

# The dispersal ability, performance and population dynamics of Cape *Xenopus* frogs

By  
Francois André de Villiers

Thesis presented in partial fulfilment of the requirements for the degree  
Master of Science in Zoology  
at Stellenbosch University



Supervisor: Dr G. John Measey

Faculty of Science

Department of Botany and Zoology

March 2016

## **Declaration**

By submitting this thesis/dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

March 2016

## **Abstract**

Dispersal is an important life history trait which is present in most organisms, and can affect the population structure, such as survival and age structure, of a species. An organism's dispersal ability is related to the individual's performance ability, which is ultimately determined by the individual's morphology. Amphibians have been classically viewed as poor dispersers, but studies have shown that there are some exceptions. However, these studies represent terrestrial frog species and lack aquatic frog species. Frogs in the genus *Xenopus* are principally aquatic, and have been known to make use of water corridors for dispersal, however overland dispersal has been observed. There are two *Xenopus* present in the south Western Cape; *X. gilli* and *X. laevis*. In this study I compare and determine the dispersal ability, performance and morphology of *X. gilli* and *X. laevis*. I hypothesize that *X. laevis* will outperform *X. gilli* in both dispersal and relative performance. Two sites were used in this study; an area east of Kleinmond and the Cape of Good Hope section of TMNP (CoGH). In Kleinmond both *X. laevis* and *X. gilli* were marked with PIT tags, whereas only *X. gilli* was tagged in CoGH. Jumping and swimming performance was obtained by filming the frogs at 240fps, and wet and dry endurance was measured in a 4m track. Dispersal distances between two ponds were represented by Euclidean distances based on recapture of individually marked animals. The results show that *X. laevis* was the better jumper and swimmer of the two species. All performance trials that included jumping were found to be related to the leg morphology of the two *Xenopus* species. There was no difference in the dispersal distance of the two species, which was mirrored by the lack of difference in dry endurance; however *Xenopus laevis* had the highest proportion of individuals dispersing. Population structure is an important tool to determine the state of a given population. In a species that experiences high juvenile predation it is expected that the age structure would be skewed towards the older individuals and that the juveniles will have a low survival rate.

*Xenopus laevis* poses a threat to *X. gilli* through predation, competition and hybridization. I compared the survival and age structure of *X. laevis* and the two *X. gilli* populations. I hypothesized that *X. laevis* will have a negative effect on the survival and age structure of *X. gilli*. Recaptures at Kleinmond and CoGH recurred between three to six weeks. The second phalange of the outer toe of 20 males and 20 females of *X. laevis* and *X. gilli* at both sites were sectioned. The number of lines of arrested growth (LAG) were recorded as a proxy for age. All frogs that were recaptured in 2015 were photographed again and growth was determined. The results indicate that Kleinmond *X. gilli* had the lowest survival (0.319), which was accredited to competition and predation by *X. laevis*, whereas CoGH *X. gilli* had the highest survival (0.562). Age structure was not determined possibly due to the presence of artificial water-bodies and consequently the lack of LAG production in some individuals.

## Opsomming

Verspreiding is 'n belangrike lewensgeskiedenis eienskap wat teenwoordig is in meeste organismes. Prestasie vermoë is verwant aan die individuele verspreiding vermoë, wat uiteindelik geaffecteer word deur die morfologie van die individu. Amfibieë word oor die algemeen as swak verspreiers beskou, maar studies het getoon dat daar 'n paar uitsonderings is. Verspreiding vermoë word oor die algemeen gebestudeer in terrestriële paddas en nie akwatiese paddas nie. Paddas van die genus *Xenopus* is hoofsaaklik akwaties en maak meestal van waterverspreiding gebruik, alhoewel oorland verspreiding waargeneem is. Daar's twee *Xenopus* teenwoordig in die suid Wes-Kaap; *X. gilli* en *X. laevis*. In hierdie studie vergelyk en bepaal ek die verspreiding, prestasie vermoë en morfologie van *X. gilli* en *X. laevis*. Twee areas word in hierdie studie gebruik; Kleinmond en die Kaap van Goeie Hoop deel van TMNP (CvGH). In Kleinmond was beide *X. laevis* en *X. gilli* ingeënt met 'n PIT merker, terwyl slegs *X. gilli* gemerk was in CvGH. Spring en swem prestasie is verkry die paddas teen 240fps af te neem en beide nat en droë uithouvermoë is gemeet deur die paddas rondom 'n 4m te jaag baan. Verspreiding afstande tussen twee damme is verteenwoordig deur Euklidiese afstande. Die resultate toon dat *X. laevis* die beter springer en swemmer van die twee spesies was. Alle prestasie eienskappe wat spring ingesluit het, was verwant aan die been morfologie. Daar was geen verskil in die verspreiding vermoë tussen die twee spesies nie, wat aan die gebrek in verskil in droë uithouvermoë geakkrediteer word. *Xenopus laevis* het die hoogste persentasie van individue wat versprei het gehad.

Die oorlewing en ouderdom struktuur is belangrike fasette om bevolking struktuur te verstaan. Hier word twee hipotetiese bevolkings aangebied; een gesonde bevolking en een met 'n bevolking met eensydige predasie druk. In die tweede bevolking sal die oorlewing van jeugdige verwagting laag wees en die ouderdom struktuur sal na verwagting swyk na volwassenes. *Xenopus laevis* hou 'n bedreiging in vir *X. gilli* deur predasie, kompetisie en

verbastering. Ek vergelyk die oorlewing en ouderdom struktuur van *X. laevis* en die twee *X. gilli* bevolkings. Die paddas was in Kleinmond en CvGH elke drie tot ses weke gevang en hervangs was in binêr aangeteken. Die tweede kootje van die buitenste toon van 20 maanetjies en 20 wyfies van *X. laevis* en *X. gilli* in beide areas was gesny. Die aantal lyne van stuitgroei (LVS) is aangeteken as 'n aanduiding van die ouderdom. Al die paddas wat in 2015 gevang is was weer afgeneem en groei is bepaal. Die resultate dui daarop dat Kleinmond *X. gilli* die laagste oorlewing (0.319) het, wat aan die kompetisie en predasie deur *X. laevis* geakkrediteer. Die ses maandelikse oorlewings skatting van *X. laevis* was 0.381. Ouderdom struktuur kon nie vasgestel word as gevolg van die teenwoordigheid van 'n kunsmatige waterliggame en gevolglik is die gebrek aan LVS produksie.

## **Acknowledgements**

I would like to thank the Centre for Invasion Biology (CIB), INVAXEN and the NRF for funding. I would also like to thank my supervisor for his help and patience with me over the course of this project. I would also like to thank the Measey lab, Res Altwegg, Marisa de Kock, Mike McCoy and Solveig Vogt for their assistance with this project. A special word of thanks goes to my wife Nikita de Villiers who stood by me since my undergraduate degree and also my family who supported me since I started studying. I would also like to thank the owners of the two farms in Kleinmond as well as SANParks who allowed me to conduct research in one of their property. Lastly I would like to thank the University of Stellenbosch for allowing me the opportunity to complete my masters.

## **Table of Contents**

Declaration.....	i
Abstract .....	ii
Opsomming .....	iv
Acknowledgements .....	vii
List of Figures .....	x
List of Tables.....	xii
<b>Chapter 1: The morphology, performance and dispersal ability of Cape <i>Xenopus</i> .....</b>	<b>1</b>
1.1 Introduction .....	1
1.2 Materials and Methods .....	6
1.2.1 Sampling sites .....	6
1.2.2 Morphology.....	8
1.2.3 Performance .....	9
1.2.4 Performance ~ morphology correlations .....	12
1.2.5 Dispersal .....	13
1.3 Results.....	15
1.3.1 Morphology .....	15
1.3.2 Performance .....	19
1.3.3 Performance ~ morphology correlations .....	24
1.3.4 Dispersal .....	28
1.4 Discussion .....	31



<b>Chapter 2: The Survival, age structure and the growth of Cape <i>Xenopus</i></b> .....	37
2.1 Introduction .....	37
2.2 Materials and Methods .....	43
2.2.1 Sampling sites .....	43
2.2.2 Age structure .....	43
2.2.3 Growth .....	44
2.2.4 Survival .....	45
2.3 Results.....	47
2.3.1 Age structure.....	47
2.3.2 Growth .....	49
2.3.3 Survival.....	52
2.5 Discussion.....	56
Literature Cited.....	62
Addendum A.....	79
De Villiers, F. A., De Kock, M. & Measey, G. J. (2016). Controlling the African clawed frog <i>Xenopus laevis</i> to conserve the Cape platanna <i>Xenopus gilli</i> in South Africa. <i>Conservation Evidence</i> , <b>12</b> . .....	76

## List of Figures

Figure 1.1: The sites and species that were used in this study.....	7
Figure 1.2: The measurements that were used to determine $\alpha$ .....	11
Figure 1.3: The body size differences of the <i>X. laevis</i> and two <i>X. gilli</i> populations. ....	15
Figure 1.4: The log transformed relative mass of the frogs that were used in the performance trails.....	18
Figure 1.5: The jumping performance of <i>X. laevis</i> and two <i>X. gilli</i> populations.....	20
Figure 1.6: The swimming speed of <i>X. laevis</i> and the two populations of <i>X. gilli</i> .....	21
Figure 1.7: The endurance distances of <i>X. laevis</i> and two <i>X. gilli</i> populations. ....	22
Figure 1.8: The log transformed dispersal distances of <i>X. laevis</i> and the two <i>X. gilli</i> populations.....	29
Figure 1.9: The dispersal frequency of the <i>X. laevis</i> and <i>X. gilli</i> . The black bars represent <i>X. laevis</i> and the clear bars represent <i>X. gilli</i> .....	30
Figure 1.10: The dispersal kernel of A) <i>X. laevis</i> and B) <i>X. gilli</i> .....	30
Figure 2.1: The age structure of two hypothetical populations .....	39
Figure 2.2: Indicating the groups that were used for the survival analyses that were based on the mean sizes of <i>X. gilli</i> and <i>X. laevis</i> .....	47
Figure 2.3: The age of <i>Xenopus</i> frogs as a function of the size of the animal.....	49
Figure 2.4: The daily growth of <i>X. laevis</i> and the two <i>X. gilli</i> populations.....	51

Figure 2.5: The summer and winter survival estimates of *X. laevis* and two *X. gilli* populations.....55

Figure 2.6: Pictures of the same *X. laevis* at two different time periods, indicating the loss in body mass that resulted from a harsh summer season .....59

Figure 2.7: A partly digested adult *X. gilli* that was regurgitated by a *X. laevis* .....61

## **List of Tables**

Table 1.1: The size corrected morphological characters of <i>X. laevis</i> and the two <i>X. gilli</i> populations that show sexual differences. ....	17
Table 1.2: The size corrected morphological characters of <i>X. laevis</i> and the two <i>X. gilli</i> populations that show no sexual differences .....	19
Table 1.3: The raw data from the performance trail for both <i>X. gilli</i> populations and <i>X. laevis</i> .....	23
Table 1.3: Model selection for the morphological characters that explain performance traits of <i>X. laevis</i> and <i>X. gilli</i> . ....	24
Table 2.1: Model selection for <i>X. laevis</i> and the two <i>X. gilli</i> populations .....	53

## **Chapter 1:**

### **The morphology, performance and dispersal ability of Cape**

#### **Xenopus**

##### **1.1 Introduction**

The ability to disperse is present in most organisms (Clobert *et al.*, 2009) and is one of the most important characteristics of an organism (Wilson *et al.*, 2009). Dispersal entails the movement of individuals from one habitat patch to another (Clobert *et al.*, 2009). As such, dispersal not only affects individual traits, but also population characteristics, such as community structure (Holt, 1985; Johnson & Gaines, 1990; Hanski & Gyllenberg, 1993; Goldwasser *et al.*, 1994; Doebeli, 1995; Dunning *et al.*, 1995). Dispersal is not a static event but as several studies suggest, differs between, as well as, within species (Altwegg *et al.*, 2000; Schneider *et al.*, 2003; Mennechez *et al.*, 2004; Bowler & Benton, 2009; Clobert *et al.*, 2009; 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, 2005; Clobert *et al.*, 2009). For example, Massot *et al.* (2002) have shown that juvenile *Zootoca vivipara* (common lizard) that were released in a dry environment would have a higher percentage of dispersers compared to those released in a colder habitat. A review by Matthysen (2005) has shown that birds and mammals had a positive relationship between dispersal and population density. South and Kenward (2001) have shown that mate finding could have a negative effect on the dispersal ability of invasive species, as species with low dispersal and high mate finding showed positive population growth.

The typical view of an invasive species is an alien species that invades a foreign geopolitical range, through human mediated means (Bean, 2007), however a species from the same geopolitical area can also become invasive within that geopolitical range (better known as extra-limital or domestic exotic; Spear & Chown, 2009). This is the case when a species undergoes a range expansion which is assisted, either directly or indirectly, by humans (Pyšek *et al.*, 2004). For example, Davies *et al.* (2013) have shown that *Hyperolius marmoratus* made use of farm dams to facilitate a range expansion from its natural range in Eastern Cape towards the Western Cape, in South Africa. Dispersal from the introduction point, or in the case of extra-limital species, dispersal from the native range into the extra-limital range, is an essential step for a species to be considered invasive (Wilson *et al.*, 2009; Blackburn *et al.*, 2011). As such it is important to understand the dispersal ability of the species in question, as this will provide valuable information with regards to further invasion and the control of the species (see Blackburn *et al.*, 2011). Also, understanding the dispersal ability of an invasive species in its natural habitat provides valuable information about its potential range expansion ability. Dispersal is generally expressed in the form of a dispersal kernel (Nathan, 2006): displaying the different distances that different individuals have dispersed (see Robledo-Arnuncio & Garcia, 2007). The individuality of the dispersal kernel is similar to that of performance ability, as performance ability refers to a single individual.

Dispersal ability is ultimately related to the animal's individual performance ability, which in turn is related to the morphology of that animal (Stevens *et al.*, 2010). Performance ability represents the animal's maximum performance ability whereas dispersal ability represents the animal's observed dispersal ability (Garland & Losos, 1994). As such, performance ability can be a good indicator as to the dispersal ability of the 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. It has also been shown that

the male cabbage butterflies (*Pieris brassicae*) have higher flight endurance in order to reach more disconnected habitat patches (Ducatez *et al.*, 2012). Morphology ultimately determines the performance ability of the animal and consequently the animal's dispersal ability (Zug, 1972; Arnold & Bennett, 1984; Hertz *et al.*, 1998). For example, O'Riain *et al.* (1996) have shown that the naked mole-rat has a distinctive dispersal morph, which differs in respect to morphology as well as locomotion. In another case it has been shown, through a combination of studies, that Cane toad (*Rhinella marina*) populations, in 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).

Amphibians in general have been classified as poor dispersers (Awise, 2000), due to their physiology and their tendency to have high site fidelity (Duellman & Trueb, 1986; Blaustein *et al.*, 1994). However, it has been shown that this is not the case for all amphibians (Smith & Green, 2005). Smith & Green (2005) have shown that 44% of the anurans, which they reviewed in their study, had a maximum dispersal distance greater than one kilometer. However this review only reports on individual frogs that have moved the maximum distance. If the mean dispersal distances or a dispersal kernel were to be reported in this study a different result is to be expected. What is also lacking in this study is the dispersal ability of aquatic anurans.

The genus *Xenopus* occurs throughout sub-Saharan Africa, occupying almost every aquatic habitat found within this range (Tinsley & Kobel, 1996). The frogs in this genus are highly adapted for an aquatic lifestyle (Trueb, 1996), as most of their life is spent in the water (Tinsley *et al.*, 1996). Water corridors (i.e. rivers, streams, irrigation system, etc.) are readily used by these frogs to migrate to other habitats that are connected via these corridors (Tinsley *et al.*, 1996; Lobos & Measey, 2002; Measey, 2004a). This has led to the classical view that these frogs are fully aquatic (e.g. Elepfandt *et al.*, 2000), however this view has been

challenged by several observations of overland migrations (see Loveridge, 1953; Kalk, 1960; Passmore & Carrunthers, 1979; Picker, 1985; Schramm, 1987; Measey & Tinsley, 1998; Lobos & Measey, 2002a; Lobos & Measey, 2002b; Measey, 2004; Eggert, & Fouquet, 2006; Fouquet & Measey, 2006; Faraone *et al.*, 2008), which suggest that these frogs are capable of dispersing overland, and that they might better be termed “principally aquatic” rather than “fully aquatic”. When it comes to the dispersal ability of *Xenopus* species, not much is known about what proportion of the population does disperse, what time of year they disperse, and the function of the dispersal kernel.

There are two *Xenopus* species present in the south-western Cape (Kobel *et al.*, 1981; Picker & De Villiers, 1989; Minter *et al.*, 2004): *Xenopus gilli*, a small (SVL<70mm) restricted endemic (De Villiers, 2004; Fogel *et al.*, 2013; Figure 1D), which is listed by the IUCN as Endangered (SA-FRoG & IUCN 2015), and *X. laevis*, a larger (SVL<130mm) widespread southern African species which is also invasive on four continents (see Measey *et al.*, 2012).

*Xenopus laevis* occurs in sympatry throughout the range of *X. gilli* (Picker & De Villiers, 1989). Poynton is of the opinion that *X. laevis* made use of artificial water-bodies to expand their range and become an extra-limital species (see De Moor & Bruton, 1988). *Xenopus laevis* is known to readily occupy and breed in artificial water-bodies, i.e. farm dams (Van Dijk, 1977; Schoonbee *et al.*, 1992; Tinsley *et al.*, 1996), whereas *Xenopus gilli* naturally occupy temporary water-bodies (De Villiers, 2004), which fill up during the winter rainfall. Through overland dispersal *X. laevis* would be able to occupy the same temporary water-bodies that contain *X. gilli*. When *X. gilli* and *X. laevis* occupy the same water-body, *X. laevis* poses a threat to *X. gilli* through predation (see De Villiers, 2004; Vogt *et al.*, Unpublished data), competition (Vogt *et al.*, Unpublished data) and hybridization (Kobel *et al.*, 1981; Picker, 1985; Picker & De Villiers, 1989; Evans *et al.*, 1998)



In this study I make use of capture-mark-recapture data to determine the dispersal ability of *Xenopus gilli* and *X. laevis*. I also determine the performance ability of these two species through laboratory based performance trails, which are used to further assess any difference in dispersal ability. Individual performance ability is compared to morphological measures of each individual and used to determine which morphological character is associated with which performance trait. I aim to determine and compare the dispersal and relative performance ability of the Endangered Cape platanna (*Xenopus gilli*) and the widespread common platanna (*X. laevis*) to give insight into the conservation of *X. gilli* as well as to the invasion potential of *X. laevis*. The hypothesis for this study was that *Xenopus laevis* will outperform *X. gilli* in both dispersal and relative performance.

## 1.2 Methods and materials

### 1.2.1 Sampling sites

Two of the remaining four sites, which currently contain *Xenopus gilli* populations, were used in this study: Cape of Good Hope section of TMNP (CoGH) and Kleinmond (see Fogell, 2012; Figure 1.1 C). In both these sites there are permanent and temporary water-bodies. All permanent water-bodies are artificial and have water in them year round. The temporary water-bodies are natural and only fill during the austral winter rains (April – September). These temporary water-bodies are situated within a wetland and are the natural habitat for *X. gilli* (De Villiers, 2004). In CoGH I sampled three permanent and four temporary ponds (Figure 1.1D). In Kleinmond I sampled eight ponds, three of which are permanent and five temporary (Figure 1.1E).



Figure 1.1: The sites and species that were used in this study. The frogs that were used in study; A) *Xenopus gilli* and B) *X. laevis*. C) The red squares indicate the sites used for this study, Kleinmond and the Cape of Good Hope section of Table Mountain National Park (CoGH). The ponds that were used in E) CoGH and in D) Kleinmond. PP indicates permanent ponds and TP indicates temporary ponds.

Frogs were collected from sites using either seining or trapping (Kobel *et al.*, 1981; Picker & De Villiers, 1989; Evans *et al.*, 1998; Measey 2001; Lobos & Measey, 2002). Seining

entailed dragging a 10m purse seine net through the water, from the middle of the dam to the edge, collecting all frogs that were trapped in the net. This was done annually, in association with South African National Parks (SANParks), as part of an effort to conserve *X. gilli* by removing *X. laevis* (De Villiers *et al.*, 2016). During this exercise all *X. laevis* captured were removed and euthanized by SANParks. Seining was done only in CoGH. Traps used were either baited bucket traps or fyke net traps (see Measey 2001; Lobos & Measey, 2002). The traps were set each evening and collected again the following morning for three consecutive days. This was done at both Kleinmond and CoGH. Ethical clearance was obtained from Stellenbosch University (SU-ACUD14-00028). The relevant field work and collection permits were obtain from the South African National Parks and from CapeNature (AAA007-00092-0056).

