

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

1

First revision

Please read the **Important notes** below, the **Review guidance** on page 2 and our **Standout reviewing tips** on page 3. When ready [submit online](#). The manuscript starts on page 4.

Important notes

Editor

Donald Kramer

Files

1 Tracked changes manuscript(s)
1 Rebuttal letter(s)
4 Figure file(s)
2 Table file(s)
1 Other file(s)

Please visit the overview page to [download and review](#) the files not included in this review PDF.

Declarations

Involves vertebrate animals.
Involves a field study on animals or plants.



Please read in full before you begin

How to review

When ready [submit your review online](#). The review form is divided into 5 sections. Please consider these when composing your review:

1. BASIC REPORTING

2. EXPERIMENTAL DESIGN

3. VALIDITY OF THE FINDINGS

4. General comments

5. Confidential notes to the editor

 You can also annotate this PDF and upload it as part of your review

To finish, enter your editorial recommendation (accept, revise or reject) and submit.

BASIC REPORTING

-  Clear, unambiguous, professional English language used throughout.
-  Intro & background to show context. Literature well referenced & relevant.
-  Structure conforms to [PeerJ standards](#), discipline norm, or improved for clarity.
-  Figures are relevant, high quality, well labelled & described.
-  Raw data supplied (see [PeerJ policy](#)).

EXPERIMENTAL DESIGN

-  Original primary research within [Scope of the journal](#).
-  Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
-  Rigorous investigation performed to a high technical & ethical standard.
-  Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

-  Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
-  Conclusions are well stated, linked to original research question & limited to supporting results.
-  Speculation is welcome, but should be identified as such.
-  Data is robust, statistically sound, & controlled.

The above is the editorial criteria summary. To view in full visit <https://peerj.com/about/editorial-criteria/>

7 Standout reviewing tips

3



The best reviewers use these techniques

Tip

Example

Support criticisms with evidence from the text or from other sources

Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.

Give specific suggestions on how to improve the manuscript

Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).

Comment on language and grammar issues

The English language should be improved to ensure that your international audience can clearly understand your text. I suggest that you have a native English speaking colleague review your manuscript. Some examples where the language could be improved include lines 23, 77, 121, 128 - the current phrasing makes comprehension difficult.

Organize by importance of the issues, and number your points

1. Your most important issue
2. The next most important item
3. ...
4. The least important points

Give specific suggestions on how to improve the manuscript

Line 56: Note that experimental data on sprawling animals needs to be updated. Line 66: Please consider exchanging "modern" with "cursorial".

Please provide constructive criticism, and avoid personal opinions

I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC

Comment on strengths (as well as weaknesses) of the manuscript

I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.

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

F. André De Villiers¹, John Measey^{Corresp.}¹

¹ Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Stellenbosch, South Africa

Corresponding Author: John Measey
Email address: john@measey.com

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. Fewer males moved overland, but this was no different from the sex bias found in the population. In laboratory performance trials, we found that males outperformed 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 the first dispersal kernel for *X. laevis*, and suggest that it is similar to many non-pipid anurans with respect to dispersal.

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

3

4 F. André de Villiers¹ & John Measey^{1*}

5

6 ¹Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Private Bag X1,
7 Matieland 7602, Stellenbosch, South Africa

8

9 **Abstract**

10 Dispersal forms an important component of the ecology of many animals, and reaches particular
11 importance for predicting ranges of invasive species. African clawed frogs (*Xenopus laevis*) move
12 overland between water-bodies, but all empirical studies are from invasive populations with none from
13 their native southern Africa. Here we report on incidents of overland movement found through a
14 capture-recapture study carried out over a three year period in Overstrand, South Africa. The maximum
15 distance moved was 2.4 km with most of the 91 animals, representing 5% of the population, moving
16 ~150 m. We found no differences in distances moved by males and females, despite the former being
17 smaller. Fewer males moved overland, but this was no different from the sex bias found in the
18 population. In laboratory performance trials, we found that males outperformed females, in both
19 distance moved and time to exhaustion, when corrected for size. Overland movement occurred
20 throughout the year, but reached peaks in spring and early summer when temporary water-bodies were
21 drying. Despite permanent impoundments being located within the study area, we found no evidence
22 for migration of animals between temporary and permanent water-bodies. Our study provides the first
23 dispersal kernel for *X. laevis*, and suggests that it is similar to many non-pipid anurans with respect to
24 dispersal.

25

26

27

28

29

30

32 Introduction

33 The ability to disperse is present in most organisms (Clobert et al. 2009), and is one of their most
34 important characteristics (Bonte & Doherty 2017). Dispersal entails the individual movement between
35 habitat patches, and as such not only affects individual traits, but also population characteristics, such as
36 community structure (Bowler & Benton 2005; Doebeli 1995; Holt 1985; Matthysen 2005). Dispersal
37 differs between as well as  in species (Altwegg et al. 2000; Bowler & Benton 2009; Schneider et al.
38 2003; Stevens et al. 2010), this is because factors, which include mate finding, habitat quality and
39 competition (both intra- and interspecific) influence the costs and benefits relationship of dispersal
40 (Bowler & Benton 2009; Clobert et al. 2009). Characterising dispersal differences is increasing its
41 significance as models and simulations require accurate character traits. To characterise the statistical
42 distribution of dispersal distances for a species, it is common to produce a dispersal kernel which is
43 made up from the different Euclidian distances between source and destination points for a population
44 (Nathan et al. 2012). This is particularly important for invasive species (Travis et al. 2009) where
45 dispersal is a key characteristic. The use of dispersal kernels in models of invasion help inform managers
46 of potential invasive spread (e.g. Vimercati et al. 2017).

47

48 Animal movement, including dispersal, has been linked to an individual's morphology by studies of
49 laboratory performance (Arnold 1983; Huey & Stevenson 1979). Performance ability represents the
50 animal's maximum exertion, whereas dispersal represents the observed distance moved. As such,
51 performance ability may be a good indicator of the relative dispersal ability of that animal. For example,
52 Leis et al. (2007) have shown that reef fish larvae with the highest swimming speed had a strong
53 influence on the population's dispersal ability. Morphology ultimately determines the performance
54 ability of the animal and consequently the animal's dispersal ability, which is why natural selection acts
55 upon morphology (Hertz et al. 1988; Zug 1972). Herrel et al. (2014) demonstrated that the influence of
56 morphology on jumping performance was sex-specific for *Xenopus tropicalis*, suggesting that this
57 differentially influenced their dispersal ability (see also Herrel & Bonneaud 2012). Another interesting
58 example was observed in cane toads (*Rhinella marina*), where populations at the invasion front were
59 found to have increased dispersal abilities (Alford et al. 2009) due to an increase in endurance (Llewelyn
60 et al. 2010) resulting from longer leg length (Phillips et al. 2006), and shifts in behavioural traits (Gruber
61 et al. 2017). This spatial sorting of a population has now been found in an increasing number of invasive
62 species, including the pipid frog, *X. laevis* (Courant et al. 2017a; Louppe et al. 2017).

63

64 *Xenopus laevis* occurs throughout southern Africa, occupying almost every aquatic habitat found within
65 this range (Furman et al. 2015; Measey 2004). The frogs in this genus are highly adapted for an aquatic
66 lifestyle (Trueb 1996), as most of their life is spent in the water. It has been suggested that dispersal is
67 facilitated through aquatic corridors (i.e. rivers, streams, irrigation ditches, etc.), leading to the classical
68 view that these frogs are fully aquatic (Fouquet & Measey 2006; Lobos & Measey 2002; Measey &
69 Channing 2003; Van Dijk 1977). However, this view has been challenged by many observations of
70 overland movements (reviewed by Measey 2016), which suggest that these frogs are capable of
71 dispersing overland, and that they might better be termed “principally aquatic”. However, the majority
72 of the literature represents anecdotal or inferred movements with little or no information on what
73 proportion of the population disperses, what time of year they disperse, and the function of the
74 dispersal kernel. It has been suggested that *X. laevis* migrates (Hey 1949), adult movements between
75 permanent and temporary habitats, but no data exist to substantiate this (Measey 2016). It is important
76 to clarify whether or not individuals migrate back to ponds or disperse between ponds, as regular
77 dispersal would mean that ponds do not represent discrete populations, and instead that *X. laevis* may
78 meet some of the conditions for a metapopulation (cf Smith & Green 2005).

