

Mating Behavior of *Xenopus wittei* (Anura: Pipidae)

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Spawning behavior in the Pipidae has been reported by many authors during the past 100 years. The first accounts comprised anecdotal commentaries (Leslie, 1890; Bles, 1901, 1905) of African *Xenopus laevis*. Half a century later, observations were made of South American *Pipa pipa*, now well known for its development of young in pockets on the mother's back (Rabb and Snedigar, 1960). Rabb and Rabb (1960) reported the first descriptions of spawning in *P. pipa*, including egg laying during midwater somersaults. The "turnover" was initiated by the female and described as a "sideways upward movement, a momentary pause in a horizontal upside-down position, and a head-first return to the tilted resting position." During this maneuver, the male and female cloacae are brought close together, and three to five eggs are laid while the pair is horizontal. On descent the male, with arched back, makes inward thrusting movements, transferring the eggs anteriorly where they become implanted into the female's swollen dorsal epidermis. Although the implanted eggs on the back of female *P. pipa* undergo direct development, those of *P. carvalhoi* hatch as tadpoles which then complete their development independently. Weygoldt (1976) described the mating of *P. carvalhoi*, recording similar behavior to Rabb and Rabb (1960) but with greater detail of the male's maneuvering eggs onto the back of the female and reducing them to a single layer with a sweeping kick.

Olsson and Österdahl (1960) reported similar turnovers in *Hymenochirus boettgeri*, a pipid from West Africa which is believed to be more closely related to *Pipa* than to sympatric *Xenopus* (Cannatella and Trueb, 1988). More detailed descriptions followed (Österdahl and Olsson, 1963; Rabb and Rabb, 1963), describing territoriality, calling, and mating behavior. In *H. boettgeri*, the turnover sequence begins with the amplexed female swimming to the surface. The pair then twists into an upside-down position, and both cloacae are brought above the water while eggs are laid into the surface film (less than 10 eggs per turnover according to Österdahl and Olsson, 1963; one to 12 eggs according to Rabb and Rabb, 1963). The pair then comes out of the upside-down position by a turn through the female's longitudinal axis and returns to the substrate. Sokol (1962) observed similar spawning movements in *H. curtipes*.

Studies of the other two African pipid genera have included observations of turnovers in *Pseudohymenochirus* (Rabb and Rabb, 1963). Swisher (1969) briefly described turnovers for *X. tropicalis*, another West African pipid, to be similar to those of *P. pipa* and *H. boettgeri*. Movements were reported as a half-roll, oviposition, and a half-roll in the opposite direction, the eggs remaining at the water surface. This behavioral characteristic was included by Cannatella and Trueb (1988) in their evidence for the separation of *X. tropicalis* and *X. epitropicalis* in a distinct genus *Silurana*, closer to *Hymenochirus* and *Pipa* than to *Xenopus*. Turnovers have not been reported in the other lineage of species, referred by Cannatella and Trueb (1988) to a separate genus, *Xenopus* (sensu stricto). Swisher (1969) noted that *X. laevis* and *X. muelleri*, kept in the same conditions as *X. tropicalis*, deposited eggs only on rocks and plants. This paper follows the nomenclature of Kobel et al. (1996) who proposed *Silurana* as a subgenus of *Xenopus*.

Most accounts of breeding behavior in *Xenopus* concentrated on *X. laevis* (Leslie, 1890; Bles, 1905; Picker, 1983). Other works concerned the mechanisms of the behavior (Russell, 1954, 1960) and the stimulus for spawning (Berk, 1938; Balinsky, 1969; Savage, 1971). Most laboratory studies used hormone injections to stimulate spawning. The only description of breeding behavior in wild *X. laevis* came from a feral population in California (McCoid, 1985). McCoid noted that lack of observations of wild populations in Africa may be because *X. laevis* typically inhabits turbid conditions (also see Picker, 1980). Such turbid conditions are typical for many of the Pipidae (Tinsley et al., 1979; Tinsley et al., 1996).

This study is based on *X. wittei*, an octoploid ($2n = 72$) species (Tinsley et al., 1979; Kobel et al., 1996) from highland areas of Uganda, Rwanda, and Zaire: *wittei* is related to the *laevis* and *fraseri* groups (Kobel et al., 1996) in the subgenus *Xenopus*. We describe, for the first time, the mating behavior of *X. wittei* from observations of wild-caught pairs in uninduced spawnings.