### **1.2.2 Morphology**

*Xenopus gilli* were collected from each site, 20 (10 males and 10 female) from Kleinmond and 20 from CoGH, and 20 (10 males & 10 females) *X. laevis* were collected from Kleinmond. Each frog was housed separately in its own aquarium at a constant temperature of 20° C (Herrel *et al.*, 2012; Careau *et al.*, 2014). Animals were fed every second day with sheep's heart, *ad libitum*, and they were weighed once a week to monitor the well-being of the frogs (Herrel *et al.*, 2012; Careau *et al.*, 2014).

Prior to performance trials each animal was measured using digital callipers. Measurements that were taken are 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). For toe length, the length of the longest toe was taken. SVL was quantified as the length from the tip of the snout to the cloacae (Herrel *et*

*al.*, 2012). Each measurement was log transformed and plotted against the log transformed snout-vent-length of the same individual. Size correction was then made by the following equation:  $\frac{\text{Measurement}}{\text{SVL}^{\text{slope of the log transformed graph}}}$ . The SVL of all frogs, that were tagged, was obtained from scaled dorsal images that were measured using Image J (Rasbrand, 2012). The SVL of these frogs were compared using a MANOVA (R Studio. 3.2; R Core team, 2015). Measurements that showed differences between sexes were compared using a MANCOVA and measurements that showed no sexual differences were compared using an ANCOVA (R Studio. 3.2; R Core team, 2015).

### 1.2.3 Performance

All performance trials were conducted in a controlled environment with a constant temperature of 20° C ( $\pm 2^\circ$  C), as this is the optimal performance temperature for the genus *Xenopus* (Miller, 1982). All animals were rested for at least 1 day between trials. The performance trails were conducted within three weeks of the capture of the frogs.

Two types of endurance were determined; dry endurance and wet endurance. 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 (Huey *et al.*, 1990; Herrel & Bonneaud, 2012). Wet endurance was determined in the same 4m circular tank which was filled with water. The water depth was 10cm and left until the water reached 20° C. The same procedure as in the dry endurance was used to determine the end of the endurance trial for each animal. Swim endurance was log transformed to meet assumptions of homoscedascity.

For both swimming speed and jumping the frog was filmed in a straight Perspex tank (2 100 × 400 mm). A mirror was placed at 45° angle above the tank to also capture the top-down view. Swimming speed was determined by chasing the frog down the Perspex tank while videoing the frog at 240 fps. The top-down view was used for the analysis as the frogs do not swim in a straight line and the x and y displacement needed to be recorded to get the actual distance moved. The section in which the animal travelled for the longest without touching the side of the tank was used in the analysis. The program Blender (Blender foundation, 1994) was used to track the animal as it swam and the x and y coordinates was recorded. The distance, in pixels, was then calculated using Pythagoras's law of triangles with a right angle, by using the x-axes and y-axes displacements as the straight sides of the triangle. The diagonal pixel distance was converted to millimetres by using lines that were drawn on the tank (250 mm apart) for calibration and the distance that was the frog moved were expressed to the nearest 0.1mm. The time the frog spent moving was determined by calculating the number of frames the frog swam (i.e. the last chosen frame minus the first chosen frame) and dividing it with the recording speed (240 fps). The average swimming speed were then expressed as  $\text{m}\cdot\text{s}^{-1}$  by dividing the distance travelled (in meter) by the time spent moving (in seconds).

For jumping performance the animal was placed on cork mats to allow for sufficient grip. Jumping was initiated by tapping the frog on its back between the legs. Each video consisted of three or four trials. The section of the video in which the frog jumped the furthest was used for the analysis. The top-down view was also used to determine the jumping distance. Jumping distance was determined in the same manner as swimming distance was determined. Jumping distance showed size dependence and was size corrected. As a result jumping distance was expressed as relative distance in mm, to the nearest 0.1mm. The frontal view of the tank was used for determining jumping height. The same jump that was used to determine

distance was also used for height. Using the program Blender (Blender foundation, 1994), the animal was tracked as it was jumping. The height in pixels was then determined by subtracting the highest y-coordinate from the lowest y-coordinate. This was then calibrated with the use of the lines on the tank and expressed in mm.

Jumping force was determined by rearranging the following equation

$$d = \left( W \times \frac{L}{m_b} \right)^{\frac{2}{3}} \times \frac{\sin 2\alpha}{g} \quad (\text{James } et \text{ al.}, 2007), \text{ so that jumping force was the subject of the}$$

$$\text{equation: } W = \frac{\left( \frac{d}{\frac{\sin 2\alpha}{g}} \right)^{\frac{3}{2}}}{\frac{L}{m_b}} \quad W \text{ represents the average force used for jumping, } d \text{ is the distance}$$

jumped,  $\alpha$  the angle at which the frog jumped,  $g$  the gravitational acceleration,  $L$  is the distance from the frogs centre of mass to the end of its toe, and  $m_b$  is the mass of the frog.

The angle at which the frog jumped ( $\alpha$ ) was determined with the use of the tangent?

$\frac{\text{Height}}{\text{Jump distance}/2}$  (see figure 1.2).  $L$  was determined by adding ilium, femur, tibia, foot and toe

length together (A. Herrel pers. comm.). Frogs were weighed once a week whilst in captivity with a Radwag WTB 2000 scale to the nearest 0.01g The mass closest to the jumping trail was used in the equation.

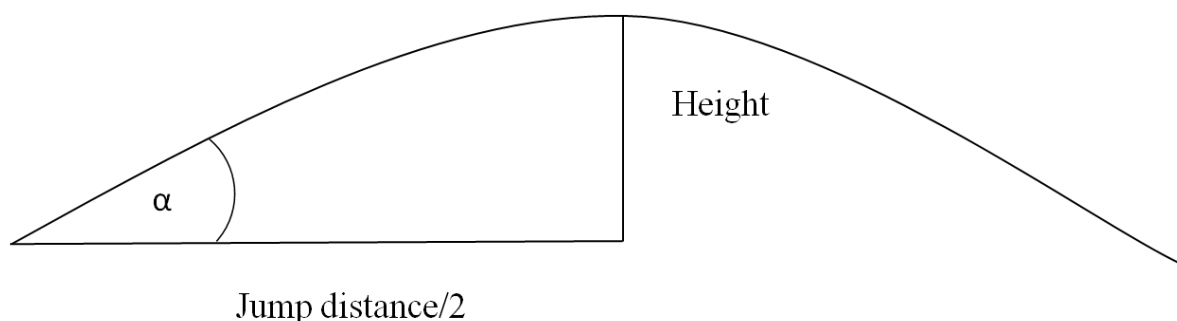


Figure 1.2: The measurements that were used to determine  $\alpha$ . The curve indicates the jumping trajectory of the frog.



Normality of data was determined by using pp-plots (i.e. the theoretical normal distribution of the data against the observed distribution of the data) and the homogeneity of the variances were determined by using a Levene's test. The data was analysed using an ANCOVA (R Studio. 3.2; R Core team, 2015). As male *Xenopus tropicalis* have a higher exertion capacity compared to females (Herrel *et al.*, 2012), it was assumed that this may hold for other *Xenopus* frogs, thus, I used sex as a factor. *Xenopus gilli* and *X. laevis* differ in size (Figure 1.2A) and the animals that were used also differed in size (Figure 1.2B) which is why SVL was used as a co-variant

All measurements of mass were log transformed to account for the assumption of homoscedascity. Mass was then compared using a MANCOVA with sex and size used as co-variants (Rstudio. 3.2; R Core team, 2015).

#### **1.2.4 Performance ~ morphology correlations**

A literature search was done to determine which morphological characters are known to be associated with a given performance trait. Jumping distance was found to be dependent on the leg length (see Tejedó *et al.*, 2000; Gomes *et al.*, 2009) and the mass (Tejedó *et al.*, 2000) of the frog. Jump force is also associated with the mass of the frog (Wilson *et al.*, 2000). Herrel *et al.* (2012) and the combination of the two studies by Phillips *et al.* (2006) and Llewellyn *et al.* (2010) has shown that leg length is important when it came to the endurance of *Xenopus tropicalis* and *Rhinella marina*. In *Xenopus* the feet (Richards, 2010) and the ilium is important for swimming (Whiting, 1980; Videler & Jorna, 1985). No literature could be found on the morphological characters which are associated with jump height and wet endurance. All other performance trials that in which jumping is involved are associated with leg length, as such it safe to assume that leg length might also be important in jumping



height. Wet endurance involves swimming as such it might be supposed that the ilium as well as toe length (as a proxy for amount of webbing) might be important for wet endurance. In support of the above literature I also used the log transformed morphological data in a stepwise regression to determine which morphological characters further explain the performance in each species (Rstudio. 3.2; R Core team, 2015). Assumptions of normality and homoscedascity were tested using a Shapiro-Wilk test in R Studio (R Core Team, 2015). All morphological parameters used in the different models were based on the above mentioned literature as well as the morphological parameters that were significant in the stepwise regression. The two *X. gilli* populations were clumped together for this analysis and as such any morphological characters that were significantly different between the two species were not used in the analyses. A general linear model was used to fit different models that included the given morphological characters to each of the associated performance traits. The best model was chosen based on the delta Akaike's information criterion ( $\Delta AICc$ ); the model with the lowest  $\Delta AICc$  represents the best model (Anderson & Burnham, 1999). The best models were then used to determine which of the given morphological characters were associated with performance traits in each of these two species.

### **1.2.5 Dispersal**

All frogs were photographed on a 10×10 mm grid paper to determine their (SVL). Frogs were sexed externally by the presence of labial lobes in females and nuptial pads on the forearms of males (Measey, 1998). The 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 needle and injected underneath the skin above the dorsal lymph sac (Donnelly *et al.*, 1994). The tag was scanned with a hand held scanner (APR 350, Agrident, Barsinghausen Germany) and a unique number was presented, which was used to identify each individual. In

CoGH only *X. gilli* were tagged (all *X. laevis* having been euthanized), whereas in Kleinmond both *X. laevis* and *X. gilli* were tagged.

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 homoscedascity. Normality of data was determined by using pp-plots and the homogeneity of the variances were determined by using Levene's test. An ANOVA was used to determine whether there were differences in dispersal distances between the two *X. gilli* populations and *X. laevis*. To compare the differences in the number of frogs that have dispersed a chi-square test was done. These analyses were used to determine which of the two species had the higher dispersal ability. All statistical analyses were done by using R Studio, 3.2 (R Core team, 2015).

### 1.3 Results

During the course of this study 3 449 individual *Xenopus* were tagged in a total of 15 water-bodies, of which six were permanent and nine temporary. In CoGH a total of 1 146 *X. gilli* were tagged. No hybrids were found in CoGH, but 410 *X. laevis* were removed (De Villiers *et al.*, 2016). In Kleinmond a total of 563 *X. gilli* were tagged as well as 1 740 *X. laevis*. Five hybrids were also tagged but not included in the study. Hybrids were identified by morphological charters as indicated by Picker (1985).

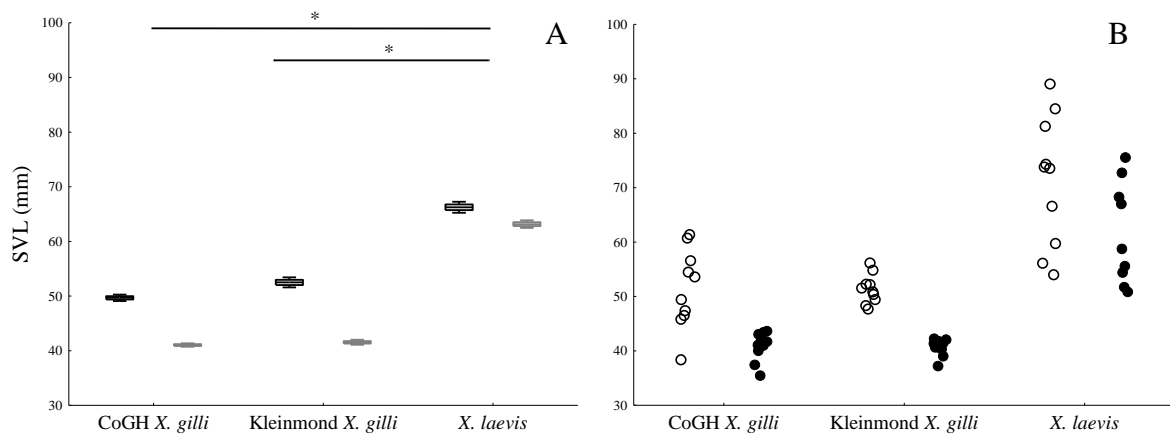


Figure 1.3: The body size differences of the *X. laevis* and two *X. gilli* populations. A) The SVL of the tagged frogs (note that raw data, outliers and extremes not shown as the number of observations was high). B) The SVL of the frogs that were used in the performance trails. The open circles indicate females and the closed circles indicate males. The boxes represent the standard error whereas the whiskers indicate the 95% confidence interval. The black lines indicate females and the gray lines indicate the males. \* indicates significant differences.

#### 1.3.1 Morphology

The size spread of the frogs that were used for the performance trials is shown in figure 1.3B. *Xenopus laevis* was the larger species of the two species (Table 1.1; Picture 1.3B). In both

*Xenopus* species the females were significantly larger than the males (Table 1.1; Figure 1.3B). The *X. gilli* females from the Kleinmond population were also significantly larger than the CoGH females (Table 1.1; Figure 1.3B). The humerus, radius and the longest toe showed significant sexual differences and were significantly larger in *X. laevis* (Table 1.1).

Table 1.1: The size corrected morphological characters of *X. laevis* and the two *X. gilli* populations that show sexual differences. <sup>a</sup> Indicate significant differences after Bonferroni corrections

	<i>X. laevis</i>		<i>X. gilli</i>				F <sub>df,n</sub>	p
			Kleinmond		CoGH			
	Male	Female	Male	Female	Male	Female		
	Mean±SD							
SVL <sup>a</sup>	63.17±9.31	66.25±16.59	41.55±3.15	52.51±8.27	41.04±3.10	49.68±7.94	463.92 <sub>5,3265</sub>	<0.001
Humerus <sup>a</sup>	0.17±0.02	0.14±0.01	0.14±0.02	0.12±0.01	0.15±0.01	0.11±0.02	19.122 <sub>5,60</sub>	<0.001
Radius <sup>a</sup>	0.31±0.03	0.24±0.03	0.24±0.02	0.21±0.02	0.27±0.02	0.21±0.03	21.56 <sub>5,60</sub>	<0.001
Toe <sup>a</sup>	0.39±0.01	0.36±0.01	0.35±0.02	0.32±0.03	0.38±0.02	0.34±0.03	15.49 <sub>5,60</sub>	<0.001

The log transformed relative mass of *X. laevis* was significantly greater than *X. gilli* ( $F_{5,60} = 26.938$ ,  $p < 0.0001$ ; Figure 1.4). Females, of both species, were also relatively heavier than males (Figure 1.4)

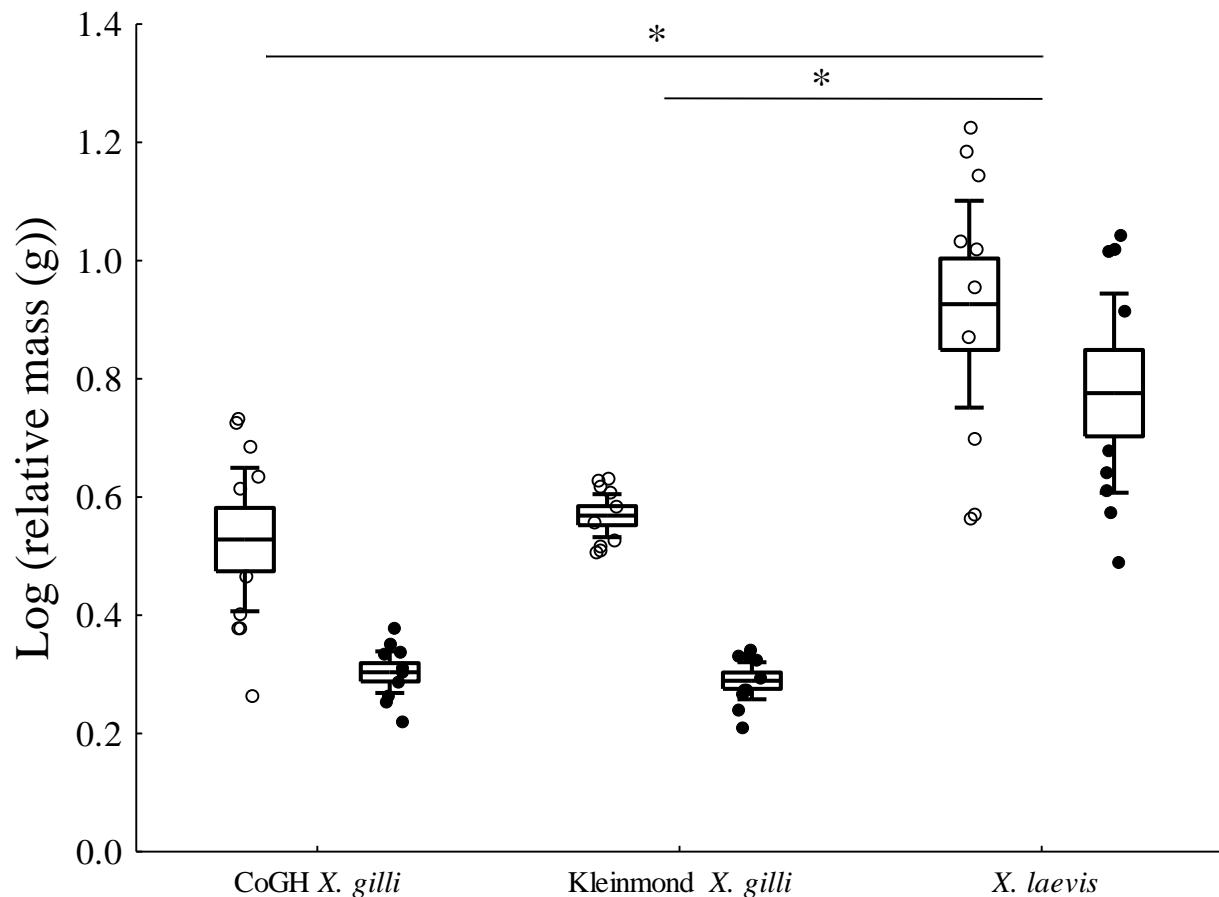


Figure 1.4: The log transformed relative mass of the frogs that were used in the performance trails. There was a significant difference, in the weight, between the sexes of both species. The boxes represent the standard error whereas the whiskers indicate the 95% confidence interval. The open circles indicate females and the closed circles indicate males. The circles indicate the raw data. \* indicates significant differences.

Head length and head width were significantly larger in *X. laevis* and the CoGH *X. gilli* than the Kleinmond *X. gilli*. The longest finger of *X. laevis* was significantly longer than the longest finger of *X. gilli* (Table 1.2).

Table 1.2: The size corrected morphological characters of *X. laevis* and the two *X. gilli* populations that showed no sexual differences in preliminary analyses. As such only comparisons between the two *X. gilli* populations and *X. laevis* are shown <sup>a</sup> Indicate significant differences after Bonferroni corrections and <sup>b</sup> indicate no significant difference after Bonferroni corrections

	<i>X. laevis</i>		<i>X. gilli</i>		p
	Kleinmond		COGH		
	Mean±SD			F <sub>df,n</sub>	
Head length <sup>a</sup>	0.37±0.02	0.34±0.03	0.37±0.02	6.81 <sub>2,60</sub>	0.005
Head width <sup>a</sup>	0.22±0.02	0.20±0.01	0.22±0.02	15.59 <sub>2,60</sub>	<0.001
Jaw <sup>b</sup>	0.15±0.01	0.14±0.01	0.15±0.01	1.82 <sub>5,60</sub>	0.12
Finger <sup>a</sup>	0.11±0.01	0.09±0.01	0.099±0.01	9.22 <sub>2,60</sub>	<0.001
Hand <sup>b</sup>	0.07±0.005	0.07±0.006	0.07±0.006	1.79 <sub>5,60</sub>	0.13
Ilium length <sup>b</sup>	0.56±0.03	0.55±0.05	0.58±0.04	1.76 <sub>5,60</sub>	0.14
Ilium width <sup>b</sup>	0.18±0.01	0.17±0.01	0.17±0.01	2.01 <sub>5,60</sub>	0.25
Femur <sup>b</sup>	0.30±0.02	0.28±0.02	0.29±0.04	2.16 <sub>5,60</sub>	0.07
Tibia <sup>b</sup>	0.49±0.03	0.46±0.03	0.48±0.06	1.37 <sub>5,60</sub>	0.25
Foot <sup>b</sup>	0.22±0.02	0.21±0.02	0.20±0.02	1.79 <sub>5,60</sub>	0.175

### 1.3.2 Performance

Both jumping distance and jumping force showed significant size dependence and as such were size corrected, whereas jumping height showed no dependence on size. *Xenopus laevis* was the better jumper as they jumped significantly further (F=9.598<sub>2, 60</sub>, p<0.0001; Figure

1.5A) and higher ( $F=63.9197_{2, 60}$ ,  $p<0.0001$ , Figure 1.5B) than both the *X. gilli* populations. There was no difference in jump distance ( $F=9.598_{2, 60}$ ,  $p=0.219$ ) or height ( $F=63.9197_{2, 60}$ ,  $p=0.584$ ) between the two *X. gilli* populations (Figure 6B). Relative jump force did not differ between the two species or within *X. gilli* ( $F=0.0553_{2, 60}$ ,  $p=0.946$ , Figure 1.5C).