79

80 Literature on the ecology of *X. laevis* is growing rapidly, due to increasing numbers of studies of invasive
81 populations (e.g. Amaral & Rebelo 2012; Courant et al. 2017b; Lillo et al. 2011). However, there have
82 been very few empirical studies conducted within its native range, despite the species being almost
83 ubiquitous in southern Africa. Here, *X. laevis* is associated with artificial impoundments, such as farm
84 dams, sewage works, fish hatcheries, etc. (Schoonbee et al. 1992; Van Dijk 1977), while their presence in
85 natural water-bodies goes almost unnoticed. Intriguingly, this species appears to occur in
86 impoundments in desert areas where it is likely to have had anything but a transient presence, making it
87 the most widespread amphibian species in South Africa (Measey 2004). This might be because there is a
88 tendency for human mediated dispersal of *X. laevis* for fishing bait and via universities (Measey et al.
89 2017; Van Sittert & Measey 2016; Weldon et al. 2007). Poynton (quoted in De Moor & Bruton 1988) was
90 of the opinion that *X. laevis* made use of artificial water-bodies to expand their range and become an
91 extra-limital species, and it has been suggested that there is leading edge dispersal in *X. laevis* which
92 could explain the near ubiquitous distribution (Measey et al. 2017; Van Dijk 1977). However, the extent
93 to which populations disperse between natural and artificial impoundments in their native southern
94 Africa is largely unknown (Measey 2016).

95

96 To redress the dearth of data on overland movement from native populations, we conducted a capture-
97 mark-recapture exercise with *X. laevis* in eight water-bodies in the Overstrand region, southwestern
98 South Africa. We conducted a study over 33 months asking the same four questions posed by Measey
99 (2016) of our data: (1) Is there evidence for overland dispersal in a native population of *X. laevis*; (2)
100 What distances are moved overland; (3) Is there evidence that overland movement is seasonal or
101 associated with rain or drying habitats; (4) Is there evidence of overland movement being migratory
102 with respect to breeding? Lastly, we use a small laboratory study of maximum performance to ask
103 whether sex and size differences match population movements in the field.

104

105 **Materials & Methods**

106 *Study site*

107 The study area (34.325° S, 19.103° E), 8 km east of Kleinmond (hereafter referred to as Kleinmond),
108 covers an area of 5.4 km² (3.5 km by 1.5 km) in the Overstrand, Western Cape Province, South Africa
109 (Figure 1). It falls within a single catchment and is relatively homogenous with a very gentle slope
110 running approximately north-south with a change of less than 10 m altitude in 1.5 km. The eight water-
111 bodies are divided between five temporary water-bodies (vleis: typically full between July and
112 November) and three permanent impoundments (dams) which contain water all year, but may vary in
113 depth. In each case, the permanent impoundments are artificial, while the vleis are natural. The study
114 area had a maximum distance between water-bodies almost spanning the entire area (3.7 km), while
115 the minimum distance was 91 m. Three streams run north-south through the study area, but flow only
116 part of the year. A paved road and several unpaved roads run through the area (Figure 1).

117 *Xenopus laevis* is known to occur in all water-bodies, but the congeneric *X. gilli* only occurs in the vleis
118 (see De Villiers et al. 2016; Fogell et al. 2013; Furman et al. 2017). (Vogt et al. 2017). The dams have only
119 *X. laevis*, *A. fuscigula* and *S. capensis*. Vegetation is lowland sand-stone fynbos (Mucina & Rutherford
120 2006), with areas particularly heavily invaded by *Acacia saligna* (Port Jackson Willow), *Hakea sericea*
121 (Silky Hakea) and *Acacia mearnsii* (Black Wattle).

122 It is noteworthy that the southwestern Cape of South Africa was undergoing a drought at the time of
123 this study, and periodicity of temporary water was affected. The temporary pools held water for 6 and 7
124 months in the first and second years of the study, and these times did not coincide with seasonal

125 changes due to a lag between the onset of rains and the filling (and emptying) of pools. In contrast, the
126 permanent dams contained water throughout the study, although the levels changed considerably.

127

128 *Capture-mark-recapture*

129 Frogs were collected from January 2014 to June 2016 by using baited traps (bucket or fyke traps; see
130 (Lobos & Measey 2002; Vogt et al. 2017). Three to five traps were set in five temporary and three
131 permanent ponds (Figure 1). Each trapping session was conducted for all water-bodies for which water
132 was deep enough to contain a trap (>20 cm deep), from one to four consecutive nights, each night the
133 traps were set and collected again the following morning. Regular trapping with three to four week
134 intervals between sessions took place from 2014 to the end of 2015. Thereafter trapping has taken place
135 at six-monthly intervals. All animals were processed at the edge of each site and returned to the site in
136 which they were trapped. In addition to the eight regular trapping sites, in June 2016 we placed traps for
137 three nights in three water-bodies immediately outside of the area, but none were found to contain *X.*
138 *laevis* leading us to believe that we were covering a discrete population. Ethical clearance for capture-
139 mark-recapture was obtained from Stellenbosch University (SU-ACUD14-00028) and permits were
140 issued from CapeNature (AAA007-00092-0056).

141

142 Upon emptying traps, all frogs were first scanned with a hand held scanner (APR 350, Agrident,
143 Barsinghausen Germany) and the unique number recorded together with the locality of the individual.
144 Frogs (>30 mm SVL) without tags were then tagged using 8 mm PIT tags, which are small glass capsules
145 with an electromagnetic coil (Guimaraes et al. 2014). The tag was placed in 15-gauge hypodermic needle
146 and injected underneath the skin above the dorsal lymph sac (Donnelly et al. 1994). Each frog was
147 photographed dorsally on a 10×10 mm grid. Image numbers were recorded together with tag numbers,
148 and the scaled images used to calculate (SVL) using ImageJ (Rasband 2012). Frogs were sexed externally
149 by the presence of labial lobes in females and nuptial pads on the forearms of males (see Measey 2001).
150 Generally, it was possible to sex individuals greater than 45 mm snout-vent length (SVL), and smaller
151 animals were classified as juveniles if sex could not be unambiguously determined.

152

153 *Performance measures*

154 Twenty (10 male and 10 female) *X. laevis* were collected from Kleinmond, and transported to and
155 housed at Stellenbosch University's Department of Botany and Zoology. Each frog was PIT tagged and
156 housed in its own aquarium at a constant temperature of 20° C (Careau et al. 2014; Herrel et al. 2012;

157 Louppe et al. 2017). Animals were fed every second day with sheep's heart, *ad libitum*, and weighed
158 once a week to monitor their well-being. Ethical clearance for performance measures was obtained
159 from Stellenbosch University (SU-ACUD14-00028).

160

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

167

168 All performance trials were conducted within three weeks of capture in a controlled environment with a
169 constant temperature of 20° C ($\pm 2^\circ$), as this is the optimal performance temperature for *X. laevis* (Miller
170 1982). All animals were rested for at least 24 hours between trials, with each animal undergoing three
171 trials where the longest distance in the shortest time was retained for analysis. Dry endurance was
172 determined on a 4 m circular track with a rubber grip mat as substrate. Each trial was timed, and the
173 distance moved was calculated from the number of laps with continuous movement insured by tapping
174 the frog between the hind legs. The trial was considered finished if the frog refused to move after
175 multiple taps, and was unable to right itself (Herrel & Bonneaud 2012).