Materials and methods.—Five female and two male *X. wittei* collected in Cyamudongo, Rwanda, in 1992, were kept in naturalized conditions

in a glass aquarium 1.2 m long, 0.35 m wide and 0.5 m high. Voucher specimens were deposited in the British Museum (Natural History) collection (BMNH 1996. 226–231). The water was maintained at a temperature of 15 C (± 1) and a depth of 0.13 m (55 liters) over a gravel substrate, with large stones and spiked water mill-foil (*Myriophyllum spicatum*). For over a year, sporadic matings occurred after the tank was topped up with water or during sunny conditions. A regular diet of chopped beef steak was supplemented by crickets (*Achaeta domestica*). There was a noticeable increase in the appetite of females prior to mating. Eggs were deposited on stones, on the vegetation, and on the glass walls of the tank. Many eggs were removed from the tank and reared separately. Duckweed (*Lemna minor*) was then introduced to the tank and grew to cover most of the water surface during the winter months when no matings were observed.

For studies of mating behavior, the movement of *X. wittei* was recorded with an NAC 400 high speed video camera through a 55 mm Micro Nikkor lens at 200 frames per second with synchronized stroboscopic lighting. The images were analyzed with (and drawings made from) Hi-8 tape archived from the camera and using acetates drawn from single frames. Stills were taken with Ilford FP4 at 1/250 sec with synchronized flash, using a 55 mm Micro Nikkor lens.

Sound recordings were made with a Sony Professional Walkman (WM D6C) and a Sony stereo microphone (ECM 909A) enclosed in a rubber sheath (Durex Gossamer) lowered into the water. Sonograms were analyzed on a Digital Sound Processing Sonograph (Kay Elemetrics, 5500, 512pt. fast fourier transformer, 400 Hz frequency resolution).

Observations were made of over 20 matings from February to May 1995. Sunrise and sunset in Bristol were at 0750 h and 1700 h, respectively, at the start of this period, and at 0500 h and 2115 h at the end (all times GMT). Natural light levels and times were occasionally supplemented by laboratory lighting. High speed video recordings were made of two matings, and still photos taken of another. Sounds were recorded from three matings.

Results.—Pre-amplexus: The two males took up a waiting stance in the evening (1600–1700 h), their feet resting on and their arms and digits splayed 10 mm above the gravel, their gloves clearly visible. In this position, the males called in bouts of about 10 sec with repeated short trills. The females remained motionless at the water surface, among weed or under rocks.

Males swam slowly about the tank calling, often coming to rest near another individual. If a female made any sudden move in the vicinity of a male during this period, a chase would occur. The chased female would flee under rocks or into weed. The males also clasped each other, but in this case release occurred immediately.

Amplexus: A grasped female elicited two alternative responses. If the female was not receptive and the male managed to contact her, she immediately took up a rigor stance, often allowing her body to fall to the bottom of the tank and even turn upside down. The female gave a shrill sound, termed the "release call" (Picker, 1980) and did not resume normal behavior until the male retreated. The male continued to call and again took up the waiting stance. Females giving a rigor stance when males first clasped them might accept a mating attempt later in the same evening. When the female was receptive, the male grasped her in an inguinal amplexus. The female initially tried to escape and went into a partial rigor stance. However, she did not stop swimming, as before, but moved her body from the amplexed point in a lateral motion, jerking 40° to each side. In one instance, this jerking behavior lasted 4 min. During this time, the male would occasionally give a tremor, bobbing with his head and tightening his grip four to five times in quick succession; this movement was accompanied by a call.

Ultimately the female became calm and periodically went to the surface to breathe. She would often rest suspended in this position (Fig. 1a) or on the bottom (Fig. 2s). To breathe while the female was at the surface, the male had to loosen his grip. When the female rested, the male began jerking pumping movements, tightening his grip at the same time as depressing his head. At this time, the male frequently swept his hind foot over the female's head, which often had the effect of changing her orientation. In Figure 1, the outside portion of the male's foot can be seen to scrape between the eye and mouth of the female, but no consistent pattern of foot sweeping was observed. The amplexed pair remained in a calmed state for some hours (generally starting at 1800 h for up to 10 h), resting on the bottom or at the surface. When live crickets were offered to all animals in the tank, amplexed females were noted to take them readily, but males in amplexus were never observed to eat.