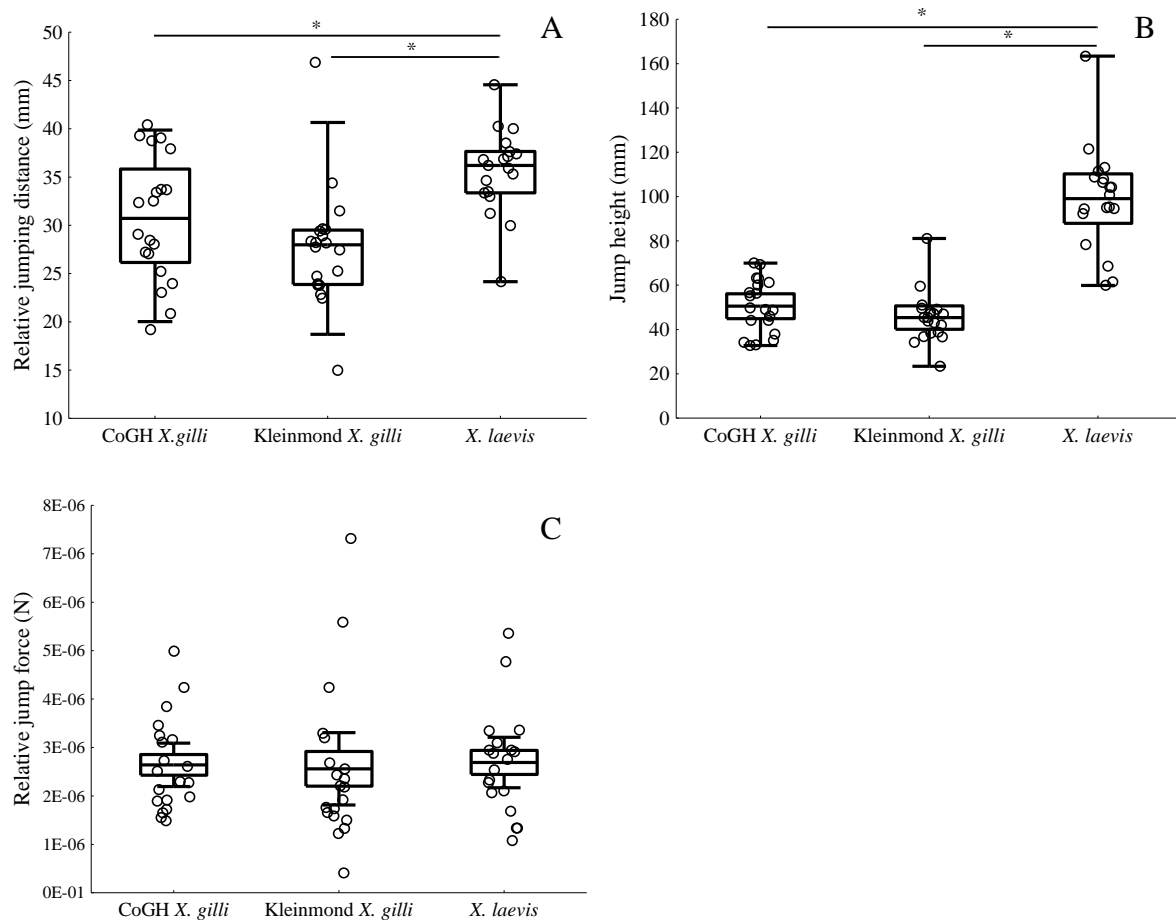


Figure 1.5: The jumping performance of *X. laevis* and two *X. gilli* populations. A) A box plot of the relative jumping distance of the two species; B) A box plot of the absolute jump heights of the two species and C) A box plot of the relative jumping force of both species. The boxes represent the standard error whereas the whiskers indicate the 95% confidence interval.  $\circ$  indicate the raw data. \* indicates significant differences.



Swim speed showed no size dependence and as such absolute values were used in comparison. *Xenopus laevis* swam significantly faster than *X. gilli* from both populations (F=9.615<sub>2, 60</sub>, p<0.001; Figure 1.6). There was no difference in swim speed between the *X. gilli* populations (p=0.969; Figure 1.6)

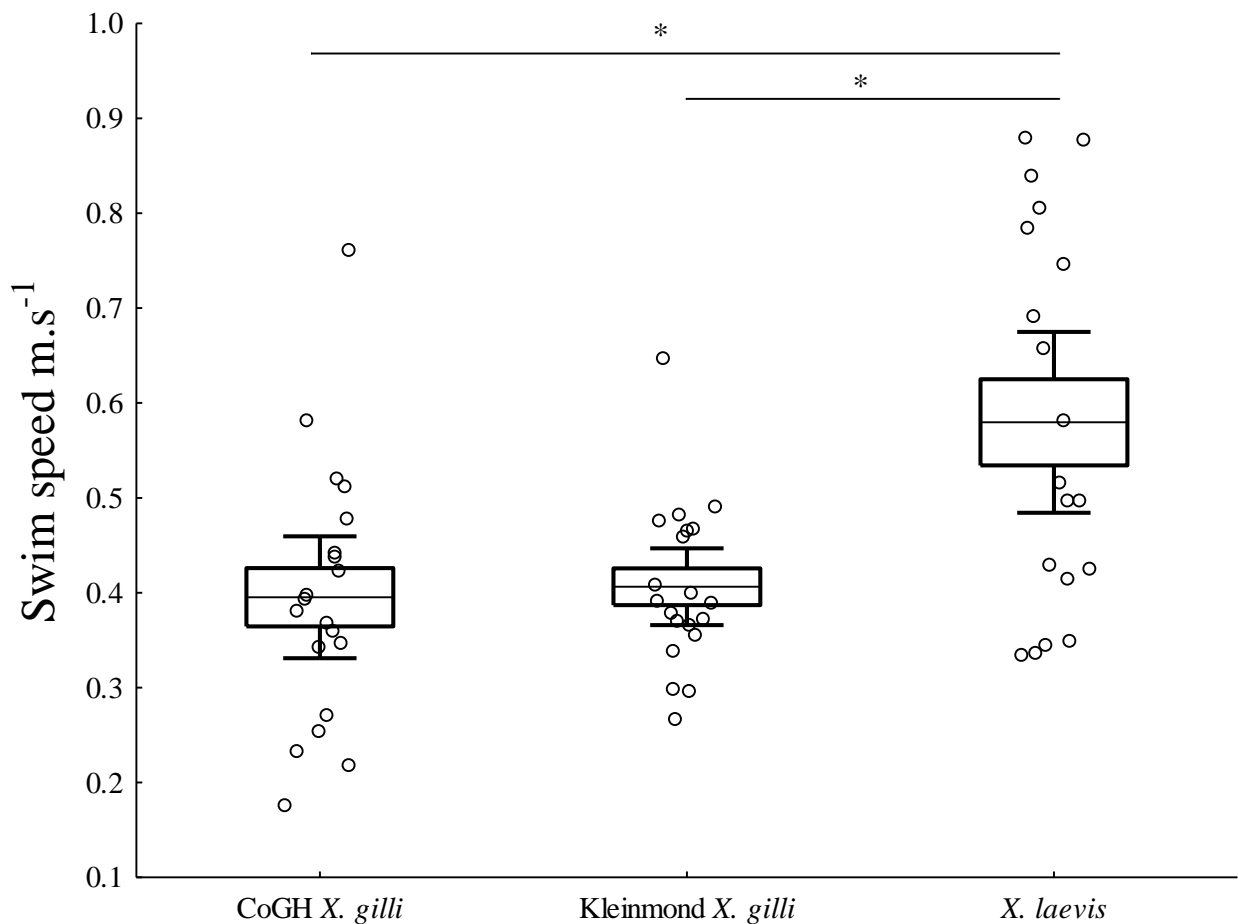


Figure 1.6: The swimming speed of *X. laevis* and the two populations of *X. gilli*. The boxes represent the standard error whereas the whiskers indicate the 95% confidence interval.  $\circ$  indicate the raw data.

\* indicates significant differences.

Dry endurance showed significant size dependence and was size corrected, whereas wet endurance showed no size dependence. There was no significant difference in the dry endurance distances (F=2.024<sub>2, 60</sub>, p=0.141; Figure 1.7A). However the CoGH *X. gilli* spent significantly more time moving than the Kleinmond *X. gilli* and *X. laevis* (F=7.517<sub>2,60</sub>,

$p < 0.01$ , Figure 1.7B). There were significant differences in wet endurance ( $F = 13.371_{2, 60}$ ,  $p < 0.0001$ ; Figure 1.7C), with both the CoGH *X. gilli* population ( $p < 0.001$ ) and *X. laevis* ( $p < 0.001$ ) having higher swim endurance than the Kleinmond *X. gilli* population (Figure 1.7C). There was no difference in swim endurance between the CoGH *X. gilli* population and *X. laevis* ( $p = 0.592$ ; Figure 1.8B). This significant result was also mirrored in the time spent moving ( $F = 4.927_{2, 60}$ ,  $p = 0.011$ ).

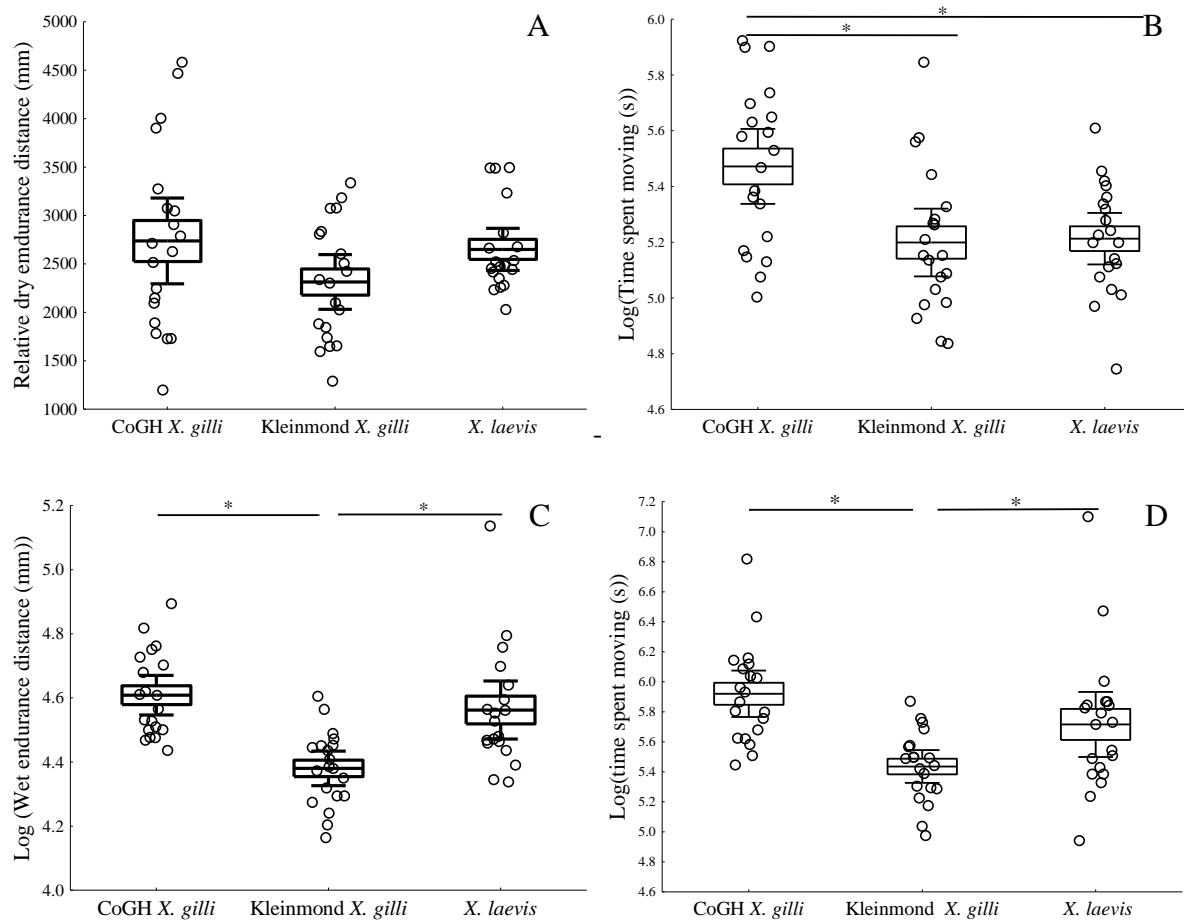


Figure 1.7: The endurance distances of *X. laevis* and two *X. gilli* populations. A) The size corrected dry endurance, B) the natural log transformed time spent moving during dry endurance, C) the log transformed wet (i.e. swimming) endurance, and D) the natural log transformed time spent moving during wet endurance. The boxes represent the standard error whereas the whiskers indicate the 95% confidence interval.  $\circ$  indicate raw data. \* indicates significant differences.

Table 1.3: Results from performance trails for both *X. gilli* populations and *X. laevis*

	CoGH <i>X. gilli</i>			Kleinmond <i>X. gilli</i>			<i>X. laevis</i>		
	Max	Min	Mean $\pm$ SD	Max	Min	Mean $\pm$ SD	Max	Min	Mean $\pm$ SD
Jumping distance (cm)	32.87	13.57	22.88 $\pm$ 4.75	32.97	11.81	20.59 $\pm$ 4.27	39.81	20.12	32.38 $\pm$ 4.73
Jumping height (cm)	11.62	2.43	6.29 $\pm$ 1.98	8.84	3.10	5.90 $\pm$ 1.42	16.34	5.99	9.93 $\pm$ 2.26
Jumping force (N)	0.99	0.18	0.45 $\pm$ 0.23	0.87	0.09	0.42 $\pm$ 0.25	4.34	0.33	1.58 $\pm$ 1.12
Swimming speed (m.s <sup>-1</sup> )	0.76	0.18	0.39 $\pm$ 0.14	0.65	0.27	0.41 $\pm$ 0.09	0.88	0.33	0.59 $\pm$ 0.20
Dry Endurance (m)	38.3	8.7	21.05 $\pm$ 7.66	26.9	9.3	17.75 $\pm$ 4.66	31.9	20.67	24.93 $\pm$ 3.53
Wet endurance (m)	78.42	27.32	42.51 $\pm$ 13.98	40.3	14.6	24.81 $\pm$ 6.61	137.04	21.8	40.95 $\pm$ 25.15

### 1.3.3 Performance ~morphology correlations

The models that best described the performance trails included jumping (i.e. jump distance, height, force and dry endurance) in both species included morphological characters which are associated with the hind legs, except for one instance where inter-axial length best explained jumping force in *X. gilli* (both populations combined) (Table 1.3). In the swimming performance trials (i.e. swimming speed and wet endurance) the morphological characters that explained each of these two performance trails differed between the two trails as well as between the two species (Table 1.3).

Table 1.4: Model selection for the morphological characters that explain performance traits of *X. laevis* and *X. gilli*. The best models that were used are indicated in bold. The abbreviations that were used are as follows: MS-mass, LL-leg length (the combination of the femur and tibia lengths), FL- total foot length (the combination of the foot length and the longest toe length), IL-ilium length, IW-ilium width, FM-femur length, TB-tibia length, FT-foot length, LT-longest toe length, HS-humerus length, RD-radius length, HD-hand length, LF-longest finger length and IA-inter axial length.

	<i>X. laevis</i>			<i>X. gilli</i>		
A) Jumping distance						
Model	$\Delta$ AIC	R <sup>2</sup>	p	$\Delta$ AIC	R <sup>2</sup>	p
MS, LL, IW, FM, TB, LT, IA	3.380067	0.391	0.421	11.00836	0.282	0.123
MS, FM, TB	4.272022	0.049	0.839	5.16614	0.242	0.018
MS, LL	2.277013	0.049	0.648	1.989565	0.264	0.003
MS	1.269526	0.001	0.877	9.742508	0.061	0.125
IW	0.941987	0.018	0.577	11.59409	0.016	0.434
LT	0	0.063	0.287	3.894558	0.189	0.005
IA	0.405891	0.044	0.377	12.24734	0	0.999

	<i>X. laevis</i>			<i>X. gilli</i>		
B) Jumping distance						
Model	$\Delta$ AIC	R <sup>2</sup>	p	$\Delta$ AIC	R <sup>2</sup>	p
LL	<b>0.321404</b>	<b>0.048</b>	<b>0.355</b>	<b>0</b>	<b>0.264</b>	<b>0.0007</b>
FM, TB	2.274383	0.0499	0.648	3.3792	0.238	0.007
FM	0.386987	0.044	0.372	2.222315	0.222	0.002
TB	0.873927	0.021	0.542	5.194996	0.162	0.01
C) Jumping height						
MS, LL, FL, IL, FM, TB, LT	4.325244	0.477	0.236	6.787546	0.347	0.041
MS, FM, TB	0.211984	0.365	0.058	1.576114	0.299	0.005
MS, LL	2.027618	0.232	0.106	<b>0</b>	<b>0.292</b>	<b>0.002</b>
MS	5.237461	0.003	0.816	3.705599	0.184	0.006
LL	1.322398	0.18	0.062	0.916337	0.239	0.001
FM, TB	<b>0</b>	<b>0.306</b>	<b>0.045</b>	3.842722	0.221	0.009
FM	0.955793	0.195	0.051	3.166632	0.195	0.004
TB	0.306441	0.221	0.037	4.496978	0.167	0.009
FL	4.446791	0.042	0.388	4.238529	0.172	0.008
LT	2.713728	0.121	0.132	7.165081	0.11	0.037
D) Jumping force						
MS, LL, FM, TB, FT, IA, LT	2.092036	0.566	0.106	9.24873	0.135	0.659
MS, IA	6.309688	0.116	0.351	1.674644	0.081	0.209
MS, LL	1.393655	0.309	0.043	4.936458	0.003	0.943
MS	6.70459	0.003	0.807	3.045867	0.001	0.901

Model	<i>X. laevis</i>			<i>X. gilli</i>		
	$\Delta$ AIC	R <sup>2</sup>	p	$\Delta$ AIC	R <sup>2</sup>	p
FM, TB	1.894977	0.291	0.054	3.962548	0.027	0.601
FM	6.392143	0.019	0.564	2.914104	0.003	0.709
LL	1.210258	0.243	0.027	2.937757	0.003	0.732
TB	<b>0</b>	<b>0.287</b>	<b>0.015</b>	2.823426	0.006	0.636
IA	4.384973	0.113	0.148	<b>0</b>	<b>0.073</b>	<b>0.09</b>
E) Swimming speed						
LL, FL, IL, IW, FM, TB, FT, LT, IA	2.602205	0.641	0.151	10.68123	0.243	0.411
IL, IW, FM, TB, FT, LT	4.338576	0.491	0.151	5.513213	0.188	0.194
IL, IW, LL	3.897399	0.302	0.116	1.999222	0.178	0.064
IL, FT, LT	3.165901	0.327	0.089	3.327372	0.15	0.115
IL, FL	1.943059	0.3	0.048	5.179455	0.064	0.293
FM, TB, FT, LT	4.939463	0.335	0.165	6.893895	0.116	0.349
LL	2.090563	0.221	0.178	4.483595	0.033	0.26
FM, TB	1.525522	0.315	0.04	4.149481	0.088	0.182
FL	2.024473	0.223	0.035	5.103578	0.018	0.408
TB	<b>0</b>	<b>0.298</b>	<b>0.013</b>	2.798301	0.073	0.092
FM	6.96173	0.006	0.742	5.564538	0.007	0.615
LT	3.671005	0.157	0.084	5.792652	0.001	0.842
IL, IW	6.262495	0.132	0.301	<b>0</b>	<b>0.178</b>	<b>0.027</b>
IL	5.215279	0.089	0.201	3.659073	0.053	0.153
IA	5.246888	0.088	0.205	5.38663	0.011	0.517