176

177 *Data analysis*

178 In order to assess potential bias in capture rates in our dataset, we first compared sex ratios and sizes of
179 animals that were captured once (26.7%) with those that were captured more than once. A chi-squared
180 test (χ^2) showed that sex ratios were the same for animals that were captured once or more than once
181 ($\chi^2 = 0.012$, p-value = 0.9123), but an ANOVA shows that there was a significant difference in size ($F_{1,1750}$
182 = 5.327, $p = 0.0211$). Therefore to test for sex bias in dispersal, we use the entire dataset. But for size,
183 we use only those animals which were captured more than once. In each case, a χ^2 test was used in R (R
184 Core Team 2017) with a P-value based on 10 000 000 bootstraps.

185

186 Sex ratio was calculated as the number of males per 100 females per capture session. The distance
187 between the pond of origin (i.e. the pond where the frog was tagged) and the destination pond were
188 measured (to the closest meter) using ArcGIS (ESRI, 2014). As such, this represented the Euclidian

189 distances between sites. Dispersal distances were log transformed to meet assumptions of
190 homoscedasticity. Normality of data was determined by using QQ-plots and the homogeneity of the
191 variances were determined by using Levene's test. Occurrence of movements (where an animal was
192 tagged in one location, but recaptured in another) were coded according to whether or not they
193 occurred within one season (dry: December to May; wet: June to November), sex and the size of the
194 individual at first capture. The dataset for comparison was made up of individuals that were marked and
195 recaptured during the same period within one of the ponds.

196

197 The dispersal kernel was fitted using all dispersal distances (including instances where individuals moved
198 more than once). We used the `fitdistrplus` package (Delignette-Muller & Dutang 2015) in R v3.3.3 (R
199 Core Team 2017) to test the fit of the data against four distribution types: exponential, lognormal,
200 Weibull and gamma. We then inferred the best fit through minimum AIC. All means are reported \pm
201 Standard Error.

202

203 For the performance data, we logged all linear measurement data to fulfill assumptions of normality and
204 homoscedasticity. To test for differences between sexes, we conducted a MANCOVA (R Core Team
205 2017) with all morphological measurements as dependent variables, with size (SVL) as a covariate with
206 Wilk's Lambda statistic. Next, we conducted another MANCOVA using the (log of) maximum distance
207 moved and time to exhaustion as dependent variables, with size (SVL) as a covariate.

208

209 **Results**

210 *Capture-mark-recapture*

211 We made 9 401 captures of 1 755 individual *X. laevis* in 80 capture nights over 28 sessions in 3 years.
212 The mean number of animals captured per session was 354 (\pm 51.21: range 1 128 to 15), and the sex
213 ratio was always female biased, varying from 30 to 74 males per 100 females. Animals found to have
214 moved more than once were larger (SVL 65.20 \pm 0.41) than those not recaptured (SVL 61.46 \pm 0.66; $F_{1,1750}$
215 = 24.660; $P < 0.0001$), the discrepancy being made by smallest marked individuals (30-49 mm SVL) for
216 which sex could often not be determined ($n = 77$), and which did not move. Juveniles (<45 mm) made up
217 a significant part of some capture sessions, averaging 9.8% (\pm 1.3). We noted large numbers of
218 metamorphs at one of the sites (Ysterklip), but animals <30 mm SVL rarely entered our traps. The
219 majority of individuals was recaptured at least once ($n = 1 298$), with only 26% of individuals ($n = 457$)



220 **that were** captured only once. We found significant differences between the sizes of males (SVL mean
 221 63.34 mm \pm 0.355; max 93.0 mm; n = 673) and females (SVL mean 66.49 mm \pm 0.537; max 129.6 mm; n
 222 = 1005: $F_{1,1638} = 19.527$; $P < 0.0001$).

223 Ninety-one individuals (5.2%) moved between one and four times (mean 1.19 ± 0.060) over the entire
 224 period. Of the 11 animals that moved two or more times, five returned to their original site of capture.
 225 The modal overland distance moved was 147 m, with the frequency of small movements far exceeding
 226 long ones (Figure 2). A lognormal distribution fitted the highest dispersal values best as well as
 227 performing well on the mid-range values. However, all four distributions fitted the data well, differing by
 228 less than 60 δ AIC values (Table 1). Equation 1, gives the probability density function, where Y is the
 229 expected frequency of moving frogs, and x is the distance moved.

$$230 \quad Y = \frac{1}{0.62x\sqrt{2\pi}} e^{-\frac{(\ln x - 5.575)}{0.765}} \quad (1)$$

231 The nature of capture-recapture using our baited traps does not allow for the precise timing of the
 232 majority of movements that occurred between capture sites. Of the 69 individuals for which the season
 233 of movement was known because they were recorded at both the origin and destination sites in the
 234 same season, there was no difference between seasons in either the number of animals moving ($\chi^2 =$
 235 0.552, $p = 0.519$; dry = 57, wet = 48) or in the sex of animals moving ($\chi^2 = 0.552$, $p = 0.519$ **sex ratio =**
 236 39/18, wet sex ratio = 36/12). However, we did find that individuals moved significantly **further** during
 237 the wet period (mean = 245.4 m \pm 36.75; **median = 147.7 m**) than during the dry (142.1 m \pm 54.36;
 238 **median = 344.0 m**; $F_{1,101} = 6.833$, $p = 0.0103$). The maximum dispersal distance observed was a *X. laevis*
 239 female, which travelled 2.42 km in less than six weeks, while another *X. laevis* female dispersed 1.36 km
 240 in less than three weeks. Neither of these movements was downhill or appeared to follow any form of
 241 stream or movement of water overland. In addition, we have a record of a single male animal that was
 242 caught in one temporary water site on one night and in another 147 m away on the next night. We also
 243 found some synchronous movements. For example, in October 2015 we captured five animals in
 244 Arabella that were all captured two nights later 91 m away, and in February 2015 we captured six
 245 animals at Rondegat that were all captured two months later in another water-body 147 m away.

246 Many of the movements during the dry summer season happened between adjacent temporary sites
 247 (Figure 3a). However, during the wet winter season movements happened between temporary and
 248 permanent sites, as well as between temporary sites (Figure 3b). The timing of these movement events

249 was related to drying of temporary water sites in December 2014 and in October 2015, which also
250 coincided with drying events after very poor winter rains (Figure 4). These two events encompassed the
251 majority of movement events (58.6%), but we recorded movements during almost every capture session
252 (83%; Figure 4).

253 Even though we had twice the number of females ($n = 63$) moving as males ($n = 28$), this was not
254 significantly different to the sex ratio of animals that did not move (females 988; males 672; $\chi^2 = 3.668$,
255 $P = 0.0630$). Females moved no farther than males ($F_{1,101} = 0.002$, $p = 0.967$). No significant bias was
256 found in the size of animals that were moving compared to those that were recaptured only within the
257 same water-body ($F_{1,1282} = 3.565$, $p = 0.059$).

258 *Performance*

259 We found significant differences between the sizes of male and female *X. laevis* within the small subset
260 ($n = 20$) which we tested for performance ($F_{1,18} = 10.4$; $P = 0.0047$). In this subsample, the size-corrected
261 forelimb measures of males were significantly longer than those of females. However, the relative
262 length of the longest toe on the foot was longer in females (Table 2). We found a difference in the size-
263 corrected distance moved by the two sexes before exhaustion, with males moving significantly farther
264 (Table 2). Time to exhaustion, when both sex and corrected size were included, was significant (Table 2),
265 with smaller males moving for a longer time than larger females. The mean distance moved was 24.9 m
266 (± 0.79 m) in around 3 minutes (187 s ± 8.15 s).