Oviposition: Figure 2 shows the general characteristics of the three turnover sequences filmed. Eggs were deposited at various points on the turnover in horizontal, vertical, and invert-

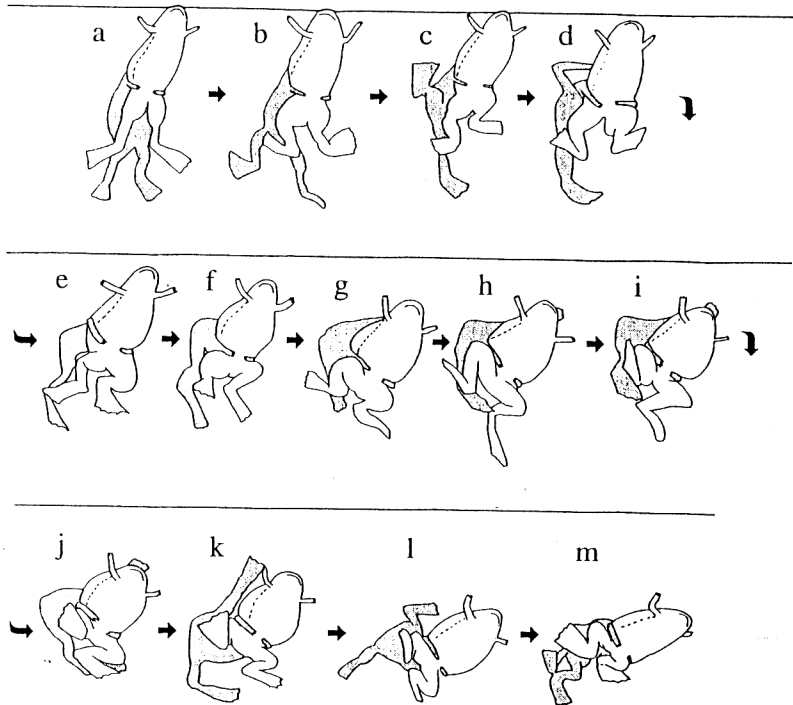


Fig. 1. Male *Xenopus wittei* (shaded) makes a sweeping kick over the head of the female while continuing to grasp in an inguinal amplexus. At (a), the female is resting at the surface, but her orientation is changed by the end of the maneuver, and in the following frames she continues to swim to the bottom of the tank. Drawn from frames of high speed video recordings at 0.1-sec intervals.

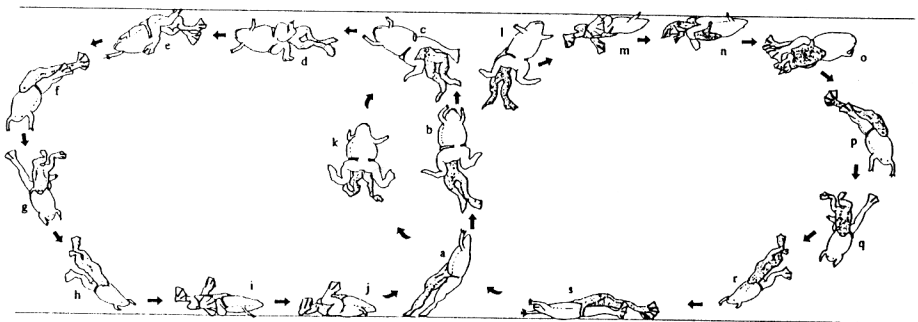


Fig. 2. Three sequences of turnover ovipositions by *Xenopus wittei* (male shaded). (a-j) shows a turnover followed by oviposition in a horizontal position onto gravel at the bottom of the tank. (a, c-h, k) shows a vertical oviposition onto glass walls of the tank, followed by a turnover. (a-b, l-s) shows an inverted oviposition, under *L. minor* thalli, followed by a turnover, and the pair resting on the bottom (s). Drawn from frames of high speed video recordings.

ed positions. Usually one egg (maximum observed = 3) was laid per turnover. Figure 2a-j shows a substrate (horizontal) laying turnover, whereas Figure 2a, k,c-h shows the female ovipositing onto the glass walls of the tank or onto strands of *M. spicatum* (vertical). Figure 2a-b, l-r shows a turnover in which eggs are deposited on the ventral surfaces of *L. minor* thalli (inverted). In this turnover sequence, the pair swam first from the bottom to the surface (Fig. 2b). At the surface, the female pushed aside the *L. minor* thalli with her forelimbs to breathe (Fig. 2l). She then instigated a move down from the surface, and the pair turned laterally about their longitudinal axis into the inverted position (Fig. 2m). Laying then occurred (Figs. 2n) as in horizontal or vertical positions but with the female seeming to put more effort into her perpendicular strokes. When more than one egg was to be laid, the pair remained in the inverted position. The male relaxed his cloacal position slightly while the female used her forelimbs to "walk" under the weed. When the last egg was laid, the female's cloaca was moved down from the *L. minor* thalli, and, as she stopped the fanning of one of her feet, the pair rolled back to the horizontal position (Fig. 2o). At no point during oviposition or turnovers were any sounds recorded from the amplexed pair.