	<i>X. laevis</i>			<i>X. gilli</i>		
F) Dry endurance						
Model	$\Delta$ AIC	R <sup>2</sup>	p	$\Delta$ AIC	R <sup>2</sup>	p
MS, LL, IL, IW, FM, TB, FT, LT	3.489101	0.729	0.024	5.821725	0.345	0.074
	<b>0</b>	<b>0.692</b>	<b>0.003</b>	9.338732	0.109	0.225
MS, FM, TB, FT, LT	5.64823	0.449	0.006	6.508913	0.101	0.141
MS, LL	8.996831	0.411	0.033	<b>0</b>	<b>0.273</b>	<b>0.009</b>
LL, IL, IW	0.27664	0.655	0.002	7.347538	0.169	0.155
FM, TB, FT, LT	9.481779	0.262	0.021	4.515337	0.101	0.046
LL	7.536315	0.395	0.014	4.072892	0.154	0.046
FM, TB	5.663656	0.391	0.003	2.770085	0.139	0.018
FM	13.88335	0.081	0.224	7.85983	0.022	0.361
TB	14.62915	0.046	0.364	8.029187	0.018	0.411
MS	12.93157	0.124	0.129	8.394044	0.009	0.563
IL						
G) Swimming (wet) endurance						
LL, FL, IL, IW, FM, TB, FT, LT, IA	3.3577	0.5396	0.342	9.70476	0.2345	0.4461
IL, IW, FM, TB, FT, LT	5.831944	0.2968	0.5148	5.34194	0.2025	0.2453
LL, FL, IL, IW	8.253565	0.0305	0.974	5.55920	0.1138	0.361
LL, FL, FM, TB, FT, LT	6.222222	0.2829	0.5515	4.66970	0.2158	0.2044
FM, TB, FT, LT	4.391168	0.2008	0.4667	2.08785	0.1875	0.1131
LL, LT	4.55636	0.0157	0.8741	1.99748	0.1041	0.131
FM, TB	2.722255	0.102	0.4009	0.45819	0.1379	0.06426
LL	2.711352	0.00805	0.7068	<b>0</b>	<b>0.104</b>	<b>0.0424</b>
TB	2.698062	0.0087	0.6956	2.59959	0.0438	0.1947

Model	<i>X. laevis</i>			<i>X. gilli</i>		
	$\Delta$ AIC	R <sup>2</sup>	p	$\Delta$ AIC	R <sup>2</sup>	p
FL	2.561557	0.01545	0.6016	0.68884	0.0884	0.0624
LT	1.445208	0.0689	0.2635	0.68884	0.0884	0.06237

### 1.3.4 Dispersal

Of the 3 449 frogs that were tagged only 142 were captured in locations other than where they had been tagged. *Xenopus laevis* (dispersing individuals: n=90, 5.17%) had significantly higher number of individuals dispersing ( $\chi^2=9.379$ , p=0.002) than *X. gilli* (dispersing individuals: n=52, 3%). The CoGH *X. gilli* population (n=46, 4.01%) had significantly higher number of individuals that dispersed ( $\chi^2=11.4334$ , p<0.001) than the Kleinmond population (n=6, 1.01%). In *X. gilli*, females (n=44, 4.1%) were more likely to disperse than males (n=8, 1.37%;  $\chi^2= 52.9176$ , p<0.001). However, in *X. laevis* there was no significant difference in the number of males or females that dispersed (females: n=62, 6.11%; Males: n=28, 4.1%; *X. laevis*:  $\chi^2=3.3144$ ; p=0.068).

Dispersal distances represents the actual Euclidean distances that was dispersed and were not size corrected. There was no significant difference in dispersal distance between males and females of both species (F=0.765, df=5, p=0.576; *X. laevis*: Female n=76, male n= 30; *X. gilli*: female n=50, male n=9; Figure 1.8). There was also no significant difference (F=0.483; df=2; p=0.618), in dispersal distance, between *X. laevis* (n=106) and either CoGH (n=53; p=0.909) or Kleinmond (n=6, p=0.616), or between the two *X. gilli* populations (p=0.732; Figure 1.8).



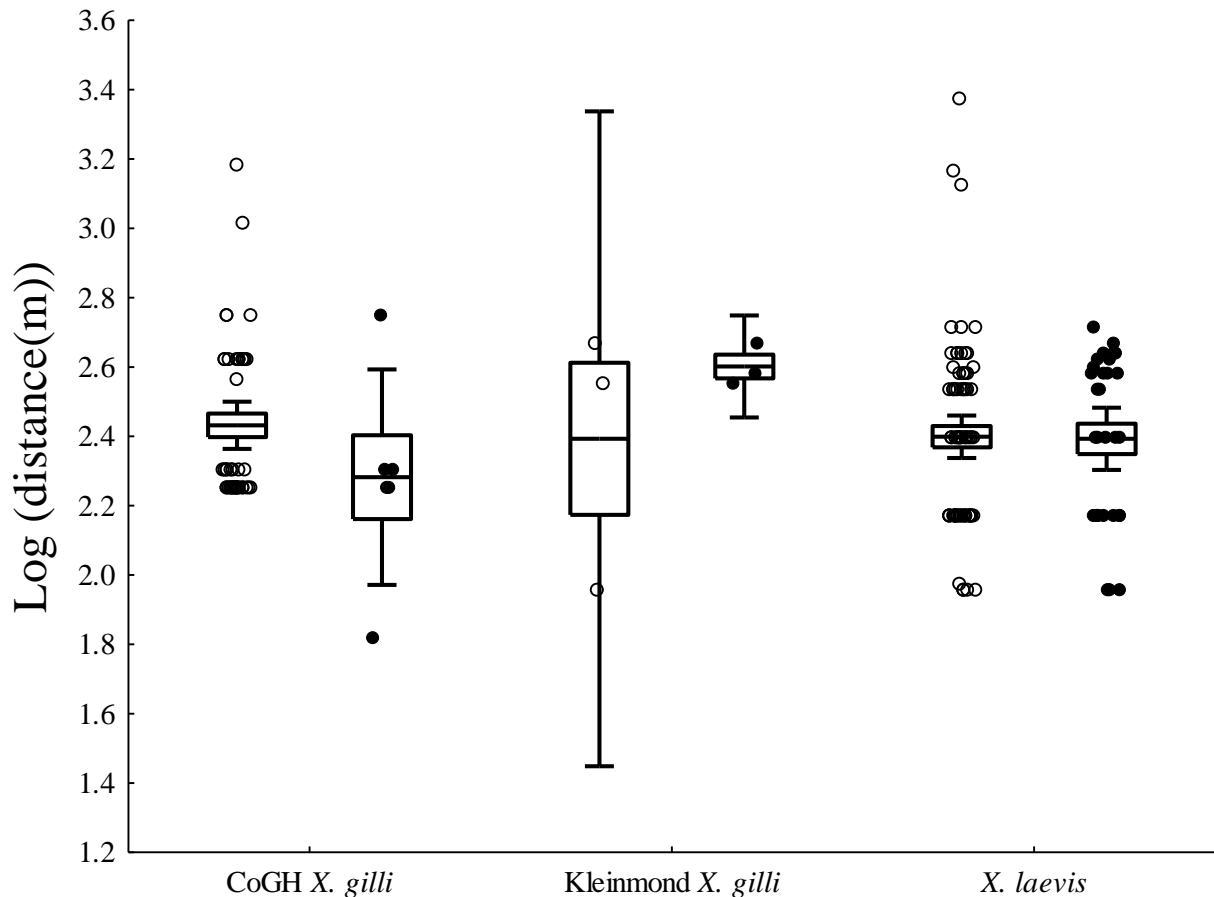


Figure 1.8: The log transformed dispersal distances of *X. laevis* and the two *X. gilli* populations. The boxes represent the standard error whereas the whiskers indicate the 95% confidence interval. The open circles indicate females and the closed circles indicate the males.  $\circ$  indicate the raw data.

Most *X. laevis* dispersed during December in 2014 and in October 2015 (Figure 1.9), representing times when the temporary water-bodies dried up. *Xenopus gilli* had the frequency highest dispersal events in August 2014 and 2015 as well as September 2015 (Figure 1.9). The distance mostly travelled by *X. laevis* were between 200 and 400m and below 200m for *X. gilli* (Figure 1.10)

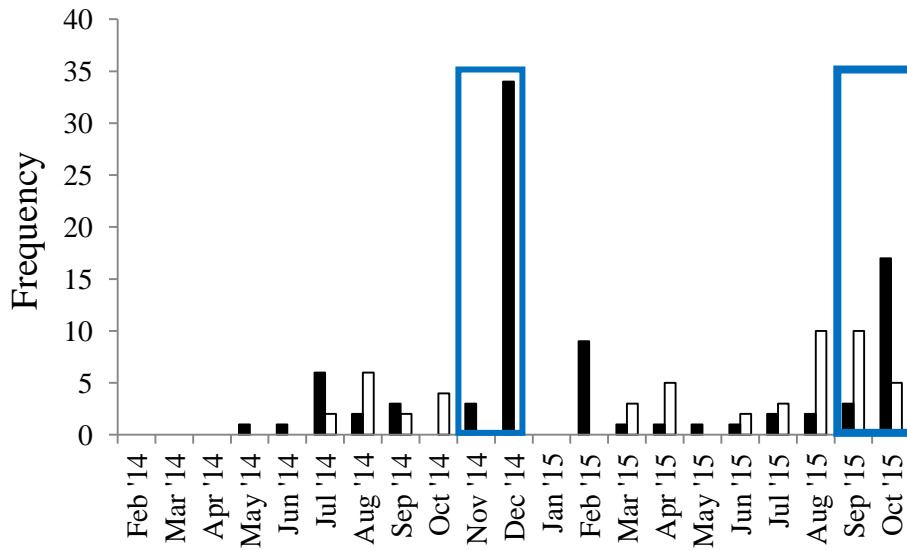


Figure 1.9: The dispersal frequency of the *X. laevis* and *X. gilli*. The black bars represent *X. laevis* and the clear bars represent *X. gilli*. The blue boxes shows the time when the temporary ponds dried up.

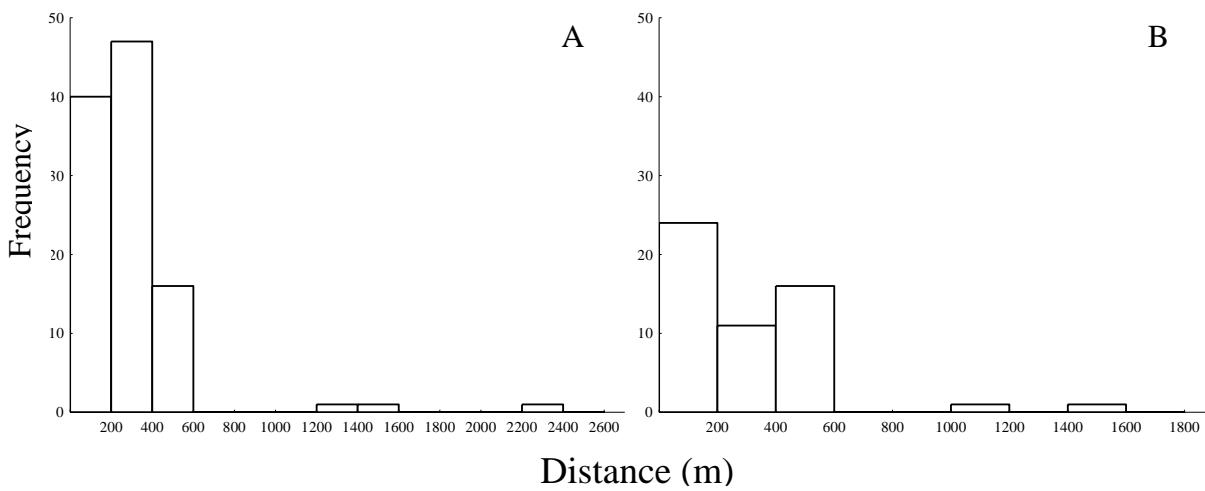


Figure 1.10: The dispersal kernel of A) *X. laevis* and B) *X. gilli*

## 1.4 Discussion

No difference was found in the dispersal distances between *Xenopus laevis* and *X. gilli*. However, *X. laevis* did have significantly more dispersal events than *X. gilli*. *X. laevis* were indeed relatively better jumpers and were absolutely faster swimmers compared to *X. gilli*. *Xenopus laevis* showed better relative swimming endurance compared to the Kleinmond *X. gilli* and no difference in the relative dry endurance. As such if a water-body, inhabited by *X. laevis*, is close enough to the habitat of *X. gilli* there is the potential for a high number of *X. laevis* to move into this habitat. Once *X. gilli* and *X. laevis* are in the same water-body it is possible for *X. laevis* to actively catch them not only because they are better swimmers but also because they can swim for longer.

Smith and Green (2005) reviewed the maximum distances travelled by several terrestrial frog species. They found that 44% of the included frog species had a maximum of higher of one kilometre. In this study I have shown that both *X. laevis* and *X. gilli* also had dispersal events over one kilometre. The maximum dispersal distance that was observed in this study was a *X. laevis* female, which travelled 2 360m (overland) in less than six weeks, another *X. laevis* female dispersed 1 460m (also overland) in less than three weeks and a *X. gilli* female that dispersed 1 540m overland. It is important to note that these are the Euclidean distances and that the actual distances moved are likely to be much more than that reported here. However what Smith and Green (2005) failed to report is the dispersal kernel of each of the species they reviewed. The maximum distances travelled by species are normally represented by a small number of individuals. This is shown by the dispersal kernel of *X. laevis* and *X. gilli* where the shorter distances had the highest frequency of dispersal events. It is also important to note that not all dispersal events might have been recorded due to the nature of the sampling effort (limited to ponds within a certain area) and that the frequency of dispersal might be higher. This frequency data is very important when it comes to comparing species.

In *X. laevis* the highest frequency of dispersal events occurred at a distance between 200 and 400m (Figure 1.10A), whereas in *X. gilli* the highest frequency dispersal events occurred at a distance lower than 200m (Figure 1.10B). This would suggest that there is a higher chance for *X. laevis* to move to the further water-body than there is for *X. gilli*.

A study by Alford *et al.* (2009) has shown that Cane toads, at the invasion front, in Australia have higher dispersal ability than the core population. Llewelyn *et al.* (2010) also found that the invasion front population have higher endurance than the core population, and suggest the higher endurance to be the reason for the increased dispersal ability. This was also found to be the case for *Xenopus laevis* and *X. gilli*, as dispersal distances between these two *Xenopus* species did not differ (Figure 1.3), which was supported by the lack of differences in dry endurance ability between these two *Xenopus* species (Figure 1.6A). There was, however, a difference in the number of frogs that dispersed, with *X. laevis* having significantly higher proportion of dispersing individuals. With *X. laevis* being the better jumper, it might be easier for them to reach other ponds and as such have a higher number of dispersal events, however this must still be tested by comparing the performance ability of known dispersers. It might also be that the close proximity of the ponds in Kleinmond made it easier for *X. laevis* to disperse from one pond to the other. It is also possible that the number of *X. gilli*, that dispersed, from the CoGH population might be underestimated.

In *X. laevis* the highest number of dispersal events was recorded in December 2014 (Figure 1.10). This was likely due to most of the frogs in temporary pond TP2 (see Figure 1.1) moving to the surrounding ponds when it dried up. Several studies have reported *X. laevis* moving *en mass* when the water-body they are in dries up (see Loveridge, 1953; Rödel, 2000; Lobos & Jaksic, 2005). What is interesting is the high incidence of dispersal events in February 2015 (Figure 1.10). Most of the dispersal events that were recorded happened during a down-pour, suggesting that *Xenopus* rely on the humid atmosphere to disperse.

However, in February the air becomes very hot and dry, suggesting that they are capable of moving under the driest of conditions. During this time dispersal probably happens at night time when it is cooler (Kalk, 1960).

Historically it was assumed that the only water-bodies, in my study area at CoGH, which contained *Xenopus gilli*, were the permanent water-bodies (see Picker & De Villiers, 1989). This was probably assumed, due to the fact that sampling was done each year in autumn (see Picker & De Villiers, 1989), which is just after a hot and dry summer (Linder, 1991). As a result all the temporary ponds are dry and most of the frogs are in the permanent ponds. This was also the reason why only the permanent water-bodies were trapped in the beginning of this study. However this study has provided more information on the ecology of the CoGH *X. gilli* and has shown that this assumption was erroneous. During the winter rainy season most of the frogs that are in the permanent water-bodies move to the adjacent temporary water-bodies to breed. When these temporary water-bodies dry up they move back into the permanent water-bodies. This was realised when trapping in the temporary ponds started in August 2014 to try and find the “missing” frogs, which is why there is a peak in dispersal event during this time. The actual dispersal events might have been earlier as the temporary water-bodies started filling up with the onset of the rainy season in May 2014 and the frogs may have started moving during this time. The other peaks in dispersal events (October 2014, August 2015 and September 2015; Figure 1.9), mostly represent the actual (within three to six weeks) movement time: determined from the capture histories. In October 2014 the ponds started to dry up after the winter rains, they then only filled again in August 2015 and dried up again in September 2015 due to the low rain fall. As such, this period coincides with the filling and drying of the temporary ponds in CoGH. It is also important to note that it would seem that a lot of these frogs that are in these temporary ponds only stay for a short while after which they move on to other ponds, which is why there was some dispersal recorded

during the rainy months (April – September). Another important point to note is that most of the area, in which these temporary ponds are found, becomes flooded during the winter rains. As such, it is entirely possible that several dispersal events by these frogs were missed due to the fact that not all ponds could be trapped as many were too shallow. There were a very low proportion of individuals that dispersed in the Kleinmond *X. gilli* population, which might be due to differences in motive to disperse. These frogs reside mostly in the temporary ponds in this area (some individuals have been caught in the permanent ponds, however this only during the start of the rainy season and they are only caught once, suggesting that they move out). As such during the summer they are believed to aestivate in the ground (see De Villiers, 2004) and emerge only when the temporary ponds have filled (pers. obs.). This would likely be the moment during which dispersal occurs, but may not be captured with our methods.

The *X. laevis* that were present in these temporary water-bodies also showed very little movement (compared to the *X. laevis* in the permanent water-bodies) between the ponds.

Gomes *et al.* (2009) have shown that this jumping performance for most anurans was related to the hind limb length, when they reanalysed the data from Zug (*Smithson. Contrib. Zool.* 1978; 276: 1–31). In an earlier study by Tejedo *et al.* (2000) they have shown that in juveniles of the European green frog (*Pelophylax esculatus*) jumping is not only related to the hind limb length of the frog but also the mass. Wilson *et al.* (2000) also found that jumping performance is related to the mass of juvenile striped march frog (*Limnodynastes peroni*), however this was not the case in adults. They also found that jumping force in the striped march frog was related to the mass of the frog. In *Xenopus laevis* and *X. gilli* both jumping distance and height were related to leg morphology (Table 1.3), which is in support of the studies done by Gomes *et al.* (2009) and Tejedo *et al.* (2000). However, jumping force in *X. laevis* was best explained by the tibia length whereas in *X. gilli* jumping force was best explained by the inter-axial length (Table 1.3). It is important to note that inter-axial length

only explained 7% of the jumping performance data, in fact there was an overall low support for the jumping force data from the morphological variables measured. This suggests that other factors besides morphology (for instance the angle of the hind legs when jumping was initiated) might have played a role in the jumping force or there was an error in data collection. This study has shown that unlike the striped marsh frog mass does not explain the jumping force of *X. laevis* and *X. gilli*.

Herrel *et al.* (2012) found that there was a difference in relative dry endurance between male and female *Xenopus tropicalis* which they accredited to the males having longer hind limbs than the females. This would suggest that in *X. tropicalis* hind limb length is important when it comes to the frog's maximal exertion capabilities. This was also shown to the case in Cane toads (*R. marina*) where Phillips *et al.* (2006) have shown the invasion front population to have longer hind limbs than the core population, which Llewelyn *et al.* (2010) have accredited to them high endurance ability than the core population. This was also the case for *X. laevis* and *X. gilli*, as leg length was included in the models that best explained dry endurance (Table 1.3). This study, in combination with the study by Herrel *et al.* (2012), suggests that leg length is important when it comes to maximal exertion and might also be important for dispersal ability. As such a study where the endurance capability of a known disperser and a *Xenopus* frog that is known to be highly site loyal is compared will yield interesting results.