267

268 **Discussion**

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

276

277 *Do Xenopus laevis migrate?*

278 Hey (1949) provided a description of *X. laevis* in Jonkershoek (45 km north-west of our study site)
279 involved in a migration from permanent impoundments into freshly filled vleis in order to breed. We
280 had expected that the combination of permanent and temporary water bodies in our study area would
281 allow us to collect data on such migration events over the three years of study, but we found none. Only
282 five animals were found to return to their original site of capture, but these movements were not
283 necessarily through permanent waters. Instead, we presume that animals that left the temporary water
284 went into subterranean aestivation (cf Balinsky et al. 1967), although efforts to find any *Xenopus*
285 through excavations in the area proved unsuccessful (Measey et al., January 2015 unpublished data).
286 Whether these animals hide collectively or are scattered throughout the area is potentially important.
287 Attempts at eradicating invasive populations may flounder if a proportion of buried animals goes
288 undetected. Like Measey (2016), we cannot discount the possibility that *X. laevis* do migrate between
289 water-bodies under particular circumstances, but we found no evidence of this in the Kleinmond
290 population. However, we did find examples of synchronous movements, both during the wet and dry
291 periods. Movements of large numbers of *X. laevis* have been witnessed (Lobos & Jaksic 2005; Measey
292 2016), but our data suggest that this may also happen on a smaller scale.

293

294 *Sexual or size difference in dispersal?*

295 Our study found no bias in sex of animals dispersing, once the highly skewed sex ratio was considered.
296 Other studies have found similar skews toward females (Lobos & Measey 2002). It could be that there is
297 dispersal bias toward smaller life-history stages (metamorphs and juveniles, see Sinsch 2014), although
298 we also found that the smallest animals we tagged did not move. If there were a male-biased dispersal
299 (as might be expected Hamilton & May 1977; Trochet et al. 2016), high mortality might help explain the
300 skewed sex ratio. Metamorph survival might be altered in densely populated water-bodies such as these
301 (see De Villiers et al. 2016) because adults are cannibalistic (Measey et al. 2015; Vogt et al. 2017).
302 Capture-mark-recapture studies on adult amphibians generally suggest no sex biased movement (e.g.
303 Sinsch 2014; Smith & Green 2006). In fact, examples of female-biased dispersal (Austin et al. 2003;
304 Lampert et al. 2003; Palo et al. 2004) and male biased dispersal (Liebgold et al. 2011) in amphibians have
305 been revealed using genetics, which suggest that juveniles (individuals that we cannot tag in most of
306 amphibian species) are responsible for most of dispersal events (inducing gene flow). Because more
307 females than males moved, a genetic study on our population would indicate female-biased dispersal.
308 However, this would not be due to a bias in dispersal of individuals, but simply reflect the already
309 skewed population sex ratio.

310

311 The fact that females were found to disperse provides important information for phylogeographic
312 studies using mitochondrial DNA (De Busschere et al. 2016; Furman et al. 2015; Measey & Channing
313 2003). African clawed frogs are known to form well defined mtDNA clades in southern Africa, and these
314 have been shown to correspond to sufficiently rapidly evolving nuclear DNA (Furman et al. 2015;
315 Furman et al. 2017). Presumably, these clades represent areas where both males and females are
316 equally inhibited from dispersing. The extent of dispersal in this study may exceed the first condition for
317 a metapopulation: that ponds sampled would represent local breeding populations (Hanski 1999). A 5%
318 movement of adults between ponds may effectively unite the study site into a single unit, or large patch,
319 with the possibility that a  population occurs at a larger spatial scale (Smith & Green 2005). Existing
320 genetic studies are too **course** to test the potential effective scale at which metapopulations exist within
321 *X. laevis*. More fine scale genetic sampling could inform the scale at which dispersal occurs as well as
322 what constitutes a dispersal barrier for this species.

323

324 In addition to the field data, we present a performance dataset that suggests that males and females are
325 equally able to move long distances. This required males to move proportionately farther and longer
326 than females before exhaustion. Distances moved in our laboratory study are around double those
327 reported by Louppe et al. (2017) for two invasive populations of *X. laevis* in France. Similarly, our
328 animals had higher stamina, being able to move for longer before exhaustion. The studies differed in the
329 temperature the trial was conducted (22° C in France and 20° C in South Africa). Despite these
330 differences, both studies found that males moved relatively farther for relatively longer such that they
331 were able to perform as well as larger females. The increased performance for males is not explained by
332 their limb morphology, as both studies show males have longer forelimbs (linked with mating), but that
333 hindlimbs are the same length, relative to size, with the exception of longer toes (larger feet) in females.
334 The time taken to move before exhaustion would make it easily possible for animals to move between
335 close sites in a single night, as we observed. However, the longest distances observed would likely have
336 taken many nights, and may have included periods in water-bodies between sites.

337

338 It is noteworthy that within our study site there were two temporary streams (Fig 2a); one not
339 associated with any water-bodies, and the other with three of the sites. While these three sites received
340 the most animals moving between them, this was largely confined to dry periods when the water did
341 not flow. This suggests that *X. laevis* are not reliant on watercourses to guide their movements.

342 However, when the weather is dry watercourses may offer increased levels of humidity that reduce
343 dehydration during overland movements. Dehydration remains an important risk for *X. laevis* moving
344 overland (Hillman 1978), as has been emphasised for other amphibians (Tingley et al. 2012).

345

346 *Seasonality and habitat drying*

347 Our data demonstrate that African clawed frogs move overland throughout the year, and that this
348 behaviour is not restricted to periods of winter rainfall. However, during the wet winter period
349 individuals moved farther. Both observations match the recent literature review (Measey 2016).
350 Additionally, movements between water-bodies peaked at the same time that the vleis were drying.
351 This suggests that the majority of animals move some distance in order to aestivate, and do not simply
352 burrow into the mud of a drying pond (although this has been observed, see Measey 2016).

353

354 *Conclusion*

355 We found that 5% of *X. laevis* moved between water-bodies within an area of 3 km², with examples of
356 animals moving nearly the full length of the study site. This suggests that frequency of movement within
357 the study site may exceed that required to maintain a metapopulation structure, and instead represent
358 a large patchy population (cf Smith & Green 2005), in what has previously been thought of as a purely
359 aquatic species (see Measey 2016). Although longer distances were moved overland during the wet
360 period, animals moved year round. More females moved than males, but this was in proportion with the
361 sex bias observed in the population. Males and females moved the same distances between sites, even
362 though males are significantly smaller; identical to results found in previous performance studies
363 (Louppe et al. 2017). Animals found in temporary water bodies did not move into permanent
364 impoundments, despite their presence in the area. We suggest instead that these animals are
365 aestivating underground at an unknown location. This is the first empirical data of overland movement
366 within the native range of *X. laevis*, and the largest mark-recapture study conducted on this species to
367 date.

368

369 **Acknowledgements**

370 We thank the Michael Lannoo and Audrey Trochet for their constructive reviews, and Donald Kramer for
371 extensive help improving readability of the manuscript. Julien Courant gave comments on previous
372 version of this manuscript. Atherton de Villiers and Andrew Turner (CapeNature) provided institutional
373 and guiding support throughout this project. Many members of the MeaseyLab helped with trapping

374 and the search for buried animals. We would like to extend our special thanks to the landowners and
375 tenants of the study area near Kleinmond.

