± 0.79 m) in around 3 minutes (187 s ± 8.15 s).

Discussion

We present the first empirical data for overland movement of *Xenopus laevis* within its native range, demonstrating that distances moved are up to 2.42 km over a period of less than 6 weeks. This finding is an important extension to the data reviewed by Measey (2016) in which the longest distance moved was 2 km in an invasive population. In addition to extending the maximum distance moved overland, we were able to calculate a dispersal kernel for this species. Over a period of 3 years, we found that 5% of individuals moved between sites, although this does not necessarily mean that 95% of the animals were philopatric, as 26% of animals were only captured once.

Do Xenopus laevis migrate?

Hey (1949) provided a description of *X. laevis* in Jonkershoek (45 km north-west of our study site) involved in a migration from permanent impoundments into freshly filled temporary vleis in order to breed. We had expected that the combination of permanent and temporary water bodies in our study area would allow us to collect data on such migrations over the three years of study, but we found none. Only five animals were found to return to their original site of capture, but these movements were not necessarily through permanent waters. Instead, we presume that animals that left the temporary water went into subterranean aestivation, although efforts to find any *Xenopus* through excavations in the area proved unsuccessful (Measey et al., January 2015 unpublished data). Whether these animals hide collectively or are scattered throughout the area is potentially important. Attempts at eradicating invasive populations may flounder if a proportion of the animals go undetected in the soil. Like Measey (2016), we cannot discount the possibility that *X. laevis* do migrate between water-bodies under particular circumstances, but we found no evidence of this in the Kleinmond population. However, we did find examples of synchronous movements, both during the wet and dry periods. Movements of large numbers of *X. laevis* have been witnessed (Lobos & Jaksic 2005; Measey 2016), but our data suggest it may also be that this happens on a smaller scale.

Sexual or size difference in dispersal?

Our study found a highly skewed sex ratio, with females outnumbering males three to one. Other studies have found similar skews toward females (Lobos & Measey 2002). Once we considered this skew, we found no bias in sex of animals dispersing. It could be that there is dispersal bias towards smaller life-history stages (metamorphs and juveniles, see Sinsch 2014) that we were not able to tag. If this were also a male biased dispersal (as might be expected Hamilton & May 1977; Trochet et al. 2016), high mortality might help explain the skewed sex ratio. However, we observed metamorphs only in one of the permanent impoundments, and metamorph survival might be altered in densely populated water-bodies such as these (De Villiers et al. 2016) for smaller cohorts as adults are cannibalistic (Measey et al. 2015; Vogt et al. 2017). Amphibians are known to have examples of female biased dispersal (Austin et al. 2003; Lampert et al. 2003; Palo et al. 2004) and male biased dispersal (Liebgold et al. 2011), although these are all genetic studies, and capture-mark-recapture studies generally suggest no sex-bias (e.g. Sinsch 2014; Smith & Green 2006). It is noteworthy that an isolated genetic study on the study population should record female biased dispersal, as more females were found to move. However, this would not be due to a bias in dispersal of individuals, but simply reflect the already skewed population bias.

The fact that females were found to disperse provides important information to phylogeographic studies using mitochondrial DNA (De Busschere et al. 2016; Furman et al. 2015; Measey & Channing 2003). African clawed frogs are known to form well defined mtDNA clades in southern Africa, and these have been shown to correspond to sufficiently rapidly evolving nuclear DNA (Furman et al. 2015). Presumably, these clades represent areas where both males and females are equally inhibited from dispersing.

In addition to the field data, we present a performance dataset that suggests that males and females are equally able to move long distances. This required males to move proportionately further and longer than females before exhaustion. Distances moved in our study are around double those reported by Louppe et al (2017) for two invasive populations of *X. laevis* in France. Similarly, our animals had higher stamina, being able to move for longer before exhaustion. The studies differed in the temperature the trial was conducted (22° C in France and 20° C in South Africa). Despite these differences, both studies found that males moved relatively further for relatively longer such that they were able to perform as well as larger females. Both studies indicate that the time taken to displace a distance to exhaustion would make it easily possible for animals to move between close sites in one night (as we observed), while the longest distances observed may have taken several days including periods in water-bodies between sites.