Videler and Jorna (1985) illustrated the importance of the sliding articulation of *Xenopus* when it came to their swimming capabilities. A study by Richard (2010) has shown that the orientation of the feet of *Xenopus* is important in providing thrust during swimming, which would suggest that foot size might also play a role in the swimming abilities of *Xenopus*. In this study, it was found that the ilium length and width was important when it came to swimming speed of *X. gilli*, as the frogs with the longest and widest illia swam the fastest

(Table 1.3), supporting the study by Videler and Jorna (1985). However, in swimming endurance the *X. gilli* frogs with the longer legs swam the furthest. In *X. laevis* the frog with the longest tibia swam the fastest but the frogs with the longest bodies (i.e. longer inter axial length) swam the furthest, which would suggest that longer legs are more important for speed but not for distance (Table 1.3). Feet size, however, did not play a role in the swimming performance of these two *Xenopus* species, which is interesting as the feet of *Xenopus* are adapted for swimming (see Richards, 2010).

In conclusion, this study has shown that there are differences in the dispersal ability and relative performance of these two *Xenopus* species. Even though *X. laevis* did not disperse significantly further than *X. gilli*, there were a higher proportion of *X. laevis* individuals dispersing and *X. laevis* dispersed further more frequently. This information suggests that *X. laevis* are capable of expanding their invasive range through overland dispersal better than *X. gilli*. *Xenopus laevis* are as such also capable of occupying the temporary ponds naturally inhabited by *X. gilli* in high numbers. It was found that *X. laevis* was able to swim faster and further than *X. gilli*, suggesting that when these two species occupy the same water-body *X. laevis* will be able to capture and actively prey on *X. gilli*. As these two species occur in sympatry throughout the range of *X. gilli*, this study underlines the threat *X. laevis* poses.



## **Chapter 2:**

### **The Survival, age structure and growth of Cape *Xenopus***

#### **1.1 Introduction**

The global decline in amphibians has become a major issue in conservation in recent years (Blaustein & Wake, 1990; Blaustein *et al.*, 1994; Alford & Richards, 1999; Houlihan *et al.*, 2000). This decline has been principally accredited to an increase in habitat alteration (see Collins & Storfer, 2003). As such population dynamic studies have become increasingly important as a method to monitor amphibian populations (Leberton *et al.*, 1992; Schmidt, 2003). This is because, with the help of population dynamics, factors like survival estimates can be determined (Biek *et al.*, 2002; Schmidt, 2003), which is important information that aids in the conservation of a certain species or populations (Biek *et al.*, 2002). Population structure, specifically demographic structure, is also important for the assessment of the animals IUCN status (see IUCN, 2012). Currently there is no data available on any of the South African frog species that allows the assessment of these frogs on criteria which rely on population structure and as such the IUCN status of all South African anurans have been assessed using category B criteria (see Measey, 2011; IUCN 2012)

There are several factors which affect demographic structure, one of them being individual longevity (or age; Driscoll, 1999). For example, if there is high mortality in any of the age classes (i.e. juvenile, adult, etc.) within a species, the age structure of that species would be skewed towards the class with lower mortality (e.g. Stewart, 1995). When a species expands its range into that of a sister species it could have detrimental effects on the age structure of the sister species, especially if the range expanding species is a better competitor and/or a predator of the sister species. In such a situation two scenarios may occur when one species 'replaces' another closely related species. Scenario 1: a healthy long lived population, of a

competitive species, would have an age class distribution that is normally distributed (Figure 2.1A; e.g. Tsiora & Kyriakopoulou-Sklavounou, 2002; Kyriakopoulou-Sklavounou & Tsiora, 2008; Bo Liao & Lu, 2010). This scenario would generally represent the species that is the better competitor. Scenario 2: in a population, of the non-competitive species, which experiences high size dependent predation pressure on smaller size classes, the age class distribution is expected to be skewed towards older individuals in the population (Figure 2.1C; e.g. Woodford *et al.*, 2005; Weyl *et al.*, 2013). For example, small mouth bass (*Micropterus dolomieu*) has invaded many rivers throughout South Africa and as a result had a negative impact on local fish species (De Moor & Bruton, 1988). Woodford *et al.* (2005) have shown that in the Rondegat river small mouth bass has exerted high predation pressure on the local fish species, however when the fish reach a size >10 cm they are able to evade the predator. As a result the age structure of the indigenous fish in this river is skewed towards the right (older individuals: Woodford *et al.*, 2005). This will generally represent the sister species that is being preyed upon.

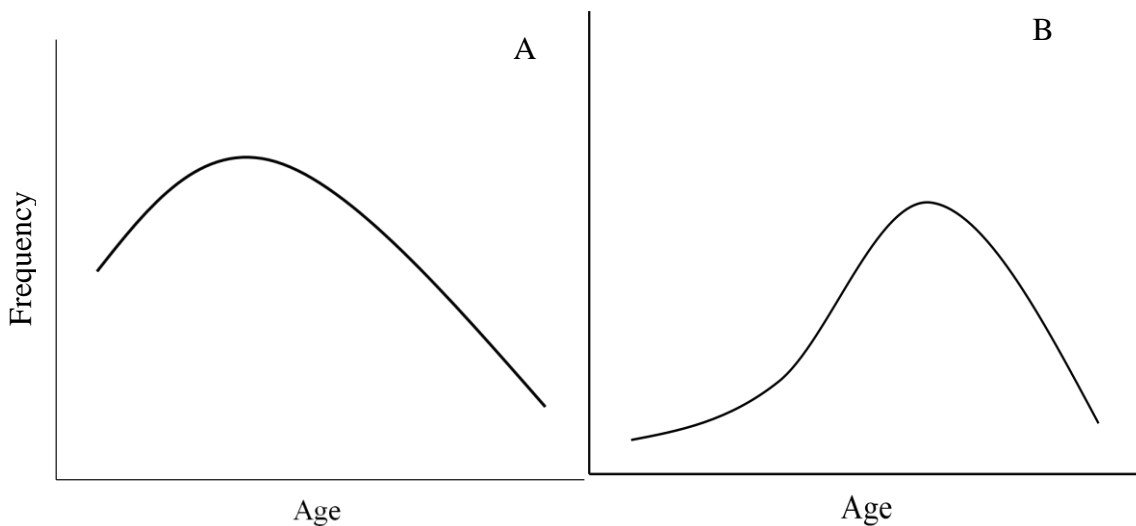


Figure 2.1: The age structure of two hypothetical populations. A) The age class distribution of a population which shows a perfectly normal distribution; B) a representation of a population experiencing high juvenile predation.

Age is particularly important when it comes to the estimation of survival, as different age classes may have different survival rates (Pollock, 1981; Driscoll, 1999). If we consider the age structure of the above mentioned hypothetical populations it is clear that survival will differ between age classes. The first population is a natural population and is only threatened by natural enemies. In this population some individuals are lost due to these natural enemies (for instance predators). There will be some fluctuation in survival over time due to seasonal changes (e.g. Schmutz & Ely, 1999). It is also expected that juveniles will have lower overall survival due to their vulnerability (see Werner, 1986; Pechmann *et al.*, 1991; Goater, 1994). In the second hypothetical population one would expect the survival of adults to be lower but not severely. However, for juveniles the survival is expected to be very low due to the impact of the predating species. For example Werner *et al.* (1995) have shown that juvenile green frogs (*Lithobates clamitans*) not only serve as prey for its sister species the American bullfrog (*L. catesbeiana*), but these two sister species also directly compete for available resources. It is expected that this will have a negative effect on the survival of juvenile green frogs. These

two scenarios are highly oversimplified when it comes to anurans, due to their complex life cycles.

The complex life histories of anurans (Wassersug, 1975; Wilbur, 1980), mean that differential predation at one life stage might have an effect on factors of adult population structure (for instance population size; see Hellriegel *et al.*, 2000; Vonesh & De la Cruz, 2002). Age structure is generally determined in post-metamorphic individuals and represents the age after metamorphosis (Smirina, 1994). The age in frogs is generally represented by an annual period of arrested growth which is represented in the bone as growth rings (Senning, 1940; Schroeder & Baskett, 1968; Smirina & Rocek, 1976). Survival, however, can be determined for all life stages (i.e. egg, larva, post-metamorph and adult; e.g. Licht, 1974), but determining survival in adults, with capture-mark-recapture, is more accurate (See Wood *et al.*, 1998; Schmidt *et al.*, 2002; Grafe *et al.*, 2004). In anurans it is also important to understand the growth rate of individuals as this will provide extra information that will corroborate the results that are found in the survival and age structure analyses (Turner, 1960a)

The genus *Xenopus* (Anura: Pipidae) is a principally aquatic group of frogs occurring throughout sub-Saharan Africa (Tinsley *et al.*, 1996). There are two *Xenopus* species present in the south-western part of South Africa (Tinsley *et al.*, 1996); the wide spread *Xenopus laevis* (see Minter *et al.*, 2004) and the Endangered *X. gilli* (SA-FRoG & IUCN 2015). These two species live in sympatry throughout the range of *X. gilli* (Kobel *et al.*, 1981; Loumont; 1984; Picker, 1985; Picker & De Villiers, 1989; Fogell *et al.*, 2013), and it is believed that *X. laevis* has a negative effect on *X. gilli* in three different ways (Kobel *et al.*, 1981; Picker, 1985; Picker & De Villiers, 1989; De Villiers; 2004). Firstly, studies have shown that *X. laevis* prey on the eggs, tadpoles and adults of *X. gilli* (De Villiers, 2004; Vogt *et al.*, Unpublished data). Secondly, these two species hybridize, giving rise to sterile males (Kobel

*et al.*, 1981; Evans *et al.*, 1998). Thirdly, when *X. laevis* invade the habitat of *X. gilli* they compete with *X. gilli* for both food and space (Vogt *et al.*, Unpublished data). Given this information it is expected that *X. laevis* should have a negative effect on the survival of *X. gilli*. In the Cape of Good Hope section of Table Mountain National Park (CoGH) *X. laevis* has been actively removed, since 1985, as a conservation effort to conserve *X. gilli* (see Picker & De Villiers 1989; De Villiers, 2004), which continues to the current day (De Villiers *et al.*, 2016). Whereas, in Kleinmond no conservation measures have been taken to conserve *X. gilli*, as they occur on privately owned land. By comparing survival of these two *X. gilli* populations I aim to determine if *X. laevis* negatively affect the survival of *X. gilli*. The survival of *X. laevis* has not yet been determined in South Africa. Survival estimates will be supported by information gathered from the age class distribution and growth. The comparison of age class distributions between these two species will give additional insight on the effect that *X. laevis* has on the local species where it invades and how effective it will be in invading a new habitat. It will further give an indication on what effect *X. laevis* has on the recruitment ability of *X. gilli*. Growth will give an indication as to the well being of the animals as well as give insight into the ecology of these two species. Growth has only been recorded in invasive *X. laevis* populations in California and Wales (see McCoid & Fritts, 1980; Measey, 2001) and as such the growth of *X. laevis* in their natural range is unknown.

The aim of this study was to obtain information about the age structure, growth and survival of *X. laevis* and *X. gilli*, as well as determine whether *X. laevis* has a negative effect on the survival and age structure of *X. gilli*. This information will be obtained using CMR data, growth data and with the use of skeletochronology. I aim to test whether the presence of *Xenopus laevis* has a negative effect on the survival as well as the age structure of *Xenopus gilli*. From this hypothesis follows the following predictions: i) The *Xenopus gilli* population in Kleinmond will have a reduced survival rate compared to the population in the Cape of

Good Hope nature reserve ii) *Xenopus laevis*, in both the permanent ponds and the temporary ponds, will have a higher survival estimate than *Xenopus gilli* individuals; iii) the Kleinmond *X. gilli* will have an age structure which is more skewed towards the older individual.

## 1.2 Materials and Methods

### 1.2.1 Sampling sites

Two sites where *X. gilli* are known to occur were used in this study: Kleinmond and the Cape of Good Hope section of Table Mountain National Park (CoGH; see Fogell *et al.*, 2012). In CoGH *X. laevis* have been actively removed since 1985 as a method to conserve *X. gilli* (Picker & De Villiers, 1989; De Villiers, 2004). In Kleinmond, to date, there has been no effort to conserve *X. gilli* as most of its occurrence is on privately owned land (De Villiers *et al.*, 2016). Both these sites are characterised by the presence of permanent and temporary fresh water-bodies. In each case the permanent water-bodies are artificial, while the temporary water-bodies are natural. In CoGH four temporary ponds and three permanent ponds were sampled, and in Kleinmond five temporary ponds and three permanent ponds were sampled (Figure 1.1). Frogs were collected by using either baited traps (bucket and fyke net traps; see Measey 2001; Lobos & Measey, 2002) or by dragging a 10m purse seine net through the water (Kobel *et al.*, 1981; Picker & De Villiers, 1989; Evans *et al.*, 1998). Trapping was done for three consecutive nights, each night the traps were set and collected again the following morning. This was done as a requirement for the robust model design (White & Burnham, 1999). Ethical clearance was obtained from Stellenbosch University (SU-ACUD14-00028) and the relevant collection and field work permits were collected from CapeNature (AAA007-00092-0056) and SANParks.

### 2.2.2 Age structure

Two phalanges (from an outer toe) from either left or right hind foot were removed from 40 frogs of each species at each site to use in skeletochronology. The two outer phalanges of each toe were removed by cutting, with a pair of scissors, through the joint of the third phalange (Measey, 2001). Each toe was placed in 2 ml of 100% ethanol directly after it had

been cut. Each toe was then transferred to a 10% formalin solution for fixation after which it was transferred to a 2.5% nitric acid (for 18h) for decalcification. After decalcification each toe was dehydrated and embedded into paraffin wax. The toes were sectioned using a microtome, and each section was between 12 and 15 $\mu$ m thick. The sections were stained using Harris' haematoxylin and eosin staining methods (Measey, 2001; Cheong *et al.*, 2007). Each section was photographed at both 40 $\times$  and 100 $\times$  magnification, using a Leica EC 3 microscope camera that was mounted on a light microscope and the number of LAG was counted (Smirina, 1994). The production of a LAG in many species of temperate anurans is suggested to be annual (see Smirina, 1994), as such the number of LAGs are used to determine the age of the individual. However, for *Xenopus* in South Africa it is not known if this technique can be used. The relationship between the number of LAGs and the snout-vent-length (SVL; i.e. the distance between the snout and the vent) were determined using a non-linear regression. All statistical analyses were done in R Studio, 3.2 (R Core team, 2015).

### **2.2.3 Growth**

All frogs that were capture were sexed, using external sexual features, and then photographed on a 10mm  $\times$  10mm grid paper to measure their SVL using ImageJ (Rasbrand, 2012). If a frog that was tagged in the first year and recaptured in the second year it would be photographed again. The photographs of these frogs were then measured again and the difference in SVL was calculated to represent growth over a known time period. The time period between the initial capture time and recapture time was determined and the difference in SVL was divided by the number of days between the two capture events. This gave an indication of the daily growth of each individual frog. The relationship between the growth and the initial SVL was then determined using a non-linear regression in R Studio, 3.2 (R Core team, 2015).



### 2.2.4 Survival

All *Xenopus* frogs were injected with an 8mm PIT tag (972 FDX-B, Planet ID, Essen Germany) that was inserted, using a 15 gauge needle, underneath the skin in the dorsal lymph sac area. Animals below a SVL of 30mm were not tagged as it was thought that doing so may affect the survival of that frog. After the frogs were tagged they were released back to their place of capture. Frogs that were recaptured were scanned using an Agrident APC 250 scanner (Agrident, Barsinghausen Germany). Each tag has a unique number which, when scanned, is displayed (and stored) by the scanner. After the frogs were released from the bucket in which they were held (less than two hours), the scanner was used to determine if any tags were lost. Untagged frogs were also checked for markings that indicated they were tagged previously: The hole in the skin that was made by the needle closed within three weeks, as such very low tag loss was recorded (only five frogs in 3 449 marked). Recapture events were recorded in binary (i.e. 1 if frog is capture and 0 if the frog was not captured). Due to the active removal of *X. laevis* by SANParks only *X. gilli* were tagged in CoGH, whereas both species were tagged in Kleinmond.

Preliminary analyses showed that there was no difference in survival between the sexes of the species and as such sexes were grouped together. For the purpose of this study the frogs were divided into two groups; small and large. This was based on the mean size of each species, with the 'small' frogs being the individuals below the mean size and the large frogs being the individuals above the mean size. The two *X. gilli* populations and *X. laevis* were each treated as separate groups. The two *X. gilli* populations were separated not only for the purpose of this study but also because they are two genetically distinct populations (see Evans *et al.*, 1998; Fogell *et al.*, 2013), whereas *X. laevis* in both sites are genetically homogenous (see Evans *et al.*, 1998; Measey & Channing, 2003). Prior to using these models Goodness-of-fit (GOF) testing was done with RELEASE in MARK (White & Burnham,

1999). The data were also checked for any over dispersion by using the  $\hat{c}$  statistic provided by MARK during GOF testing (White & Burnham, 1999). The models that were tested are represented in Table 1. During these preliminary analyses, it was found that the data violated the assumptions of a Robust Design model. Therefore, a Cormack-Jolly-Seber (CJS) model was used to determine the survival of these frogs. When the data showed strong trap dependence and transients the base model was changed to  $\phi(M-t/t)p(t^*m)$ , where (M-t/t) models for transients and (t\*m) models for trap dependence. Model fit was determined using the Akaike's information criterion (AICc), with the model with the lowest AICc being the best model (Anderson & Burnham, 1999).

## 2.3 Results

A total of 3 449 *Xenopus* frogs were tagged over a 21 month period. Of these, 1 740 were *X. laevis* and 1 709 were *X. gilli*. In Kleinmond 563 *X. gilli* was tagged and 1 146 *X. gilli* in COGH. In Kleinmond five hybrids were also tagged but not included in the study. The mean size of *X. laevis* was 65mm and the mean size of *X. gilli* was 43mm (Figure 2.2), these were the sizes that were used to differentiate between small and large individuals of the two species.

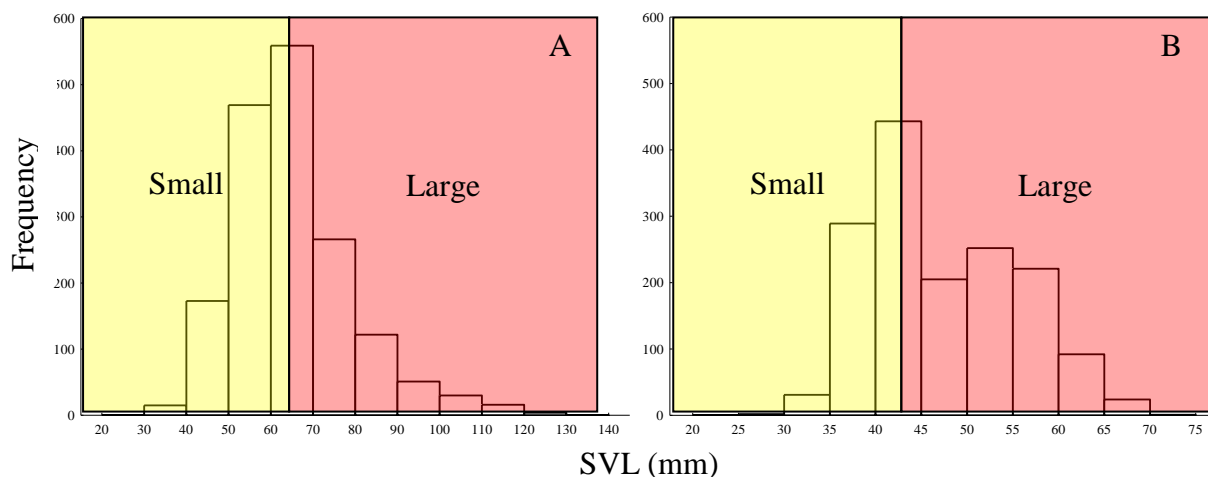


Figure 2.2: Indicating the groups that were used for the survival analyses that were based on the mean sizes of *X. gilli* and *X. laevis*. A) the size distribution of *X. laevis* and B) the size distribution of *X. gilli*.