376

377

378 Literature

- 379 Alford RA, Brown GP, Schwarzkopf L, Phillips BL, and Shine R. 2009. Comparisons through time and
380 space suggest rapid evolution of dispersal behaviour in an invasive species. *Wildlife Research*
381 36:23-28.
- 382 Altwegg R, Ringsby TH, and Sæther BE. 2000. Phenotypic correlates and consequences of dispersal in a
383 metapopulation of house sparrows *Passer domesticus*. *Journal of Animal Ecology* 69:762-770.
- 384 Amaral P, and Rebelo R. 2012. Diet of invasive clawed frog *Xenopus laevis* at Lage stream (Oeiras, W
385 Portugal). *The Herpetological Journal* 22:187-190.
- 386 Arnold SJ. 1983. Morphology, performance and fitness. *American Zoologist* 23:347-361.
- 387 Austin JD, Dávila JA, Lougheed SC, and Boag PT. 2003. Genetic evidence for female-biased dispersal in
388 the bullfrog, *Rana catesbeiana* (Ranidae). *Molecular Ecology* 12:3165-3172.
- 389 Balinsky J, Choritz E, Coe C, and van der Schans GS. 1967. Amino acid metabolism and urea synthesis in
390 naturally aestivating *Xenopus laevis*. *Comparative biochemistry and physiology* 22:59-68.
- 391 Bonte D, and Doherty M. 2017. Dispersal: a central and independent trait in life history. *Oikos* 126:472-
392 479.
- 393 Bowler DE, and Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating
394 individual behaviour to spatial dynamics. *Biological Reviews* 80:205-225.
- 395 Bowler DE, and Benton TG. 2009. Variation in dispersal mortality and dispersal propensity among
396 individuals: the effects of age, sex and resource availability. *Journal of Animal Ecology* 78:1234-
397 1241.
- 398 Careau V, Biro PA, Bonneaud C, Fokam EB, and Herrel A. 2014. Individual variation in thermal
399 performance curves: swimming burst speed and jumping endurance in wild-caught tropical
400 clawed frogs. *Oecologia* 175:471-480.
- 401 Clobert J, Galliard L, Cote J, Meylan S, and Massot M. 2009. Informed dispersal, heterogeneity in animal
402 dispersal syndromes and the dynamics of spatially structured populations. *Ecology letters*
403 12:197-209.
- 404 Courant J, Secondi J, Bereziat V, and Herrel A. 2017a. Resources allocated to reproduction decrease at
405 the range edge of an expanding population of an invasive amphibian. *Biological Journal of the*
406 *Linnean Society* 122:157-165. <https://doi.org/10.1093/biolinnean/blx048>
- 407 Courant J, Vogt S, Marques R, Measey J, Secondi J, Rebelo R, De Villiers A, Ihlow F, De Busschere C,
408 Backeljau T, Rödder D, and Herrel A. 2017b. Are invasive populations characterized by a broader
409 diet than native populations? *PeerJ* 5:e3250.
- 410 De Busschere C, Courant J, Herrel A, Rebelo R, Rödder D, Measey GJ, and Backeljau T. 2016. Unequal
411 contribution of native South African phylogeographic lineages to the invasion of the African
412 clawed frog, *Xenopus laevis*, in Europe. *PeerJ* 4:e1659.
- 413 De Moor IJ, and Bruton MN. 1988. *Atlas of alien and translocated indigenous aquatic animals in*
414 *southern Africa*: National Scientific Programmes Unit: CSIR.
- 415 De Villiers FA, de Kock M, and Measey GJ. 2016. Controlling the African clawed frog *Xenopus laevis* to
416 conserve the Cape platanna *Xenopus gilli* in South Africa. *Conservation Evidence* 13:17.
- 417 Delignette-Muller ML, and Dutang C. 2015. fitdistrplus: An R package for fitting distributions. *Journal of*
418 *Statistical Software* 64:1-34.

- 419 Doebeli M. 1995. Dispersal and dynamics. *Theoretical population biology* 47:82-106.
- 420 Donnelly M, Guyer C, Juterbock J, and Alford R. 1994. Techniques for marking amphibians. In: Heyer R,
421 Donnelly MA, Foster M, and McDiarmid R, eds. *Measuring and monitoring biological diversity:
422 Standard methods for amphibians*. Washington, D.C.: Smithsonian Institution Press, 277-284.
- 423 Fogell DJ, Tolley KA, and Measey GJ. 2013. Mind the gaps: investigating the cause of the current range
424 disjunction in the Cape Platanna, *Xenopus gilli* (Anura: Pipidae). *PeerJ* 1:e166.
- 425 Fouquet A, and Measey GJ. 2006. Plotting the course of an African clawed frog invasion in Western
426 France. *Animal Biology* 56:95-102.
- 427 Furman BL, Bewick AJ, Harrison TL, Greenbaum E, Gvoždík V, Kusamba C, and Evans BJ. 2015.
428 Pan-African phylogeography of a model organism, the African clawed frog '*Xenopus laevis*'.
429 *Molecular Ecology* 24:909-925.
- 430 Furman BL, Cauret CM, Colby GA, Measey GJ, and Evans BJ. 2017. Limited genomic consequences of
431 hybridization between two African clawed frogs, *Xenopus gilli* and *X. laevis* (Anura: Pipidae).
432 *Scientific Reports* 7:1091.
- 433 Gruber J, Brown G, Whiting MJ, and Shine R. 2017. Geographic divergence in dispersal-related behaviour
434 in cane toads from range-front versus range-core populations in Australia. *Behavioral Ecology
435 and Sociobiology* 71:38. <https://doi.org/10.1007/s00265-017-2266-8>
- 436 Guimaraes M, Corrêa DT, Sergio Filho S, Oliveira TA, Doherty PF, and Sawaya RJ. 2014. One step forward:
437 contrasting the effects of toe clipping and PIT tagging on frog survival and recapture probability.
438 *Ecology and evolution* 4:1480-1490.
- 439 Hamilton WD, and May RM. 1977. Dispersal in stable habitats. *Nature* 269:578-581.
- 440 Hanski I. 1999. *Metapopulation ecology*: Oxford University Press.
- 441 Herrel A, and Bonneaud C. 2012. Trade-offs between burst performance and maximal exertion capacity
442 in a wild amphibian, *Xenopus tropicalis*. *Journal of Experimental Biology* 215:3106-3111.
- 443 Herrel A, Gonwouo L, Fokam E, Ngundu W, and Bonneaud C. 2012. Intersexual differences in body shape
444 and locomotor performance in the aquatic frog, *Xenopus tropicalis*. *Journal of Zoology* 287:311-
445 316.
- 446 Herrel A, Vasilopoulou-Kampitsi M, and Bonneaud C. 2014. Jumping performance in the highly aquatic
447 frog, *Xenopus tropicalis*: sex-specific relationships between morphology and performance. *PeerJ*
448 2:e661.
- 449 Hertz PE, Huey RB, and Garland Jr T. 1988. Time budgets, thermoregulation, and maximal locomotor
450 performance: are reptiles olympians or boy scouts? *American Zoologist* 28:927-938.
- 451 Hey D. 1949. A report on the culture of the South African clawed frog *Xenopus laevis* (Daudin) at the
452 Jonkershoek inland fish hatchery. *Transactions of the Royal Society of South Africa* 32:45-54.
- 453 Hillman SS. 1978. Some effects of dehydration on internal distributions of water and solutes in *Xenopus
454 laevis*. *Comparative Biochemistry and Physiology Part A: Physiology* 61:303-307.
- 455 Holt RD. 1985. Population dynamics in two-patch environments: some anomalous consequences of an
456 optimal habitat distribution. *Theoretical population biology* 28:181-208.
- 457 Huey RB, and Stevenson R. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion
458 of approaches. *American Zoologist* 19:357-366.
- 459 Lampert KP, Rand AS, Mueller UG, and Ryan MJ. 2003. Fine-scale genetic pattern and evidence for
460 sex-biased dispersal in the túngara frog, *Physalaemus pustulosus*. *Molecular Ecology* 12:3325-
461 3334.
- 462 Leis JM, Wright KJ, and Johnson RN. 2007. Behaviour that influences dispersal and connectivity in the
463 small, young larvae of a reef fish. *Marine Biology* 153:103-117.
- 464 Liebgold EB, Brodie ED, and Cabe PR. 2011. Female philopatry and male-biased dispersal in a
465 direct-developing salamander, *Plethodon cinereus*. *Molecular Ecology* 20:249-257.