Before and after turnover sequences, the pair either returned to the bottom of the tank where they rested on the substrate (Fig. 2s) or else hung at the surface (Fig. 2l). During turnover sequences, the female made all the postural adjustments for the direction moved by the pair and for the laying site. It can be seen in Figure 2c that the female's left leg is pushed out to turn the pair out of the ascent and again in Figure 2g that the female's right foot turns the pair out of the descent. The feet of the male during all turnovers were kept splayed and did not contribute to the swimming effort. Female *X. wittei* in the aquarium were often observed to ingest eggs, including the ovipositing female who ate any eggs (including her own) whenever they were encountered.

The laying procedure began with the female selecting an oviposition site, during which the couple both swam with short strokes. At the selected site, the female depressed her cloaca, forcing her head up and giving a more hunched appearance; she also moved her feet so that she was pushing water perpendicular to the oviposition surface. This was a cue for the male to bring his cloaca closer to hers and to orient his feet so that a backward current was produced. The fanning of the feet was synchronized and the egg always released on a down stroke. The

egg passed along the males' genital fold and adhered to the substrate. This sequence was repeated in all orientations, including the inverted position. Eggs collected and subsequently reared separately were all viable.

In a separate spontaneous mating (16 May 1995), the water level was very low (depth 110 mm). The couple was observed laying eggs in horizontal and vertical positions for over an hour. No attempt was made by the pair to lay in an inverted position or to perform turnovers. The combined body length of the pair resting at the surface (from female snout to male feet) was around 95 mm. At this point, dechlorinated water (at 15 C) was added to the aquarium, increasing the depth by 50 mm. The amplexing couple was disturbed and rested on the substrate for around 10 min. They then began to resume laying in horizontal positions and after 5 min were laying in an inverted position onto the ventral surface of the *L. minor* thalli. Repeated turnovers were observed 20 min after the addition of the water.

Discussion.—Although *X. laevis* is one of the most intensively studied anurans, its reproductive behavior has been largely neglected. The few existing studies have been derived from spawnings induced under laboratory conditions. Descriptions of mating behavior are lacking among the subgenus *Xenopus* and have instead concentrated upon the genus *Pipa*, which is characterized by elaborate mating procedures and parental investment. There are very few records of spontaneous mating in laboratory-maintained *Xenopus* species (for instance Tinsley, 1995), and this explains why many existing accounts (Picker, 1980, 1983; Vigny, 1979) have used animals injected with gonadotrophins to stimulate reproductive behavior. Hormonally induced *X. laevis* deposit large numbers of eggs rapidly, greatly in excess of those that would occur naturally, and these have considerably lower viability (McCoid and Fritts, 1995). In this study, mating occurred spontaneously, eggs were laid individually during an extended period, and all eggs collected were viable. It is possible that other aspects of mating behavior, including call characteristics, are similarly affected by gonadotrophin injections.

This account details the reproductive behavior of *X. wittei*. During courtship, males called and chased females which subsequently fled and hid. Once a female was grasped, she either rejected the male by adopting a rigor stance or eventually accepted him. In amplexus, the male swept his foot over the head of the female (Fig. 1) during a period of calm prior to laying. Ovi-

position occurred in three orientations (vertical, horizontal, and inverted) during a turnover (Fig. 2). High speed video allowed observations which demonstrated that the female leads in all laying maneuvers. Each of these behaviors is to some extent shared with other species in the Pipidae. Comparisons incorporating a review of the literature are shown in the Appendix.

A detailed description of unsuccessful clasps has been well reported elsewhere (Russell, 1960) using *X. laevis* in aquaria. Rabb and Rabb (1963) quoted Noble and Putman's (1931) study of *Ascapus truei* to suggest that the tonic immobility of the female allows the male to secure a better grip. However, Noble and Aronson's (1942) study of *Rana pipiens* suggested that the tonic posture is to simulate a non gravid female. The tonic posture appears to be a female rejection stance in the Pipidae, a female makes the region clasped by the male very thin by extension of the pelvis and the hind limbs. The delay after a successful grasp has occurred and, before the onset of oviposition (about 10 h), may correspond to a period during which the female ovulates (but also see Aronson, 1944). Shapiro (1935) showed that ovulation had not occurred in hormonally induced *X. laevis* before or just after grasping. Leslie (1890) found that a female that had been separated during initial amplexus oviposited alone, but Russell (1960) claimed that no spontaneous ovulation occurred in *X. laevis*. On the other hand, Rabb and Rabb (1965) noted oviposition in *X. laevis* females kept in isolation and exposed to male calls. Rabb and Rabb (1960) considered that the prolonged period of amplexus before oviposition in *P. pipa* (at least 24 h) corresponded to a tumescent build up of the dorsal epidermis of the female, but this period may also incorporate ovulation.