### 2.3.1 Age structure

A total of 160 toes were sectioned, 80 from both the CoGH and the Kleinmond *X. laevis* populations, and 80 from the two *X. gilli* populations. For 27 individuals, age could not be determined due to the sections being too poor to determine LAG, and so were discarded from the study. A prescribed allometric growth function could not fit the data and as such a logarithmic function that best fitted the age data was used to explain age as a function of

SVL. For the CoGH *X. laevis* age was significantly log correlated with size for both males ( $r=0.6862$ ,  $n=16$ ,  $p=0.003$ ; Figure 2.3A) and females ( $r=0.6771$ ,  $n=16$ ,  $p=0.004$ ; Figure 2.3A). The CoGH *X. gilli* showed no log correlation for either males ( $r=0.0741$ ,  $n=17$ ,  $p=0.7773$ ; Figure 2.3B) or females ( $r=0.2648$ ,  $n=16$ ,  $p=0.3402$ ; Figure 2.3B). Only the females, of the Kleinmond *X. laevis*, ( $r=0.6008$ ,  $n=20$ ,  $p=0.005$ ; Figure 2.3C) showed a significant log correlation between age and SVL whereas there was no correlation for the males ( $r=0.2226$ ,  $n=16$ ,  $p=0.4648$ ; Figure 2.3C). This was also the case for the Kleinmond *X. gilli* where there was only a significant correlation found for females ( $r=0.5356$ ,  $n=19$ ,  $p=0.0147$ ; Figure 2.3D) and not males ( $r=0.4263$ ,  $n=13$ ,  $p=0.0997$ ; Figure 2.3D).

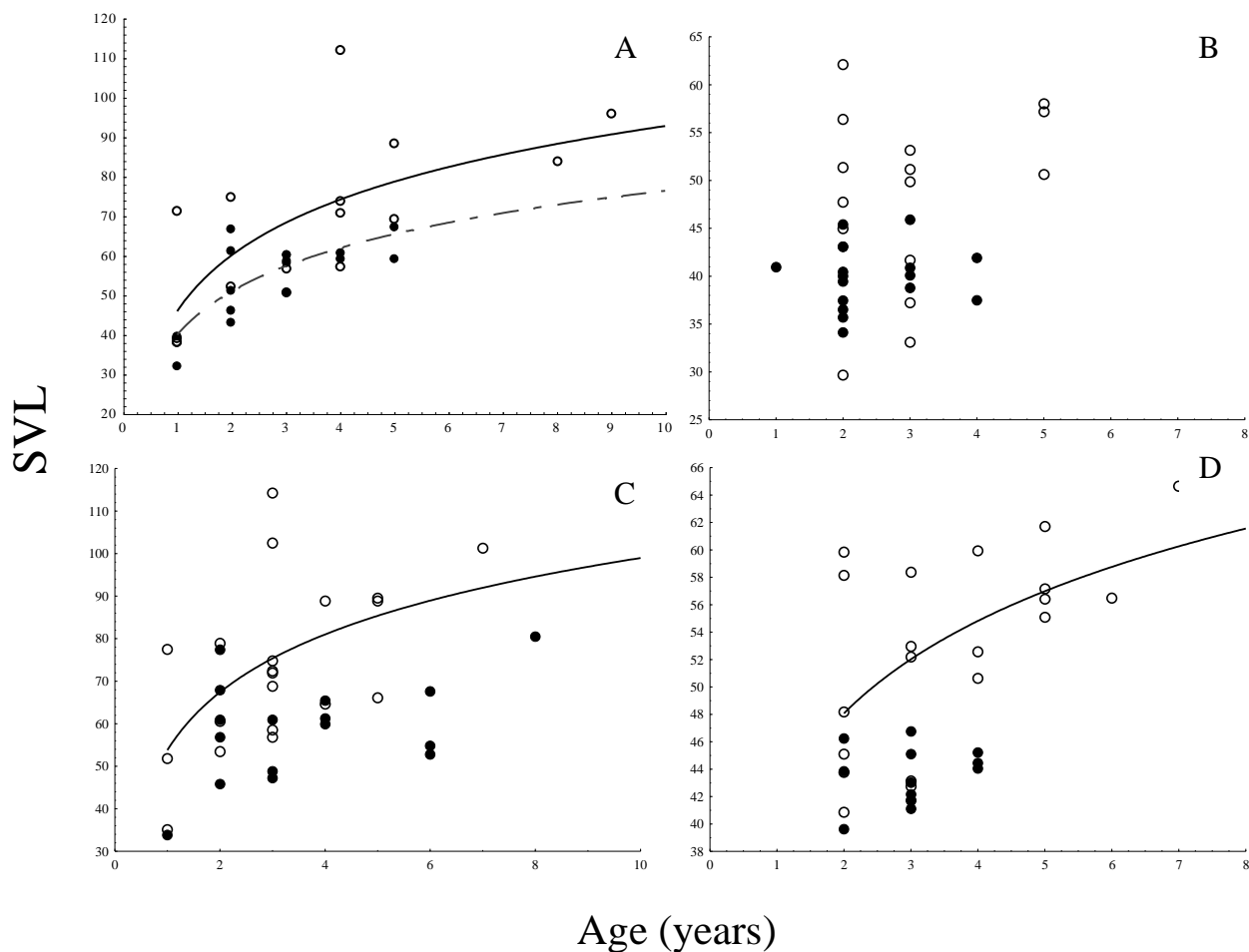


Figure 2.3: The age of *Xenopus* frogs as a function of the size of the animal. A) The age of *X. laevis* and B) *X. gilli* from CoGH. The age of the Kleinmond populations of C) *X. laevis* and D) *X. gilli*. The open black circles indicate females and the closed gray circles indicate males. Lines indicate significant log correlation, solid line for females and dashed line for males.

### 2.3.2 Growth

The daily growth of 268 frogs was determined in this study and expressed as a function of initial SVL. Initial SVL was used to determine whether the larger individuals grow slower than the smaller individuals. Both males ( $r=-0.5926$ ,  $n=67$ ,  $p<0.0001$ ; Figure 2.4A) and females *X. laevis* ( $r=-0.5028$ ,  $n=109$ ,  $p<0.0001$ ; Figure 2.4A) showed a significant inverse log correlation between daily growth and initial SVL. In the Kleinmond *X. gilli* population only the females growth was significantly correlated with SVL ( $r=-0.7549$ ,  $n=14$ ,  $p=0.0018$ ; Figure 2.4B) and not the males ( $r=-0.5320$ ,  $n=9$ ,  $p=0.1404$ ; Figure 2.4B). In the CoGH *X. gilli*

population both the males ( $r=-0.7076$ ,  $n=18$ ,  $p=0.001$ ; Figure 2.4C) and the females ( $r=-0.4309$ ,  $n=61$ ,  $p<0.001$ ; Figure 2.4C) were significantly log correlated with initial SVL.

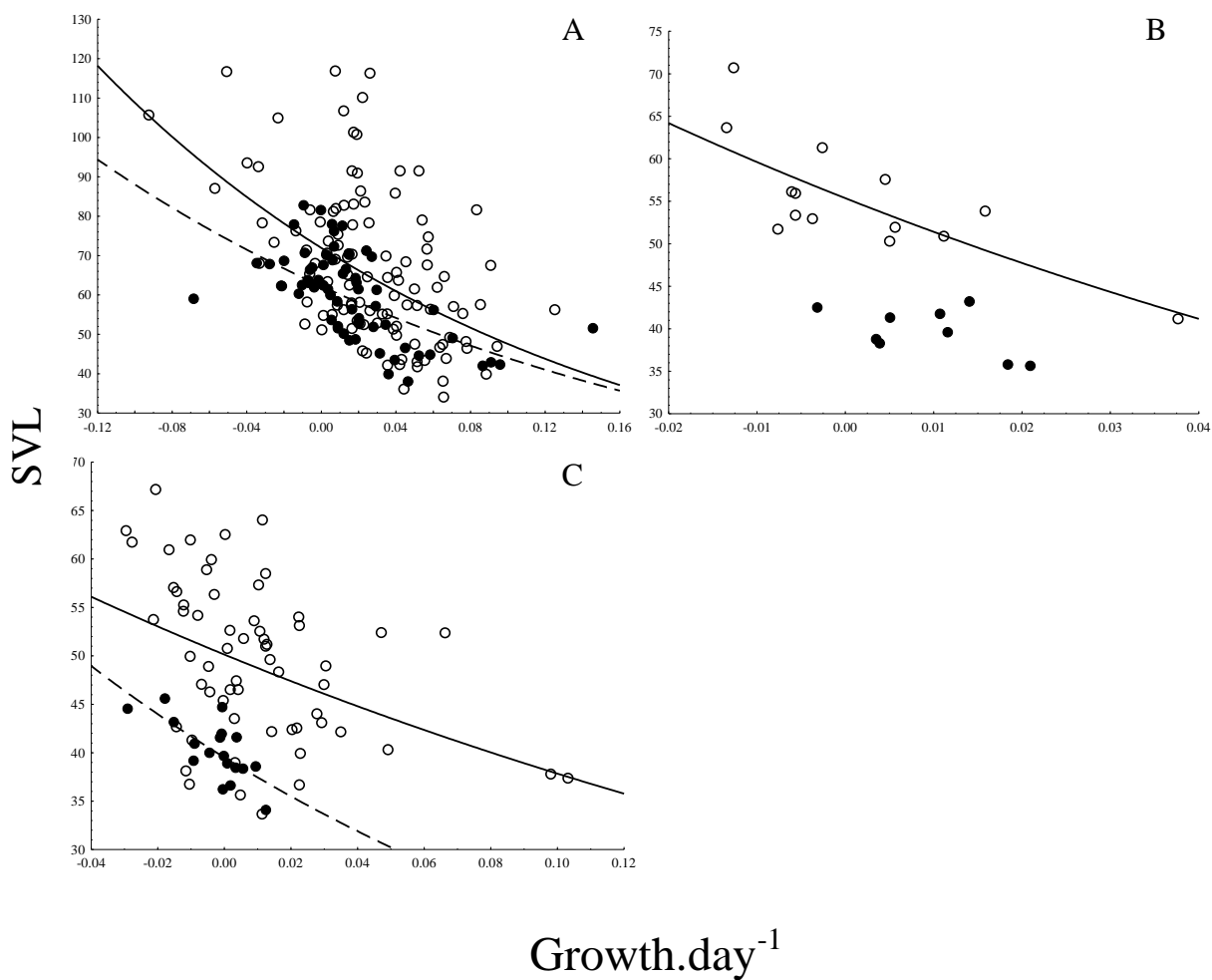


Figure 2.4: The daily growth of *X. laevis* and the two *X. gilli* populations. A) The daily growth of the males and females of *X. laevis*, B) the Kleinmond *X. gilli* population and C) the CoGH *X. gilli* population. The open black circles indicate females and the closed black circles indicate males. Black solid lines indicate log correlation significance for females and the dashed lines indicate significance for males.

### 2.3.3 Survival

The best model in all tested groups (i.e. both permanent and temporary ponds in both species) indicated that survival varied over time (Table 1A-E, Figure 2.5) In *Xenopus laevis* six monthly survival fluctuated around a mean of 0.381 (SE  $\pm$ 0.102). The Kleinmond *X. gilli* had a mean survival, over six months, of 0.319 (SE  $\pm$  0.121) and the CoGH *X. gilli* had a mean survival, over six months, of 0.562 (SE  $\pm$  0.152) In *X. laevis* the winter survival was higher than the summer survival (Figure 2.5) and in the Kleinmond *X. gilli* the survival in 2014 was constant with the smaller individuals having a higher survival (Figure 2.5). In 2015 the survival dropped lower than in 2014, with the smaller individuals having the lowest survival (Figure 2.5). Survival in the CoGH population was higher during the summer months and lower in the winter (Figure 2.5). In both *X. laevis* and the CoGH *X. gilli* the small and the large individuals had similar survival throughout the sampling period (Figure 2.5).



Table 2.1: Model selection for *X. laevis* and the two *X. gilli* populations. Only the best four models are shown. The models that were used are shown in bold. The Akaike's Information Criterion (AICc) was used to choose the best model (the lowest value indicated the best model). The delta AICc is an indication of the difference between the best model and the specific model. The AICc weight ( $w_i$ ) indicates the support of that model compared to the other models. The number of estimated parameters of each model is given in the Num. Par. column. The Deviance indicates the  $-2\log$  Likelihood between the selected model and the model with the same number of parameters as the sample size (the saturated model). Model Notation:  $\phi$  indicates survival,  $p$  indicates recapture probability. (t) Indicated that the specific variable varied over time, whereas (.) indicates that the variable is constant. If there was a transient effect it was indicated by M-x/x. Trap dependence was indicated by  $t^*m$ . If a model assumed that sex classes varied synchronously over time it was indicated with //.

Model	AICc	Delta AICc	AICc $w_i$	Num. Par.	Deviance
A) Models selection for <i>X. laevis</i> captured in the permanent water bodies					
<b>1 <math>\phi(\text{Size}+\text{M}-t//t)\text{P}(\text{Size}+t^*m)</math></b>	<b>11952.44</b>	<b>0.00</b>	<b>1.0</b>	<b>51</b>	<b>11849.21</b>
2 $\phi(\text{Size}+\text{M}-//.)\text{P}(\text{Size}+t^*m)$	11999.25	46.81	0.00	29	11940.85
3 $\phi(\text{Size}+\text{M}-t//t)\text{P}(\text{Size}^*m)$	12147.64	195.19	0.00	29	12089.24
4 $\phi(\text{Size}^*\text{M}-t/t)\text{P}(\text{Size}^*t^*m)$	11334.39	208.9856	0.00	6	11322.37
B) Model selection for <i>X. laevis</i> that were captured in temporary ponds					
<b>1 <math>\phi(\text{Size}+t)\text{P}(\text{Size}+t^*m)</math></b>	<b>2779.29</b>	<b>0.00</b>	<b>1.0</b>	<b>25</b>	<b>2728.28</b>
2 $\phi(\text{Size})\text{P}(\text{Size}+t^*m)$	2806.51	27.22	0.00	15	2776.14
3 $\phi(\text{Size}+t)\text{P}(\text{Size}^*m)$	2850.70	71.61	0.00	15	2820.33
4 $\phi(\text{Size}^*t)\text{P}(\text{Sex}^*t^*m)$	2860.71	81.41	0.00	38	2782.37
C) Model selection for the Kleinmond <i>X. gilli</i> population					
<b>1 <math>\phi(\text{Large}+\text{M}-t//t)\text{P}(\text{Size}+t^*m)</math></b>	<b>1400.69</b>	<b>0.00</b>	<b>0.997</b>	<b>24</b>	<b>1350.98</b>
2 $\phi(\text{Large}+\text{M}-//.)\text{P}(\text{Size}+t^*m)$	1412.57	11.88	0.003	15	1381.89
3 $\phi(\text{Large}+\text{M}-t//t)\text{P}(\text{Size}^*m)$	1438.02	37.33	0.00	16	1405.25
4 $\phi(\text{Large}+\text{M}-//.)\text{P}(\text{Size}^*m)$	1493.59	92.9053	0.00	6	1481.48

Model	AICc	Delta AICc	AICc wi	Num. Par.	Deviance
D) Model selection for the CoGH <i>X. gilli</i> population					
<b>1 <math>\varphi(\text{Size}+\text{M}-\text{t}/\text{t})\text{P}(\text{Size}+\text{t}^*\text{m})</math></b>	<b>4276.58</b>	<b>0.00</b>	<b>1.00</b>	<b>35</b>	<b>4205.08</b>
2 $\varphi(\text{Size}*\text{M}-\text{t}/\text{t})\text{P}(\text{t}^*\text{m})$	4310.65	34.07	0.00	61	4184.09
3 $\varphi(\text{M}-\text{t}/\text{t})\text{P}(\text{t}^*\text{m})$	4339.36	62.79	0.00	42	4253.21
4 $\varphi(\text{M}-\text{t}/\text{t})\text{P}(\text{Size}*\text{t}^*\text{m})$	4339.97	63.39	0.00	54	4228.41

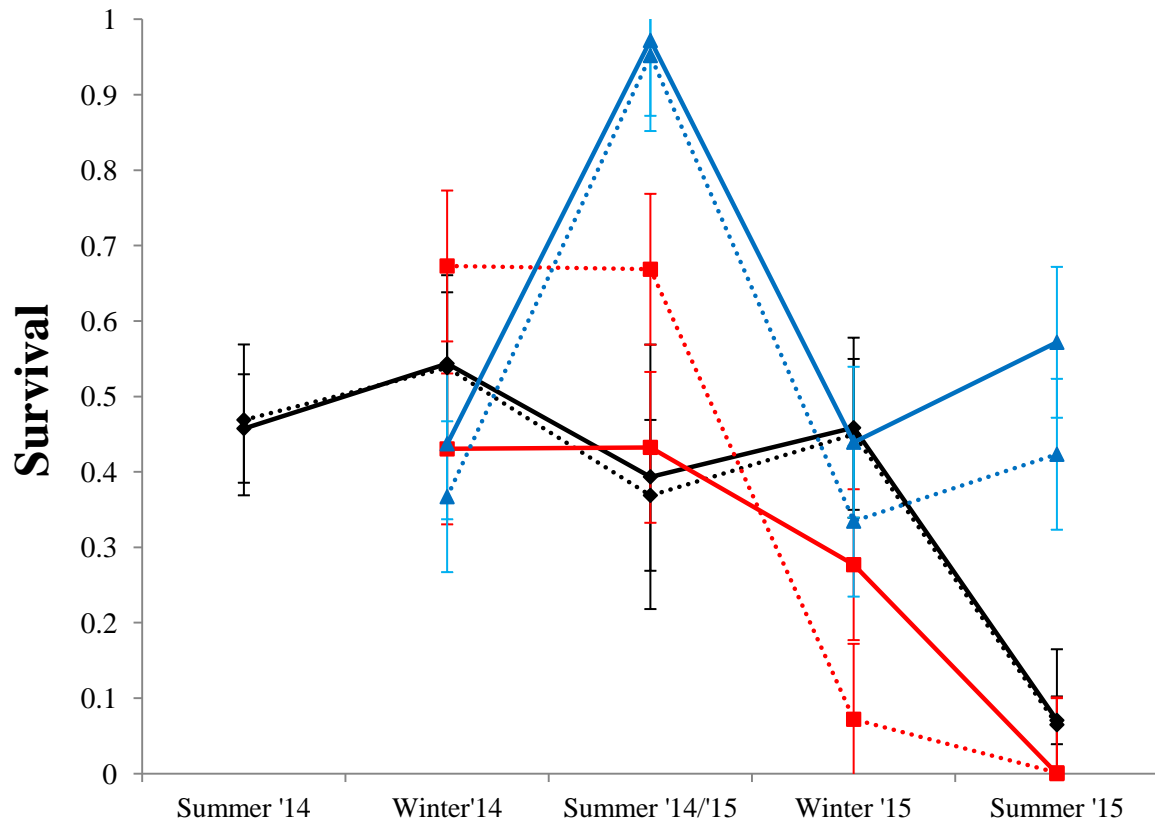


Figure 2.5: The summer and winter survival estimates of *X. laevis* and two *X. gilli* populations. The black lines represent the fluctuation in survival of *X. laevis*, whereas the blue lines represent the survival of the CoGH *X. gilli* and the red lines the Kleinmond *X. gilli*. The small individuals are represented by the non-continuous line, whereas the large individuals are represented by solid line. The error bars represent the standard error.

## 2.4 Discussion

The main findings for this study are firstly, that all the *X. gilli* from Kleinmond that could be aged was older than two years of age. This suggests a lack of recruitment for at least the last two years, or it could be due to sampling error. De Villiers *et al.* (2016) have shown that in Kleinmond there is a lack of smaller *X. gilli* which could be indicative of a lack of recruitment. Secondly, that CoGH generally had a higher survival than the Kleinmond population (the only exception being the 2014 winter), which also suggests that *X. laevis* does have a negative effect on the survival of *X. gilli*.