- 466 Lillo F, Faraone FP, and Valvo ML. 2011. Can the introduction of *Xenopus laevis* affect native amphibian
467 populations? Reduction of reproductive occurrence in presence of the invasive species.
468 *Biological Invasions* 13:1533-1541.
- 469 Llewelyn J, Phillips BL, Alford RA, Schwarzkopf L, and Shine R. 2010. Locomotor performance in an
470 invasive species: cane toads from the invasion front have greater endurance, but not speed,
471 compared to conspecifics from a long-colonised area. *Oecologia* 162:343-348.
- 472 Lobos G, and Jaksic FM. 2005. The ongoing invasion of African clawed frogs (*Xenopus laevis*) in Chile:
473 causes of concern. *Biodiversity and Conservation* 14:429-439.
- 474 Lobos G, and Measey GJ. 2002. Invasive populations of *Xenopus laevis* (Daudin) in Chile. *Herpetological*
475 *Journal* 12:163-168.
- 476 Louppe V, Courant J, and Herrel A. 2017. Differences in mobility at the range edge of an expanding
477 invasive population of *Xenopus laevis* in the west of France. *Journal of Experimental Biology*
478 220:278-283.
- 479 Matthysen E. 2005. Density-dependent dispersal in birds and mammals. *Ecography* 28:403-416.
- 480 Measey GJ. 2001. Growth and ageing of feral *Xenopus laevis* (Daudin) in South Wales, UK. *Journal of*
481 *Zoology* 254:547-555.
- 482 Measey GJ. 2004. Species account: *Xenopus laevis* (Daudin 1802). In: Minter LR, Burger M, Harrison JA,
483 Braack HH, and Bishop PJ, eds. *Atlas and Red Data Book of the Frogs of South Africa, Lesotho*
484 *and Swaziland*. Washington, D.C.: Smithsonian Institution Press, 266-267.
- 485 Measey GJ, and Channing A. 2003. Phylogeography of the genus *Xenopus* in southern Africa. *Amphibia-*
486 *Reptilia* 24:321-330.
- 487 Measey GJ, Vimercati G, De Villiers FA, Mokhatla MM, Davies SJ, Edwards S, and Altwegg R. 2015. Frog
488 eat frog: exploring variables influencing anurophagy. *PeerJ* 3:e1204.
- 489 Measey J. 2016. Overland movement in African clawed frogs (*Xenopus laevis*): a systematic review. *PeerJ*
490 4:e2474.
- 491 Measey J, Davies SJ, Vimercati G, Rebelo A, Schmidt W, and Turner A. 2017. Invasive amphibians in
492 southern Africa: A review of invasion pathways. *Bothalia-African Biodiversity & Conservation*
493 47:1-12.
- 494 Miller K. 1982. Effect of temperature on sprint performance in the frog *Xenopus laevis* and the
495 salamander *Necturus maculosus*. *Copeia* 1982:695-698.
- 496 Mucina L, and Rutherford M. 2006. *The vegetation of South Africa, Lesotho and Swaziland: Strelitzia* 19.
497 Pretoria: South African National Biodiversity Institute.
- 498 Nathan R, Klein E, Robledo-Arnuncio JJ, and Revilla E. 2012. Dispersal  review. In: Clobert J,
499 Baguette M, Benton TG, and Bullock JM, eds. *Dispersal Ecology and Evolution*. Oxford: Oxford
500 University Press, 187-210.
- 501 Palo J, Lesbarreres D, Schmeller D, Primmer C, and Merilä J. 2004. Microsatellite marker data suggest
502 sex-biased dispersal in the common frog *Rana temporaria*. *Molecular Ecology* 13:2865-2869.
- 503 Phillips BL, Brown GP, Webb JK, and Shine R. 2006. Invasion and the evolution of speed in toads. *Nature*
504 439:803-803.
- 505 R Core Team. 2017. R: a language and environment for statistical computing. Vienna: R Foundation for
506 Statistical Computing.
- 507 Rasband W. 2012. ImageJ. Bethesda, MD: US National Institutes of Health. Available on [http://rsb.info](http://rsb.info.nih.gov/ij)
508 [nih.gov/ij](http://rsb.info.nih.gov/ij).
- 509 Schneider C, Dover J, and Fry GL. 2003. Movement of two grassland butterflies in the same habitat
510 network: the role of adult resources and size of the study area. *Ecological Entomology* 28:219-
511 227.

- 512 Schoonbee H, Prinsloo J, and Nxiweni J. 1992. Observations on the feeding habits of larvae, juvenile and
513 adult stages of the African clawed frog, *Xenopus laevis*, in impoundments in Transkei. *Water SA*
514 18:227-227.
- 515 Sinsch U. 2014. Movement ecology of amphibians: from individual migratory behaviour to spatially
516 structured populations in heterogeneous landscapes. *Canadian Journal of Zoology* 92:491-502.
- 517 Smith MA, and Green DM. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and
518 conservation: are all amphibian populations metapopulations? *Ecography* 28:110-128.
- 519 Smith MA, and Green DM. 2006. Sex, isolation and fidelity: unbiased long-distance dispersal in a
520 terrestrial amphibian. *Ecography* 29:649-658.
- 521 Stevens VM, Pavoine S, and Baguette M. 2010. Variation within and between closely related species
522 uncovers high intra-specific variability in dispersal. *PLoS One* 5:e11123.
- 523 Tingley R, Greenlees M, and Shine R. 2012. Hydric balance and locomotor performance of an anuran
524 (*Rhinella marina*) invading the Australian arid zone. *Oikos* 121:1959-1965.
- 525 Travis JM, Mustin K, Benton TG, and Dytham C. 2009. Accelerating invasion rates result from the
526 evolution of density-dependent dispersal. *Journal of theoretical biology* 259:151-158.
- 527 Trochet A, Courtois EA, Stevens VM, Baguette M, Chaine A, Schmeller DS, and Clobert J. 2016. Evolution
528 of Sex-Biased Dispersal. *The Quarterly Review of Biology* 91:297-320. 10.1086/688097
- 529 Trueb L. 1996. Historical constraints and morphological novelties in the evolution of the skeletal system
530 of pipid frogs (Anura: Pipidae). In: Tinsley RC, and Kobel H-R, eds. *The biology of Xenopus*.
531 Oxford: Oxford University Press, 349-377.
- 532 Van Dijk D. 1977. Habitats and dispersal of southern African Anura. *African Zoology* 12:169-181.
- 533 Van Sittert L, and Measey GJ. 2016. Historical perspectives on global exports and research of African
534 clawed frogs (*Xenopus laevis*). *Transactions of the Royal Society of South Africa* 71:157-166.
- 535 Vimercati G, Hui C, Davies SJ, and Measey GJ. 2017. Integrating age structured and landscape resistance
536 models to disentangle invasion dynamics of a pond-breeding anuran. *Ecological Modelling*
537 356:104-116.
- 538 Vogt S, De Villiers FA, Ihlow F, Rödder D, and Measey J. 2017. Competition and feeding ecology in two
539 sympatric *Xenopus* species (Anura: Pipidae). *PeerJ* 5:e3130.
- 540 Weldon C, De Villiers AL, and Du Preez LH. 2007. Quantification of the trade in *Xenopus laevis* from
541 South Africa, with implications for biodiversity conservation. *African Journal of Herpetology*
542 56:77-83.
- 543 Zug GR. 1972. Anuran locomotion: structure and function. I. Preliminary observations on relation
544 between jumping and osteometrics of appendicular and postaxial skeleton. *Copeia* 1972:613-
545 624.
546
547

Table 1 (on next page)

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

Models are based on capture-mark-recapture data of 108 movements of 91 individuals over a 3 year period.