It is noteworthy that within our study site there were two temporary streams (Fig 2a); one not associated with any water-bodies, and the other with three of the sites. While these three sites received the most movement between them, this was largely confined to dry periods when the water did not flow. This suggests that *X. laevis* are not reliant on water courses to guide their movements. However, when the weather is dry watercourses may offer increased levels of humidity which reduce dehydration during overland movements. Dehydration remains an important risk for *X. laevis* moving overland, as has been stressed with other amphibians (Tingley et al. 2012; Vimercati et al. sub).

Seasonality and habitat drying

Our data demonstrate that African clawed frogs do move overland throughout the year, and that this behaviour is not restricted to periods of winter rainfall. However, more dispersal events occurred during the wet winter period, when individuals also moved further. Both observations match the recent literature review (Measey 2016). Additionally, movements between water-bodies peaked at the same time that the vleis were drying. This suggests that the majority of animals move some distance in order to aestivate, and do not simply burrow into the mud of a drying pond (although this has been observed, see Measey 2016). There was no notable directionality in this movement.

Conclusion

This is the first empirical data of overland movement within the native range of *X. laevis*, and the largest mark-recapture study conducted on this species to date. We found that 5% of *Xenopus laevis* moved between one or more of eight water-bodies within an area of 3 km^2, with examples of animals moving the full length of the study site. Longer distances were moved overland during the wet period, but animals moved all year round. More females moved than males, but this was in proportion with the sex-bias observed in the population. Males and females moved the same distances between sites, even though males are significantly smaller; identical to results found in performance studies (Louppe et al. 2017). Animals found in temporary water bodies did not move into permanent impoundments, despite their presence in the area. We suggest instead that these animals are aestivating underground at an unknown location.

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Table 1(on next page)

Model testing for distributions of dispersal kernel of *Xenopus laevis* from Kleinmond.

Based on 108 movements of 91 individuals over a 3 year period.

Table 1. Model testing for distributions of dispersal kernel of *Xenopus laevis* from Kleinmond.

Distribution	Akaike's Information Criterion (AIC)	∆AIC	Bayesian Information Criterion	Anderson-Darling Statistic
Log normal	1410.92	0	1416.29	3.069861
Gamma	1433.32	22.40	1438.69	3.927477
Weibull	1450.97	40.05	1456.33	5.497646
Exponential	1469.55	58.63	1472.23	10.39505

Table 2 (on next page)

MANCOVA performed on the morphometric data of *Xenopus laevis* from Kleinmond with SVL as covariate.

All hand, arm, and foot measurements were found to be significantly different.

Effect	Variable	Pillai test	F	df	Error	P	
Sex		0.9962	168.91	11		0.0004	*
	Mass		0.23	1		0.6381	
	Ilium length		2.52	1		0.1306	
	Ilium width		1.63	1		0.2195	
	Femur		3.24	1		0.0898	
	Tibia		3.63	1		0.0738	
	Astragalus		3.45	1		0.0808	
	Longest toe		41.59	1		<0.0001	*
	Humerus		10.64	1		0.0046	*
	Radius		36.07	1		<0.0001	*
	Hand		17.1	1		0.0007	*
	Longest finger		4.97	1		0.0395	*

Figure 1

Dispersal kernel of *Xenopus laevis* at Kleinmond, South Africa

Based on 108 movements of 91 individuals over a 3 year period.