Skeletochronology has been used as a method to determine age structure in temperate (see Halliday & Verrell, 1988; Smirina, 1994), desert (e.g. Kuzmin & Ischenko, 1997), and tropical climates (Khonsue *et al.*, 2000; Kumbar & Pancharatna, 2001), however these are all terrestrial frogs. Measey (2001) has also shown that skeletochronology is an effective way to determine age structure in the invasive *X. laevis* population of Wales. However in this study I was unable to determine the age structure, from SVL, of all the *X. gilli* and *X. laevis* that were captured, because of the lack of fit in the data. This requires future research to determine if LAG are produced each year. In a natural system the temporary ponds, in which *X. gilli* reside, would fill up in the rainy winter season and then dry up again in the dry summer season. As such these frogs aestivate to survive the dry summer months and as a result growth is ceased and LAG are formed. In the current non-natural system there are artificial permanent water-bodies present which provide an alternative to aestivating. Frogs are now able to spend the dry summer months feeding in the permanent water-bodies. In this situation, as growth continues, due to the continuous availability of food, LAG are not produced. In such situations it is possible that large animals only have a single LAG (Figure 2.3), this then does not represent the actual age of the animals as LAG might not have formed each year. *Xenopus gilli* naturally occur in the temporary water-bodies and aestivate during the summer

(De Villiers, 2004). This was indicated by the significant log correlation of SVL and age in the Kleinmond *X. gilli* females (Figure 2.3D). Interestingly, there was a lack of fit in the Kleinmond *X. gilli* males (Figure 2.3D), however, this might be explained by the lack of smaller individuals in the sample. The smallest *X. gilli* from the Kleinmond population that was used had a SVL of 39mm which is already a reproductively active frog (the smallest *X. gilli* that was reproductively active was 35mm; pers. obs.). This lack of smaller frogs does not represent collection bias but rather the lack of smaller *X. gilli* in the Kleinmond population (see De Villiers *et al.*, 2016). In CoGH three artificial permanent water-bodies are present making the area a non-natural system. As such the lack of fit between age and SVL, in the CoGH *X. gilli*, was not surprising as these frogs make use of the alternative option and spend their summers in the permanent water-bodies. *Xenopus laevis* are known to prefer permanent water-bodies (Measey, 2004b), and as such are expected to have a lack of fit. However, there was a significant log correlation found between age and SVL in *X. laevis* (except for the *X. laevis* males from Kleinmond). This would suggest that either they also aestivate during the summer (see McCoid & Fritts, 1980) or they cease growth due to other factors, for example low food availability and water levels in summer.

Both species showed a reduced growth rate with an increase in SVL (Figure 2.3). This is the case for most amphibians (see Turner, 1960a). Even though amphibians have indeterminate growth (Woolbright, 1983), growth is reduced when the animal gets older (Turner, 1960a, Woolbright, 1983). In both species it was shown that males had a lower growth rate than females, which were supported by data from McCoid and Fritts (1989) and Measey (2001). The lack of fit that was shown for the Kleinmond *X. gilli* males might be due to the lack of data. The temporary water bodies in Kleinmond had low water levels due to the low rainfall that was experienced. This resulted in only certain number of animals emerging from their aestivation, which resulted in low recaptures and the lack of growth data. Both species

showed some negative growth, with the extreme cases in *X. laevis* (Figure 2.3). This negative growth is due to the way the SVL of the animals were measured. The genus *Xenopus* is unique in the sliding articulation of the ilium, as it slides back and forth rather than articulate (Videler & Jorna, 1985). As such, if the ilium was in a more backwards position (i.e. the frog was more stretched out) when first photographed compared to the second time it may result in negative growth. As such the growth rate could be under estimated. Whiting (1960) has shown that the sliding action of the *Xenopus* ilium could reduce body length by up to 18%. However, in *X. laevis* there were two instances where a negative growth greater than 18% was recorded (-25.96% & -33.31%), which may indicate that Whiting (1960) under-estimated the amount by which the sliding articulation could reduce body length. McCoid and Fritts (1989) has shown that the growth rate of *X. laevis* in California could be expressed by the equation  $y^3 = 0.96x + 18.04$  for females and  $y^3 = 0.44x + 58.65$  for males. In the equation  $y$  is the size of the animal in centimetre and  $x$  is time in days Measey (2001) had a lower growth rate in the Welsh population (males:  $y^3 = 0.14x + 147.41$  and females:  $y^3 = 0.27x + 104.26$ ), which he accredited to a shorter growth season. In this study the growth rate (Males:  $y^3 = 0.32x + 178.47$ ; Females:  $y^3 = 0.62x + 252.56$ ) was approximately double that of the Welsh population, however it was still lower than the growth rate recorded for the California population. The lower growth rate of the Welsh population is to be expected as the Welsh population has a shorter growth season as accredited by Measey (2001). However the higher growth rate in the California population is unexpected. California also has a Mediterranean climate and as such the growth rate should be similar. The lower growth rate can be accredited to the harsh summer that these animals experienced (Figure 2.6), which could have led to a lower growth rate due to the lack of food.



Figure 2.6: Pictures of the same *X. laevis* at two different time periods, indicating the difference in SVL between capturing sessions. The SVL at initial capture was 105mm and at the second capture event 82mm. This is also an indication of the harsh summer that was experienced by these animals

Wood *et al.* (1998) found that in the males and the juveniles of the pig frog (*Lithobates grylio*) had very similar monthly survival (0.75 for males and 0.72 for juveniles). However in general it is found that, in anurans, juvenile survival is lower than adult survival (see Turner, 1960b). Survival of *Xenopus* frogs are unknown as this is the first study to report on the survival of adult *Xenopus* species. In this study each species was divided into small and large, depending on the species' mean size, rather than adults and juvenile (Figure 2.2). This was due to the low capture and recapture rates that were experienced in the juvenile frogs. In both *X. laevis* and the CoGH *X. gilli*, the small and large individuals had similar survival throughout the duration of this study, which was in accordance with that of Wood *et al.* (1998). The Kleinmond *X. gilli* had the lowest mean survival of three groups tested (i.e. *X. laevis*, CoGH *X. gilli* and Kleinmond *X. gilli*). This negative effect might be mainly through competition rather than predation. Vogt *et al.* (Unpublished data) have shown that *X. laevis* prey on all life stages of *X. gilli* (Figure 2.7), however most of the predation occurs on the eggs and the larva of *X. gilli*. As such with high predation of the early life stages (i.e. eggs

and larva) the number of metamorphs is expected to be low. Results from De Villiers *et al.* (2016) indicate that there is a lack in recruitment in the Kleinmond *X. gilli*. With this lower metamorph density it is possible that the survival of the smaller *X. gilli* to be higher due to reduced intraspecific competition. Purrenhage and Boone (2009) have shown that the survival of northern leopard frog (*Rana pipiens*) metamorphs increased with a decrease in metamorph density. This might be one reason for smaller *X. gilli* individuals having higher survival than the larger individuals. Evidence has been found that *X. laevis* actively prey on adult *X. gilli* (Vogt *et al.*, Unpublished data; Figure 2.7), which also has an effect on the overall survival and might be one of the reason for the Kleinmond *X. gilli* having lower survival than the CoGH *X. gilli*. Another reason for the lower survival of Kleinmond *X. gilli*, compared to the CoGH *X. gilli*, might be due to interspecific competition. Vogt *et al.* (Unpublished data) have shown that there is an overlap in diet between *X. laevis* and *X. gilli* in both Kleinmond and CoGH indicating that there is direct competition for food resources. With the removal of *X. laevis* in CoGH there is allot less *X. laevis* present in the same water-bodies than *X. gilli* compared to Kleinmond. As such the potential for competition is a lot higher in Kleinmond and might be the reason for the lower overall survival of the Kleinmond *X. gilli*. In the summer of 2014/2015 the CoGH *X. gilli* have an exceptionally high survival. During the summer months these frogs reside in the permanent water-bodies and do not move between ponds, as previously mentioned. As a result all of the frogs are concentrated in a small area and are easier to catch. During this specific time these permanent water-bodies had extremely low water levels and as such it was even easier to capture these animals. This resulted in a high recapture rate (i.e. most of the frogs present in the specific pond were captured each sampling occasion) which resulted in the high survival.





Figure 2.7: A partly digested adult *X. gilli* that was regurgitated by a *X. laevis*.

In conclusion, this study has shown that *Xenopus laevis* has a negative effect on the survival of *X. gilli*, however the effect that *X. laevis* had on the age structure of *X. gilli* could not be determined. The CoGH *X. gilli* had the highest survival whereas the Kleinmond *X. gilli* had the lowest survival. This low survival in the Kleinmond *X. gilli* was accredited to the competition and predation by *X. laevis*. The age structure of *X. laevis* and *X. gilli* was not obtainable by means of skeletochronology, due to the presence of artificial water-bodies and the lack of aestivation, which lead to a lack of LAG production.

## **Literature cited**

- Alford, R. A., & Richards, S. J. (1999). Global amphibian declines: a problem in applied ecology. *Annual review of Ecology and Systematics*, **30**, 133-165.
- Alford, R. A., Brown, G. P., Szwarczopf, L., Phillips, B. L. & Shine, R., (2009). Comparisons through time and space suggest rapid evolution of dispersal behaviour in an invasive species. *Wildlife Research* **36**, 23-28.
- Altwegg, R., Ringsby, T. H., & SÆther, B. E. (2000). Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows *Passer domesticus*. *Journal of Animal Ecology*, **69**, 762-770.
- Anderson, D. R., & Burnham, K. P. (1999). Understanding information criteria for selection among capture-recapture or ring recovery models. *Bird Study*, **46**, S14-S21.
- Arnold, S. J. & Bennett, A. F., (1984). Behavioural variation in natural populations. III. Antipredator displays in the garter snake *Thamnophis radix*. *Animal Behavior*, **32**, 1108-1118.
- Awise, J. C. (2000). *Phylogeography: the history and formation of species*. Harvard university press. Pp170-180.
- Bean, A. R. (2007). A new system for determining which plant species are indigenous in Australia. *Australian Systematic Botany*, **20**, 1-43.
- Biek, R., Funk, W. C., Maxell, B. A., & Mills, L. S. (2002). What is missing in amphibian decline research: insights from ecological sensitivity analysis. *Conservation Biology*, **16**, 728-734.

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U. & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, **26**, 333-339.

Blaustein, A. R., & Wake, D. B. (1990). Declining amphibian populations: a global phenomenon. *Trends in Ecology and Evolution*, **5**, 203-204.

Blaustein, A. R., Wake, D. B., & Sousa, W. P. (1994). Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology*, **8**, 60-71.

Blender Foundation, 1994. *Blender 2.74*. [blender.org](http://blender.org). March 31, 2015. Retrieved June ,2015.

Bo Liao, W. & Lu, X., (2010). Age structure and body size of the Chuanxi Tree Frog (*Hyla annectans chuanxiensis*) from two different elevations in Sichuan (China). *Zoologischer Anzeiger-A Journal of Comparative Zoology*, **248**, 255-263.

Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, **80**, 205-225.

Bowler, D. E., & Benton, T. G. (2009). Variation in dispersal mortality and dispersal propensity among individuals: the effects of age, sex and resource availability. *Journal of Animal Ecology*, **78**, 1234-1241.

Careau, V., Biro, P. A., Bonneaud, C., Fokam, E. B., & Herrel, A. (2014). Individual variation in thermal performance curves: swimming burst speed and jumping endurance in wild-caught tropical clawed frogs. *Oecologia*, **175**, 471-480.

- Cheong, S. W., Park, D. S., Sung, H. C., Lee, J. H., & Park, S. R. (2007). Skeletochronological age determination and comparative demographic analysis of two populations of the gold-spotted pond frog (*Rana chosenica*). *Journal of Ecology and Environment*, **30**, 57-62.
- Clobert, J., Oppliger, A., Sorci, G., Ernande, B., Swallow, J. G., & Garland, T. (2000). Trade-offs in phenotypic traits: endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*. *Functional Ecology*, **14**, 675-684.
- Clobert, J., Galliard, L., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, **12**, 197-209.
- Collins, J. P., & Storfer, A. (2003). Global amphibian declines: sorting the hypotheses. *Diversity and Distributions*, **9**, 89-98.
- Davies, S. J., Clusella-Trullas, S., Hui, C., & McGeoch, M. A. (2013). Farm dams facilitate amphibian invasion: Extra-limital range expansion of the painted reed frog in South Africa. *Austral Ecology*, **38**, 851-863.
- De Bruyn, L., Kazadi, M., & Hulselmans, J. (1996). Diet of *Xenopus fraseri* (Anura, Pipidae). *Journal of Herpetology*, **30**, 82-85.
- De Moor, I. J., & Bruton, M. N. (1988). *Atlas of alien and translocated indigenous aquatic animals in southern Africa*. National Scientific Programmes Unit: CSIR.
- De Villiers, A. L., 2004. *Xenopus gilli* Rose and Hewitt, 1927. In: Minter, L. R., Burger, M., Harrison, J. A., Braack, H. H. Bishop, P. J. and Kloepfer, D. eds. *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland*. SIMAB Series #9. Smithsonian Institution, Washington, DC. Pp. 260-263.

De Villiers, F. A., De Kock, M. & Measey, G. J. (2016). Controlling the African clawed frog *Xenopus laevis* to conserve the Cape platanna *Xenopus gilli* in South Africa. *Conservation Evidence*, **12**.

Doebeli, M. (1995). Dispersal and dynamics. *Theoretical Population Biology*, **47**, 82-106.

Donnelly, M. A., Guyer C., Juterbock, E. J. & Alford, R. A., (1994). Techniques for marking amphibians. In: WR Heyer, ed. *Measuring and monitoring biological diversity: standard methods for amphibians*. Smithsonian Institution Press, Washington. 277–284.

Driscoll, D. A. (1999). Skeletochronological assessment of age structure and population stability for two threatened frog species. *Australian Journal of Ecology*, **24**, 182-189.

Ducatez, S., Baguette, M., Trochet, A., Chaput-Bardy, A., Legrand, D., Stevens, V., & Fréville, H. (2013). Flight endurance and heating rate vary with both latitude and habitat connectivity in a butterfly species. *Oikos*, **122**, 601-611.

Duellman, W. E., & Trueb, L. (1986). *Biology of amphibians*. JHU Press.

Dunning Jr, J. B., Stewart, D. J., Danielson, B. J., Noon, B. R., Root, T. L., Lamberson, R. H. & Stevens, E. E. (1995). Spatially explicit population models: current forms and future uses. *Ecological Applications*, **5**, 3-11.

Eggert, C., & Fouquet, A. (2006). A preliminary biotelemetric study of a ferai invasive *Xenopus laevis* population in France. *Alytes*, **23**, 144-149.

Elepfandt, A., Eistetter, I., Fleig, A., Gunther, E., Hainich, M., Hepperle, S., & Traub, B. (2000). Hearing threshold and frequency discrimination in the purely aquatic frog *Xenopus laevis* (Pipidae): measurement by means of conditioning. *Journal of Experimental Biology*, **203**, 3621-3629.

Emerson, S. B. (1978). Allometry and jumping in frogs: helping the twain to meet. *Evolution*, **32**, 551-564.

Evans, B. J., Morales, J. C., Picker, M. D., Kelley, D. B. & Melnick, D. J., (1997). Comparative molecular phylogeography of two *Xenopus* species, *X. gilli* and *X. laevis*, in the south-western Cape Province, South Africa. *Molecular Ecology*, **6**, 333-343.

Evans, B. J., Morales, J. C., Picker, M. D., Melnick, D. J. & Kelley, D. B., (1998). Absence of extensive introgression between *Xenopus gilli* and *Xenopus laevis laevis* (Anura: Pipidae) in Southwestern Cape Province South Africa. *Copeia* **1998**, 504-509.

Faraone, F. P., Lillo, F., Giacalone, G., & Valvo, M. L. (2008). The large invasive population of *Xenopus laevis* in Sicily, Italy. *Amphibia-Reptilia*, **29**, 405-412.

Fogell, D. J., Tolley, K. A. & Measey, G. J., (2012). Mind the gaps: investigating the cause of the current range disjunction in the Cape Platanna, *Xenopus gilli* (Anura: Pipidae). *PeerJ* **DOI10.7717/peerj.166**, 1-23.

Fouquet, A. & Measey, G. J., (2006). Plotting the course of an African clawed frog invasion in Western France. *Animal Biology* **56**, 95-102.

Garland Jr, T., & Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In: Wianwright, P. C. & Reilly, S. M. eds. *Ecological morphology: integrative organismal biology*, University of Chicago Press, Chicago. Pp 240-302.

Goater, C. P. (1994). Growth and survival of postmetamorphic toads: interactions among larval history, density, and parasitism. *Ecology*, **75**, 2264-2274.

Goldwasser, L., Cook, J., & Silverman, E. D. (1994). The effects of variability on metapopulation dynamics and rates of invasion. *Ecology*, **75**, 40-47.

- Gomes, F. R., Rezende, E. L., Grizante, M. B., & Navas, C. A. (2009). The evolution of jumping performance in anurans: morphological correlates and ecological implications. *Journal of Evolutionary Biology*, **22**, 1088-1097.
- Grafe, T. U., Kaminsky, S. K., Bitz, J. H., Lüssow, H., & Linsenmair, K. E. (2004). Demographic dynamics of the afro-tropical pig-nosed frog, *Hemissus marmoratus*: effects of climate and predation on survival and recruitment. *Oecologia*, **141**, 40-46.
- Guimaraes, M., Corrêa, D. T., Sergio Filho, S., Oliveira, T. A., Doherty, P. F., & Sawaya, R. J. (2014). One step forward: contrasting the effects of Toe clipping and PIT tagging on frog survival and recapture probability. *Ecology and evolution*, **4**, 1480-1490.
- Halliday, T. R., & Verrell, P. A. (1988). Body size and age in amphibians and reptiles. *Journal of Herpetology*, **22**, 253-265.
- Hanski, I., & Gyllenberg, M. (1993). Two general metapopulation models and the core-satellite species hypothesis. *American Naturalist*, **142**, 17-41.
- Hellriegel, B. (2000). Single-or multistage regulation in complex life cycles: does it make a difference? *Oikos*, **88**, 239-249.
- Herrel, A., Gonwouo, L. N., Fokam, E. B., Ngundu, W. I. & Bonneaud, C., (2012). Intersexual differences in body shape and locomotor performance in the aquatic frog, *Xenopus tropicalis*. *Journal of Zoology*, **287**, 311-316.
- Herrel, A., & Bonneaud, C. (2012). Temperature dependence of locomotor performance in the tropical clawed frog, *Xenopus tropicalis*. *The Journal of Experimental Biology*, **215**, 2465-2470.



Hertz, P. E., Huey, R. B., & Garland, T. (1988). Time budgets, thermoregulation, and maximal locomotor performance: are reptiles olympians or boy scouts? *American Zoologist*, **28**, 927-938.

Holt, R. D. (1985). Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology*, **28**, 181-208.

Houlahan, J. E., Findlay, C. S., Schmidt, B. R., Meyer, A. H., & Kuzmin, S. L. (2000). Quantitative evidence for global amphibian population declines. *Nature*, **404**, 752-755.

Huey, R. B. & Stevenson, R. D., (1979). Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist*, **19**, 357-366.

IUCN. (2012). *Guidelines for Application of IUCN Red List Criteria at Regional and National Levels: Version 4.0*. Gland, Switzerland and Cambridge, UK: IUCN. iii + 41pp.

Johnson, M. L., & Gaines, M. S. (1990). Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual review of ecology and systematic*, **21**, 449-480.

Kalk, M. (1960). Climate and breeding in *Xenopus laevis*. *South African Journal of Science*, **56**, 271-276.

Khonsue, W., Matsui, M., & Misawa, Y. (2000). Age determination by skeletochronology of *Rana nigrovittata*, a frog from tropical forest of Thailand. *Zoological Science*, **17**, 253-257.

Kobel, H. R., Du Pasquier, L. & Tinsley, R. C. (1981). Natural hybridization and gene introgression between *Xenopus gilli* and *Xenopus laevis laevis* (Anura: Pipidae). *J. Zool., Lond.*, **194**, 317-322.



- Kumbar, S. M., & Pancharatna, K. (2001). Determination of age, longevity and age at reproduction of the frog *Microhyla ornata* by skeletochronology. *Journal of Biosciences-Bangalore*, **26**, 265-270.
- Kuzmin, S. L., & Ischenko, V. G. (1997). Skeletochronology of *Bufo raddei* from the Gobi Desert. *Journal of Herpetology*, **31**, 306-309.
- Kyriakopoulou-Sklavounou, P, Stylianou, P & Tsiora, A. (2008). A skeletochronological study of age, growth and longevity in a population of the frog *Rana ridibunda* from southern Europe. *Zoology*, **111**, 30-36.
- Leberon, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67-118.
- Leis, J. M., Wright, K. J., & Johnson, R. N. (2007). Behaviour that influences dispersal and connectivity in the small, young larvae of a reef fish. *Marine Biology*, **153**, 103-117.
- Licht, L. E. (1974). Survival of embryos, tadpoles, and adults of the frogs *Rana aurora aurora* and *Rana pretiosa pretiosa* sympatric in southwestern British Columbia. *Canadian Journal of Zoology*, **52**, 613-627.
- Linder, H. P. (1991). Environmental correlates of patterns of species richness in the southwestern Cape Province of South Africa. *Journal of Biogeography*, **18**, 509-518.
- Llewelyn, J., Phillips, B. L., Alford, R. A., Schwarzkopf, L. & Shine R., (2010). Locomotor performance in an invasive species: cane toads from the invasion front have greater endurance, but not speed, compared to conspecifics from a long-colonized area. *Oecologia*, **162**, 343-348.