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

Distribution	Akaike's Information Criterion (AIC)	Δ 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

2

3

Table 2 (on next page)

Morphological variables measured for *Xenopus laevis* used in performance tests.

Results from a MANCOVA (with SVL as the covariate) show that sexes are morphologically different. Means (in mm \pm Standard Error) are given for measures of females (n = 10) and males (n = 10), together with tests which show that significant differences centred on limb measures. Distance (in m \pm SE) and Time (in s \pm SE) for stamina performance trials are also given. Stars (*) indicate statistical significance.

Effect	Variable	Wilk's Lambda	Mean females	±SE	Mean males	±SE	F	df	P	
Sex		0.035					17.52	11	0.0004	*
	Mass		38.46	6.49	25.6	4.04	0.23	1	0.6381	
	Ilium length		31.53	1.82	26.25	1.17	2.52	1	0.1306	
	Ilium width		14.41	0.71	13.12	0.61	1.63	1	0.2195	
	Femur		22.31	1.16	20.66	0.85	3.24	1	0.0898	
	Tibia		22.37	1.33	20.64	0.78	3.63	1	0.0738	
	Astragalus		15.95	1.09	14.55	0.75	3.45	1	0.0808	
	Longest toe		23.89	1.22	22.87	1.03	41.59	1	<0.0001	*
	Humerus		11.27	0.61	11.39	0.51	10.64	1	0.0046	*
	Radius		10.27	0.59	11.55	0.64	36.07	1	<0.0001	*
	Hand		4.26	0.24	4.08	0.23	17.1	1	0.0007	*
	Longest finger		10.32	0.56	10.02	0.51	4.97	1	0.0395	*
	Distance		23.23	0.47	26.63	1.33	10.4	1	0.0047	**
	Time		167.50	10.45	206.50	9.33	5.113	1	0.0182	*

1

Figure 1

Position of the study site

(a) Southern Africa, with black dots showing known locations of *Xenopus laevis*. (b) The site in the extreme southwest is 8 km East of Kleinmond (red star) borders the Botrivier Estuary to the South. The position of Jonkershoek (45 km north-west of the study site) is shown with a yellow star. Map shows local relief of Cape Fold Mountains (brown to yellow) and extensive lowland (gray) areas. (c) A simplified schematic of the site (34.325° S, 19.103° E) is approximately 3.5 km by 1.5 km with both permanent (dark blue) and temporary (light blue) water bodies.

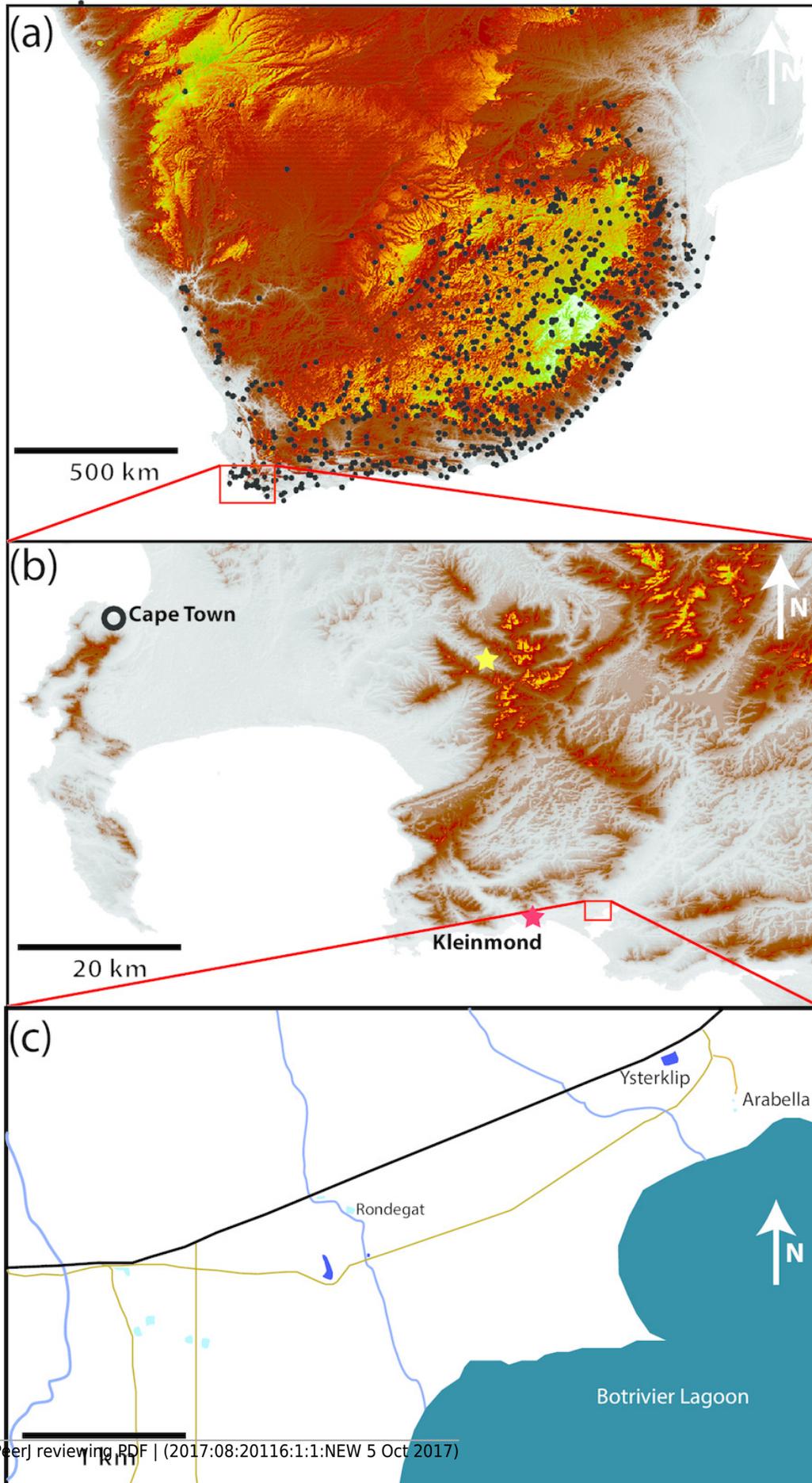


Figure 2

Schematic of movement by marked *Xenopus laevis* in (a) summer and (b) winter between water-bodies.

Thickness of red (a) and green (b) lines is proportionate to the amount of dispersal movements within that season. The site 5 km East of Kleinmond has natural temporary vleis (light blue) and anthropogenic impoundments (dark blue), and lies north of the brackish Botrivier Estuary. Paved (black line) and unpaved (brown lines) roads run through the area together with three temporary streams (blue lines).