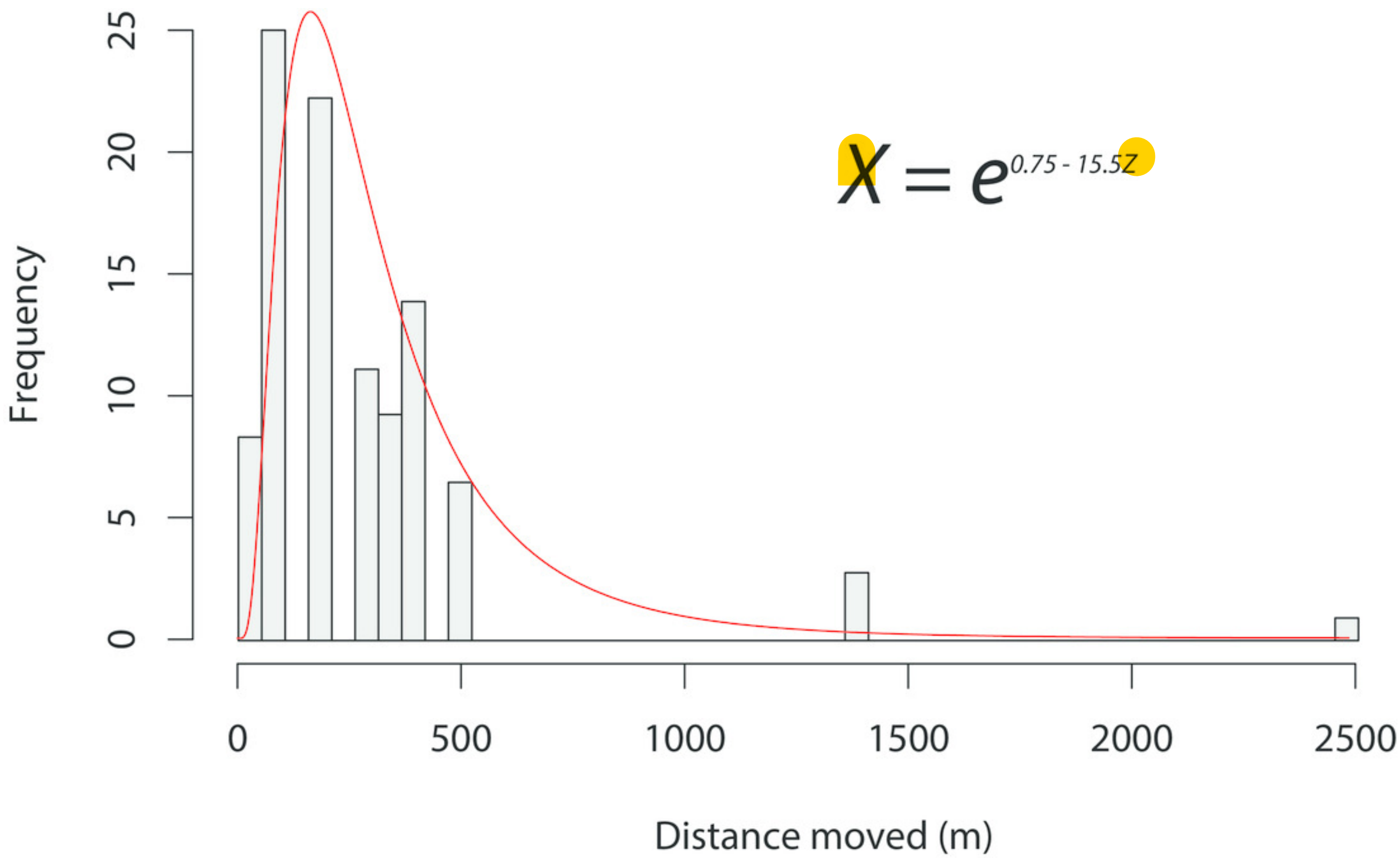

Figure 2

Study site location and detail of mark-recapture work on *Xenopus laevis*.

(a) Location of study site near Kleinmond in the extreme southwest of the Western Cape, South Africa. Note that the study area (red box) is on level ground with only light relief toward the saltwater Botrivier Lagoon. Yellow star shows the location of Jonkershoek (Hey 1949 ; Van Sittert & Measey 2016) . (b) Study site in detail with satellite image of ground cover in the area. Artificial impoundments are in dark blue while light blue shows temporary vleis. The tar road is shown with a black line, while dirt roads are shown with brown lines. Temporary streams are shown with blue lines. Simplified schematic of sampling area with overland movements of *Xenopus laevis* during (c) the dry summer (January to June), and (d) the wet winter (June to December). Red and green lines are proportional to the numbers of movements in summer and winter, respectively.