Lobos, G., & Measey, G. J. (2002). Invasive populations of *Xenopus laevis* (Daudin) in Chile. *Herpetological Journal*, **12**, 163-168.

Lobos, G., & Garin, C. (2002). *Xenopus laevis*: behavior. *Herpetological Review*, **33**, 132.

Lobos, G., & Jaksic, F. M. (2005). The ongoing invasion of African clawed frogs (*Xenopus laevis*) in Chile: causes of concern. *Biodiversity & Conservation*, **14**, 429-439.

Loumont, C. (1984). Current distribution of the genus *Xenopus* in Africa and future prospects. *Revue suisse de Zoologie*, **91**, 725-746.

Loveridge, A. (1953). Zoological results of a fifth expedition to East Africa. IV-Amphibians from Nyasaland and Tete. *Bulletin of Museum of Comparative Zoology, Harvard*, **110**, 325-406.

Mennechez, G., Petit, S., Schtickzelle, N., & Baguette, M. (2004). Modelling mortality and dispersal: consequences of parameter generalisation on metapopulation dynamics. *Oikos*, **106**, 243-252.

Marsh, D. M., & Trenham, P. C. (2001). Metapopulation dynamics and amphibian conservation. *Conservation Biology*, **15**, 40-49.

Massot, M., Clobert, J., Lorenzon, P., & Rossi, J. M. (2002). Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. *Journal of Animal Ecology*, **71**, 253-261.

Matthysen, E. (2005). Density-dependent dispersal in birds and mammals. *Ecography*, **28**, 403-416.

- McCoid, M. J., & Fritts, T. H. (1980). Observations of feral populations of *Xenopus laevis* (Pipidae) in southern California. *Bulletin of the Southern California Academy of Sciences*, **79**, 82-86.
- McCoid, M. J., & Fritts, T. H. (1989). Growth and fatbody cycles in feral populations of the African clawed frog, *Xenopus laevis* (Pipidae), in California with comments on reproduction. *The Southwestern Naturalist*, **34**, 499-505.
- Measey, G. J. & Tinsley, R. C., (1998). Feral *Xenopus laevis* in south Wales. *Herpetological Journal*, **8**, 23-27.
- Measey, G. J. (2001). Growth and ageing of feral *Xenopus laevis* (Daudin) in South Wales, UK. *Journal of Zoology*, **254**, 547-555.
- Measey, G. J., & Channing, A. (2003). Phylogeography of the genus *Xenopus* in southern Africa. *Amphibia-Reptilia*, **24**, 321-330.
- Measey, G. J. (2004a). Genus *Xenopus* Wagler, 1827 (Family Pipidae). In: Minter, L. R., Burger, M., Harrison, J. A., Braack, H. H. Bishop, P. J. and Kloepfer, D. eds. *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland*, Pp 266-267.
- Measey, G. J. (2004b). Species account: *Xenopus laevis* (Daudin 1802). In: Minter, L. R., Burger, M., Harrison, J. A., Braack, H. H. Bishop, P. J. and Kloepfer, D. eds. *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland*, Pp 266-267.
- Measey, G. J. (2011). *Ensuring a future for South Africa's frogs: a strategy for conservation research*. South African National Biodiversity Institute.

- Measey, G. J., Rödder, D., Green, S. L., Kobayashi, R., Lillo, F., Lobos, G., Rebelo, R. & Thirion, J-M., (2012). Ongoing invasions of the African Clawed frog, *Xenopus laevis*: a global review. *Biological Invasions*, **14**, 2255-2270.
- Mennechez, G., Petit, S., Schtickzelle, N., & Baguette, M. (2004). Modelling mortality and dispersal: consequences of parameter generalisation on metapopulation dynamics. *Oikos*, **106**, 243-252.
- Miller, K., (1982). Effect of temperature on sprint performance in the frog *Xenopus laevis* and the salamander *Nectrurus maculosus*. *Copeia*, **1982**, 695-698.
- Nathan, R. (2006). Long-distance dispersal of plants. *Science*, **313**, 786-788.
- O'Riain, M. J., Jarvis, J. U., & Faulkes, C. G. (1996). A dispersive morph in the naked mole-rat. *Nature*, **380**, 619-621.
- Passmore, N. I., & Carruthers, V. (1979). *South African frogs*. ISBS. Pp 194-201.
- Pechmann, J. H., Scott, D. E., Semlitsch, R. D., Caldwell, J. P., Vitt, L. J., & Gibbons, J. W. (1991). Declining Amphibian Populations: The Problem of Separating Human Impacts from Natural Fluctuations. *Science*, **253**, 892-895.
- Pergl, J., Perglová, I., Pyšek, P., & Dietz, H. (2006). Population age structure and reproductive behavior of the monocarpic perennial *Heracleum mantegazzianum* (Apiaceae) in its native and invaded distribution ranges. *American Journal of Botany*, **93**, 1018-1028.
- Phillips, B. L., Brown, G. P., Webb, J. K., & Shine, R. (2006). Invasion and the evolution of speed in toads. *Nature*, **439**, 803-803.
- Picker, M. D. & De Villiers, A. L., (1989). The distribution and conservation status of *Xenopus gilli* (Anura: Pipidae). *Biological Conservation*, **49**, 169-183.

Picker, M. D. (1985). Hybridization and habitat selection in *Xenopus gilli* and *Xenopus laevis* in the South-Western Cape Province. *Copeia*, **1985**, 574-580.

Picker, M. D., Harrison, J. A. & Wallace, D., (1996). Natural hybridization between *Xenopus laevis laevis* and *X. gilli* in the south-western Cape Province, South Africa. In: Tinsley, RC & Kobel, H. R. eds. *The biology of Xenopus*. Oxford University Press Inc. New York. Pp 61-71.

Pollock, K. H. (1981). Capture-recapture models allowing for age-dependent survival and capture rates. *Biometrics*, **37**, 521-529.

Purrenhage, J. L., & Boone, M. D. (2009). Amphibian community response to variation in habitat structure and competitor density. *Herpetologica*, **65**, 14-30.

Pyšek, P., Richardson, D. M., Rejmánek, M., Webster, G. L., Williamson, M., & Kirschner, J. (2004). Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, **53**, 131-143.

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

Rasband W. S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, <http://imagej.nih.gov/ij/>, 1997-2012.

Richards, C. T. (2010). Kinematics and hydrodynamics analysis of swimming anurans reveals striking inter-specific differences in the mechanism for producing thrust. *The Journal of Experimental Biology*, **213**, 621-634.

Robledo-Arnuncio, J. J., & Garcia, C. (2007). Estimation of the seed dispersal kernel from exact identification of source plants. *Molecular Ecology*, **16**, 5098-5109.

Rödel, M. O. (2000). *Herpetofauna of West Africa: Amphibians of the West African Savanna* (Vol. 7). Chimaira.

Schmidt, B. R., (2003). Count data, detection probabilities, and the demography, dynamics, distribution, and decline of amphibians. *Comptes Rendus Biologies*, **326**, 119-124.

Schmidt, B. R., Schaub, M., & Anholt, B. R. (2002). Why you should use capture-recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration, overdispersion, and common toads. *Amphibia-Reptilia*, **23**, 375-388.

Schmutz, J. A., & Ely, C. R. (1999). Survival of greater white-fronted geese: effects of year, season, sex, and body condition. *The Journal of wildlife management*, **63**, 1239-1249.

Schneider, C., Dover, J., & Fry, G. L. (2003). Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. *Ecological Entomology*, **28**, 219-227.

Schoonbee, H. J., Prinsloo, J. F., & Nxiweni, J. G. (1992). Observations on the feeding habits of larvae, juvenile and adult stages of the African clawed frog, *Xenopus laevis*, in impoundments in Transkei. *Water SA*, **18**, 227-227.

Schramm, M., (1987). Control of *Xenopus laevis* (Amphibia: Pipidae) in fish ponds with observations on its threat to fish fry and fingerlings. *Water SA*, **13**, 53-56.

Schroeder, E. E., & Baskett, T. S. (1968). Age estimation, growth rates, and population structure in Missouri bullfrogs. *Copeia*, **3**, 583-592.

Senning, W. C. (1940). A study of age determination and growth of *Necturus maculosus* based on the parasphenoid bone. *American Journal of Anatomy*, **66**, 483-495.

- Smirina, E. M., (1994). Age determination and longevity in amphibians. *Gerontology*, **40**, 133-146.
- Smirina, E. M., & Rocek, Z. (1976). On the possibility of using annual bone layers of alpine newts, *Triturus alpestris* (Amphibia: Urodela), for their age determination. *Vestnik Ceskoslovenske Spolcnosti Zooloigicke*, **3**, 232-237.
- Smith, M. A., & M Green, D. (2005). Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations?. *Ecography*, **28**, 110-128.
- South, A. B., & Kenward, R. E. (2001). Mate finding, dispersal distances and population growth in invading species: a spatially explicit model. *Oikos*, **95**, 53-58.
- South African Frog Re-assessment Group (SA-FRoG), IUCN SSC Amphibian Specialist Group (2010). *Xenopus gilli*. The IUCN Red List of Threatened Species. Version 2014.2. <[www.iucnredlist.org](http://www.iucnredlist.org)>. Downloaded on **10 August 2014**.
- Spear, D., & Chown, S. L. (2009). The extent and impacts of ungulate translocations: South Africa in a global context. *Biological Conservation*, **142**, 353-363.
- Stevens, V. M., Pavione, S. & Baguette, M. (2010) Variation within and between closely related species uncover high intra-specific variability in dispersal. *PLoS ONE*, **5**, e11123.
- Stewart, M. M., (1995). Climate driven population fluctuations in rain forest frogs. *Journal of Herpetology*, **29**, 437-446.
- Tejedo, M., Semlitsch, R. D., & Hotz, H. (2000). Covariation of morphology and jumping performance in newly metamorphosed water frogs: effects of larval growth history. *Copeia*, **2000**, 448-458.

- Themudo, G. E., & Arntzen, J. W. (2007). Newts under siege: range expansion of *Triturus pygmaeus* isolates populations of its sister species. *Diversity and Distributions*, **13**, 580-586.
- Tinsley, R. C. & Kobel, H. R., (1996). The biology of *Xenopus*. Oxford University Press Inc. New York.
- Tinsley, R. C., Loumont, C. & Kobel, H. R., (1996). Geographical distributions and ecology. In: Tinsley, R. C. & Kobel, H. R. eds. The biology of *Xenopus*. Oxford University Press Inc. New York. Pp 35-59.
- Trueb, L., (1996). Historical constraints and morphological novelties in the evolution of the skeletal system of pipid frogs (Anura: Pipidae). In: Tinsley, R. C. & Kobel, H. R. eds. The biology of *Xenopus*. Oxford University Press Inc. New York. Pp 349-377.
- Tsiora, A. & Kyriakopoulou-Sklavounou, P., (2002). A skeletochronological study of age and growth in relation to adult size in the water frog *Rana epeirotica*. *Zoology*, **105**, 55-60.
- Turner, F. B. (1960a). Postmetamorphic growth in anurans. *American Midland Naturalist*, **64**, 327-338.
- Turner, F. B. (1960b). Population structure and dynamics of the western spotted frog, *Rana p. pretiosa* Baird & Girard, in Yellowstone Park, Wyoming. *Ecological Monographs*, **30**, 251-278.
- Van Dijk, D. E., (1977). Habitats and dispersal of southern African Anura. *African Zoology*, **12**, 169-181.
- Vences, M., & Köhler, J. (2007). Global diversity of amphibians (Amphibia) in freshwater. In: Balian, E. V., Lévêque, C., Segers, H., & Martens, K. eds. *Freshwater Animal Diversity Assessment*. Springer Netherlands. Pp 569-580.



Videler, J. J., & Jorna, J. T. (1985). Functions of the sliding pelvis in *Xenopus laevis*. *Copeia*, **1985**, 251-254.

Vonesh, J. R., & De la Cruz, O. (2002). Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. *Oecologia*, **133**, 325-333.

Wassersug, R. J. (1975). The adaptive significance of the tadpole stage with comments on the maintenance of complex life cycles in anurans. *American Zoologist*, **15**, 405-417.

Werner, E. E. (1986). Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *American Naturalist*, **128**, 319-341.

Werner, E. E., Wellborn, G. A., & McPeck, M. A. (1995). Diet composition in postmetamorphic bullfrogs and green frogs: implications for interspecific predation and competition. *Journal of Herpetology*, **29**, 600-607.

Weyl, O. L. F., Ellender, B. R., Woodford, D. J., & Jordaan, M. S., (2013). Fish distributions in the Rondegat River, Cape Floristic Region, South Africa, and the immediate impact of rotenone treatment in an invaded reach. *African Journal of Aquatic Science*, **38**, 201-209.

White, G. C. & Burnham, K. P., (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, 120-139.

Whiting, H. P. (1961). Pelvic girdle in amphibian locomotion. *Symposium of the Zoological Society of London*, **5**, 43-57.

Wilbur, H. M. (1980). Complex life cycles. *Annual Review of Ecology and Systematics*, **11**, 67-93.

Wilson, J. R., Dormontt, E. E., Prentis, P. J., Lowe, A. J., & Richardson, D. M. (2009). Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology & Evolution*, **24**, 136-144.

Wilson, R. S., Franklin, C. E., & James, R. S. (2000). Allometric scaling relationships of jumping performance in the striped marsh frog *Limnodynastes peronii*. *Journal of Experimental Biology*, **203**, 1937-1946.

Wood, K. V., Nichols, J. D., Percival, H. F., & Hines, J. E. (1998). Size-sex variation in survival rates and abundance of pig frogs, *Rana grylio*, in northern Florida wetlands. *Journal of Herpetology*, **32**, 527-535.

Woodford, D. J., Impson, N. D., Day, J. A. & Bills, I. R., (2005). The predatory impact of invasive alien smallmouth bass, *Micropterus dolomieu* (Teleostei: Centrarchidae), on indigenous fishes in a Cape Floristic Region mountain stream. *African Journal of Aquatic Science*, **30**, 167-173.

Woolbright, L. L. (1983). Sexual selection and size dimorphism in anuran amphibia. *American Naturalist*, **121**, 110-119.

Zug, G. R., (1972). Anuran locomotion: structure and function. I. Preliminary observations on relation between jumping and osteometrics of appendicular and postaxial skeleton. *Copeia* **1972**, 613-624.

## Addendum A

### SHORT COMMUNICATION

#### **Controlling the African clawed frog *Xenopus laevis* to conserve the Cape platanna *Xenopus gilli* in South Africa**

F. André de Villiers<sup>1</sup>, Marisa de Kock<sup>2</sup> & G. John Measey\*<sup>1</sup>

<sup>1</sup>Centre for invasion biology, Department of Botany & Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, Stellenbosch, South Africa <sup>2</sup>South African National Parks, Plateau Road, Simons Town 7975, Cape Town, South Africa

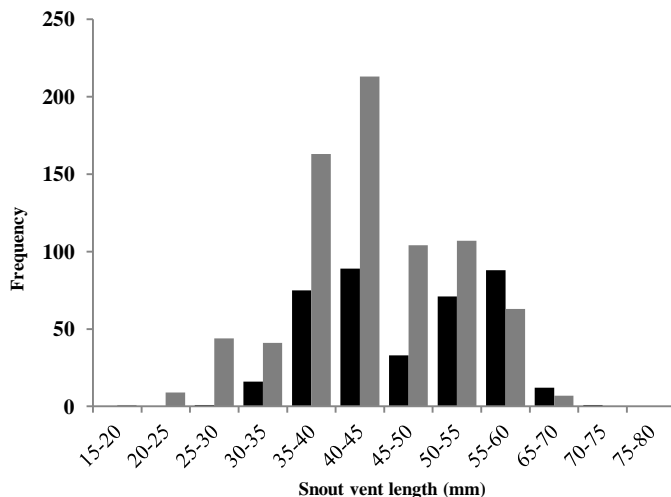
**SUMMARY: A five year control programme of the African clawed frog *Xenopus laevis* resulted in improved population demographics in the Cape platanna *Xenopus gilli* in comparison to a population without removal.**

**BACKGROUND:** The Cape platanna *Xenopus gilli* is a pipid frog endemic to the south-western Cape, occurring in only four locations, with IUCN Endangered status. The African clawed frog *Xenopus laevis* occurs in sympatry with Cape platanna throughout its distribution (Picker & De Villiers 1989, Fogell *et al.* 2013), and is thought to threaten Cape plantanna via predation, hybridization and competition (Picker & De Villiers 1989, Fogell *et al.* 2013). In this study we compared two of four known Cape platanna populations: Kleinmond and the Cape of Good Hope Section of Table Mountain National Park (CoGH). The Kleinmond population is situated on privately owned land without active conservation interventions. In CoGH, active Cape platanna conservation began in 1985 with annual removal of African clawed frogs (Picker & De Villiers 1989, De Villiers 2004), but removal of clawed frogs ceased in 2000 after CoGH came under new management (De Villiers 2004).

**ACTION:** In 2010 we began monitoring Cape platanna at CoGH in collaboration with South African National Parks (SANParks). African clawed frogs were removed annually from all areas by seine netting. Each impoundment was seined until the net came back three consecutive times without any clawed frogs. In 2014 we started monitoring the effect of clawed frogs on Cape plantanna demographics. Both species were collected by seining and trapping at each site. Trapping sessions were within three to six weeks of each other and lasted three days. In Kleinmond, both species were tagged (9/10 mm passive integrated transponder) and released at the point of capture. In CoGH all Cape platanna caught were tagged and released, but all African clawed frogs were euthanized using tricaine methane-sulfonate (MS222: Sandoz) by SANParks staff. All Cape platanna were also photographed on a scaled background to measure snout vent length (Measey *et al.* 2003). A total of 2,126 clawed frogs were removed from CoGH in the five year control period, while we tagged 1,699 common platanna over 18 months in Kleinmond.

**CONSEQUENCES & DISCUSSION:** A marked increase in CoGH juvenile and young adult Cape platanna (<45 mm) corresponded to the same five years during which clawed frogs were controlled. In Kleinmond, recruitment appears suppressed, with a lower overall number of platanna (Figure 1). Our treatments

\* To whom correspondence should be addressed: [john@measey.com](mailto:john@measey.com)



**Figure 1.** The frequency of snout vent length classes of two populations of the Cape platanna. Grey bars represent frogs from CoGH (n=752), black bars frogs from Kleinmond (n=386).

were not replicates, but we have no reason to believe that other factors caused the observed differences. Our data suggest that (a) the African clawed frog does have a negative impact on Cape platanna through predation and/or competition, and (b) control of clawed frogs by regular seining and/or trapping is a viable way to conserve Cape platanna. We found that small numbers of clawed frogs can produce hundreds of adults within relatively short periods (e.g. 18 months). Such events then take a concerted effort to clear (27 person days for 338 clawed frogs from one impoundment in this study), while regular seining can be as little as 8 person days per year. This underlines the importance of regular, consistent monitoring. Our study also illustrates the importance of institutional formalisation of conservation actions. The regular removal of clawed frogs at CoGH is now part of the Annual Plan of Operations for SANParks, and we intend to negotiate a formal arrangement for the Kleinmond site.

**ACKNOWLEDGEMENTS:** We thank the numerous field assistants who have aided in *X. laevis* control. This research was funded by the National Research Foundation of South Africa (NRF Grant No. 87759), NRF incentive funding, the DST-NRF Centre of Excellence for Invasion Biology and BiodivERSA:INVAXEN. Research permission came from CapeNature (AAA007-01867) and SANParks.

## REFERENCES

- De Villiers A.L. (2004) *Xenopus gilli* Rose and Hewitt, 1927. Pages 260-263. In: Minter L.R., Burger M., Harrison J.A., Braack H.H., Bishop P.J. & Kloepfer D. (eds.) *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland*. SI/MAB Series #9. Smithsonian Institution, Washington, DC.
- Fogell D. J., Tolley K.A. & Measey G.J. (2013) Mind the gaps: investigating the cause of the current range disjunction in the Cape Platanna, *Xenopus gilli* (Anura: Pipidae). *PeerJ*, **1**, e166.
- Picker M.D. & De Villiers A.L. (1989) The distribution and conservation status of *Xenopus gilli* (Anura: Pipidae). *Biological Conservation*, **49**, 169-183.