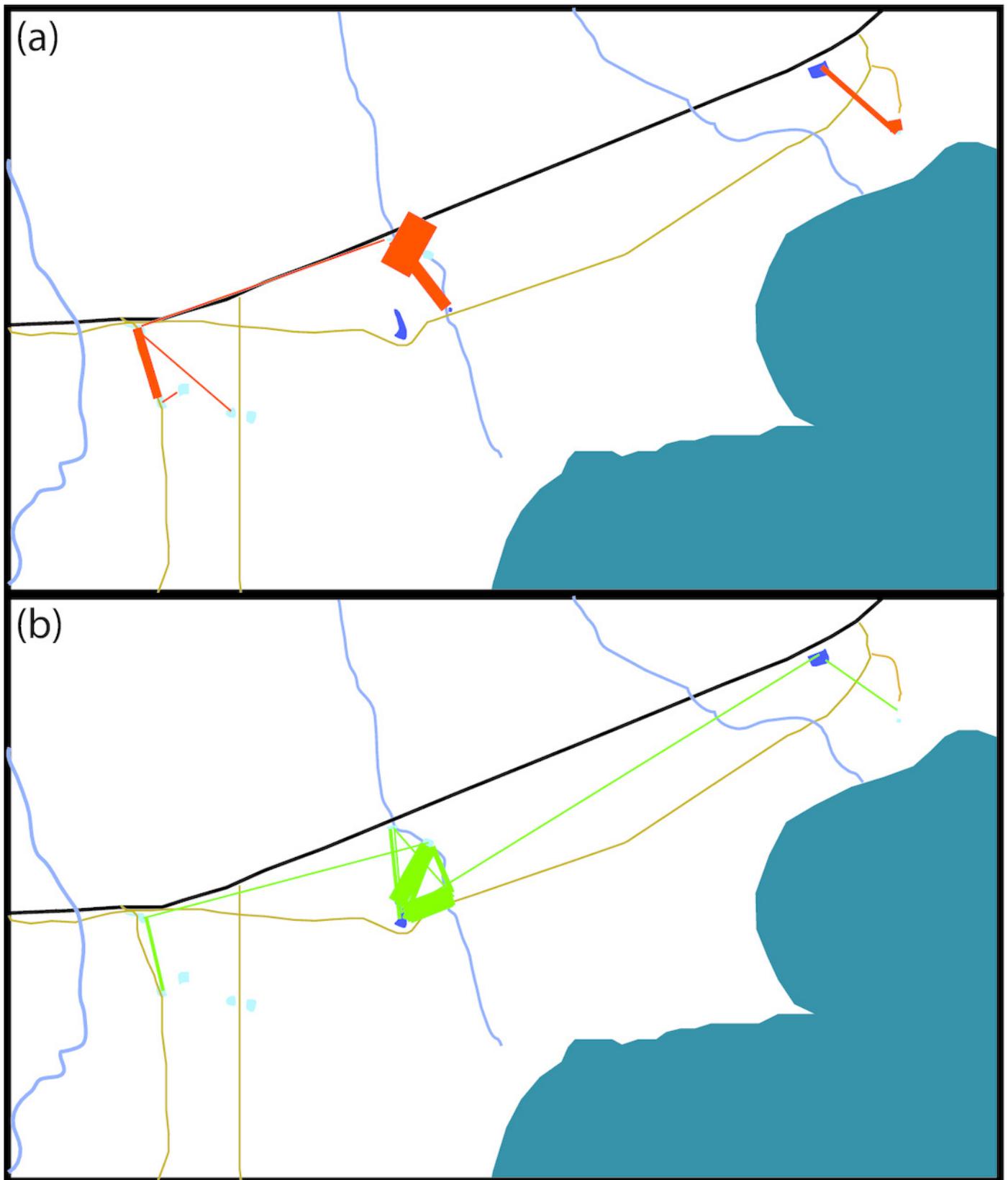


Figure 3

Dispersal kernel of *Xenopus laevis* at a site near Kleinmond, South Africa.

Bars show the frequency of distances moved between water-bodies by individuals during capture-mark-recapture based on 108 movements of 91 individuals over three years. The data is best described by a lognormal curve (red line), for which the probability density function is provided (Y is the expected frequency of moving frogs, and x is the distance moved).

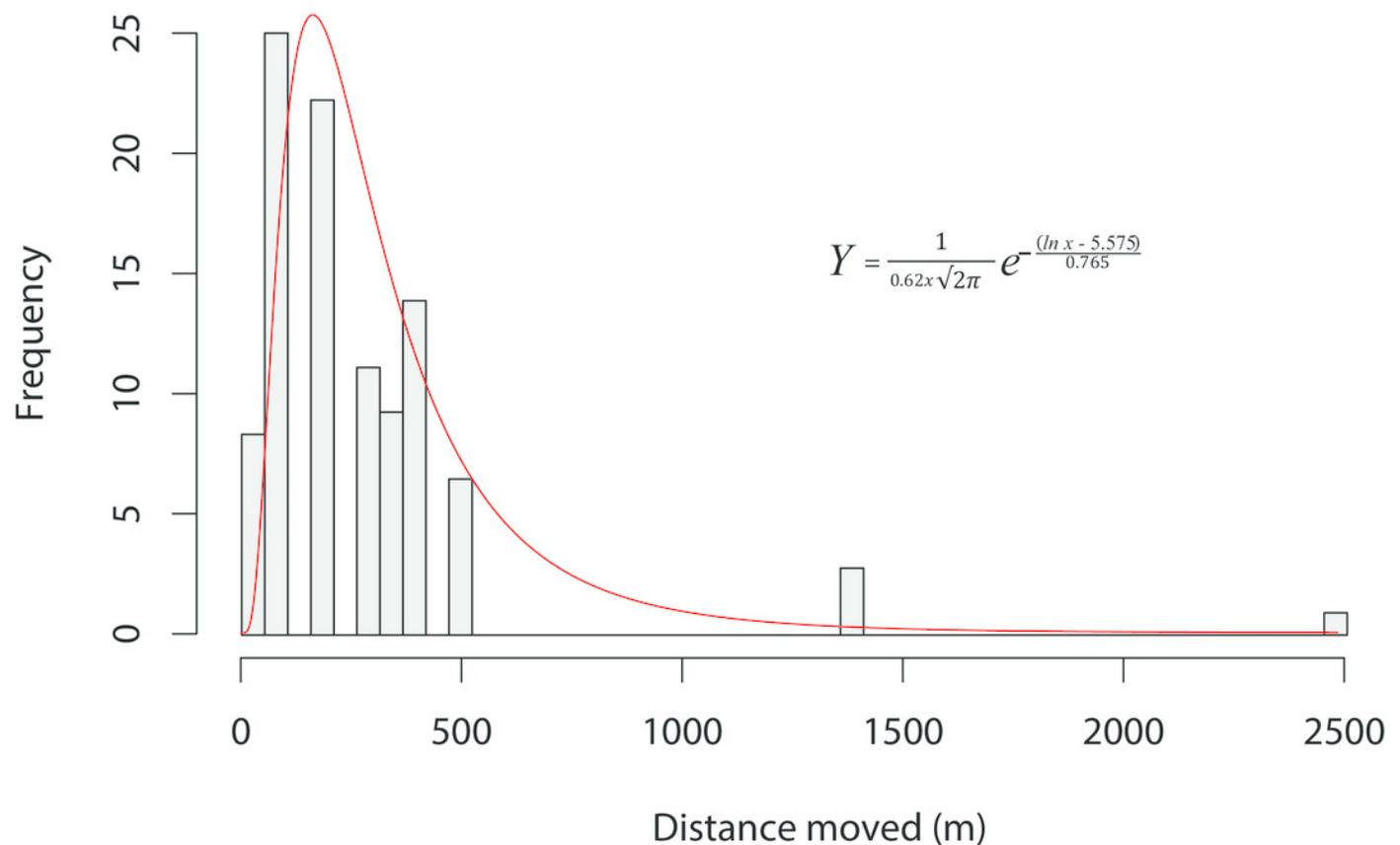


Figure 4

Numbers of *Xenopus laevis* caught per month 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 waterbodies in those years.