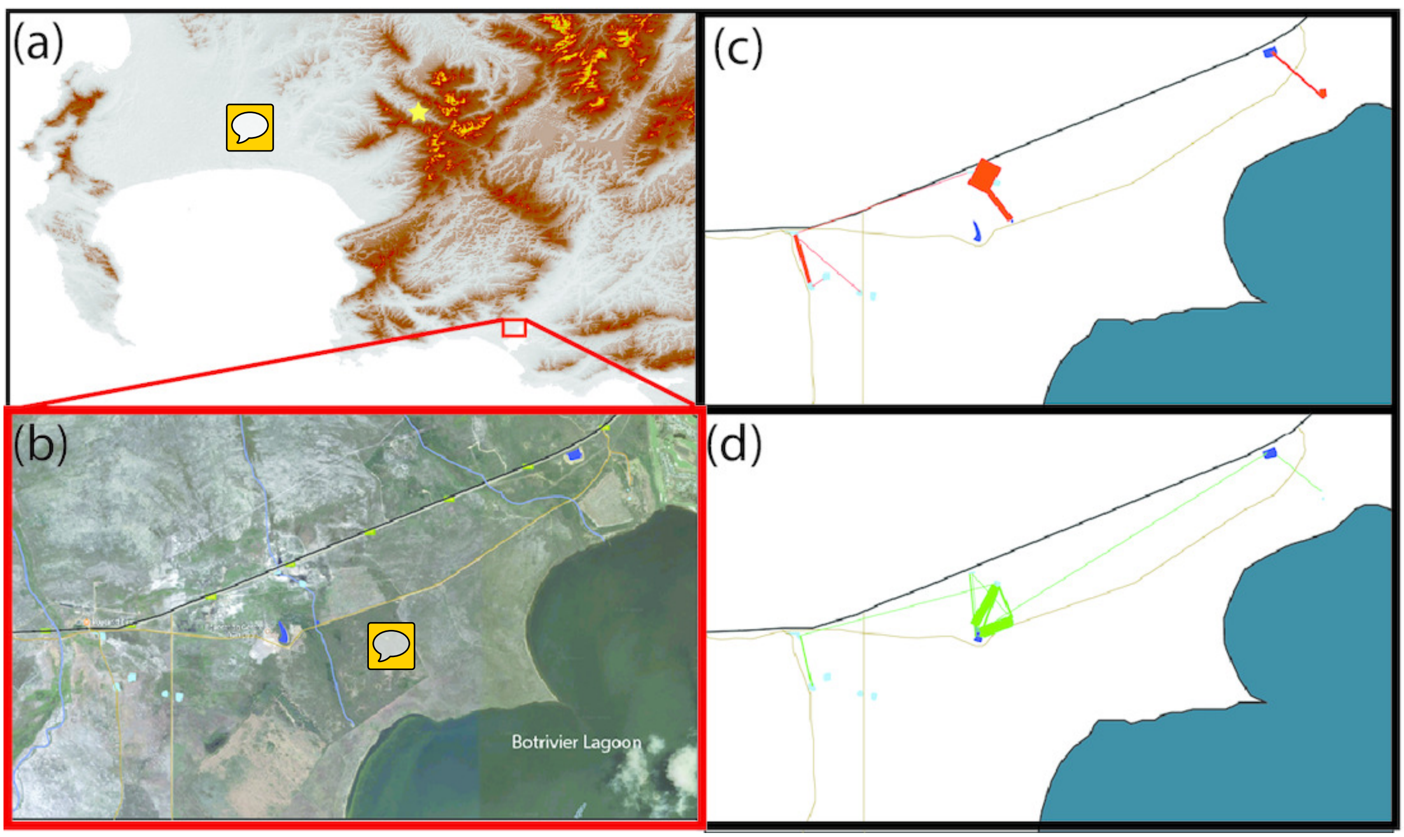

Figure 3

Frequency of incidents of *Xenopus laevis* caught in a pond other than the one in which they were marked.

Spikes in December 2014 and October 2016 coincide with the drying of temporary water-bodies in those years. Note that movements are binned by month and not by capture session.