Postural adjustments have been noted by many workers describing pipid mating behavior. Rabb and Rabb (1963) noted that a breath is sometimes taken prior to inverted laying by *H. boettgeri*. This breath in *X. wittei* may have a function to buoy up the body of the female during oviposition. Rabb and Rabb (1960, 1963) and McCoid (1985) described small swimming movements with the legs brought close to the body in both sexes. This was observed in all of the *X. wittei* layings: the feet were oriented upward (Fig. 2j,k,n), and when this occurred, there was no forward propulsion of the couple. Rabb and Rabb (1963) described this movement in *H. boettgeri* as having a "balancing function." In *X. wittei*, the same movement was observed at the substrate where balancing would not be necessary. In all positions (horizontal,

vertical, and inverted), the female moved her feet out of the way of the male and oriented her strokes perpendicular to the pair, thus keeping her cloaca close to the substrate. The fanning by the male facilitated the movement of the egg along the male's genital fold and kept the emission of sperm in the same area as the egg, maximizing the possibility of fertilization. Although no emission of sperm could be detected in the film, in vivo observations showed a thin white streak of fluid emanating from the male and traveling in a line directly toward the egg.

There are differing explanations in the literature that correspond to the forward kick of the male (Fig. 1). A similar movement has been recorded for *P. pipa*, *P. carvalhoi*, *H. boettgeri*, *Ps. merlini*, *X. laevis*, and now for *X. wittei* (Appendix). Rabb and Rabb (1960) suggested that this action compressed the female *P. pipa* and stimulated her to complete the laying. Weygoldt (1976) observed that the forward kick kept the eggs in one layer on the back of female *P. carvalhoi*. In *H. boettgeri*, the forward kick was noted to occur soon after initial amplexus (described as "stroking" by Rabb and Rabb, 1963, and as "movement 5" by Österdahl and Olsson, 1963). Österdahl and Olsson offered no explanation for this behavior, but Rabb and Rabb regarded "stroking as primarily stimulatory." The effect of the forward kick in *X. wittei* seems to be stimulatory, changing the orientation of the female while she is quiescent. Rabb (1973) listed five basic components to anuran courtship. Despite the variations associated with inguinal amplexus and turnovers, all the components recorded in the rest of the Pipidae are represented in *X. wittei* (Appendix).

The pattern of calls made by *X. wittei* are in general agreement with the description of the phonoresponse of breeding *X. laevis* by Picker (1980). However, a specific amplexant call (Picker, 1980) was not recorded; instead males continued their mating calls while in amplexus. The mating calls of male *Xenopus* are considered to be species specific (Vigny, 1979), and our recordings agree with those given for *X. wittei* by Kobel et al. (1996).

It is considered that the genus *Xenopus* includes two distinct lineages. Cannatella and Trueb (1988) proposed that these represent separate genera, *Xenopus* and *Silurana*, mainly based on morphology and osteology, with some behavioral and reproductive characteristics. They argued that *Silurana* is closer to *Pipa*, *Hymenochirus*, and *Pseudhymenochirus* than to other *Xenopus*. The occurrence of turnovers was regarded as a synapomorphy among these genera, not found in the genus *Xenopus* (sensu stricto).

The importance of behavioral observations to taxonomic relationships has been discussed by de Queiroz and Wimberger (1993; see also Duellman, 1985 and references therein). Within the Pipidae behavioral characteristics have been included in the separation of genera (Cannatella and Trueb, 1988). de Sá and Hillis (1990) showed that, on the basis of nuclear ribosomal DNA sequencing, *Silurana* is more closely related to *Xenopus* than to *Hymenochirus* and *Pipa*. Cannatella and de Sá (1993) suggested that the observations made by Swisher (1969) are "possibly in error," thus increasing the support for *Silurana* being closer to *Xenopus*. However, our demonstration that turnovers occur in *X. wittei*, an allopolyploid with a hybrid origin presumed to have included *X. fraseri* and *X. laevis* (Tinsley et al., 1979; Tymowska, 1991), suggests that inverted oviposition may have been present in one or both of the two presumed ancestral species lineages.

There is some anecdotal documentation that aquarium-maintained *X. laevis* also oviposit in an inverted position (Sughrue, 1969). This evidence suggests that the observations of Swisher (1969) should be accepted. Indeed, it is now clear that these behavioral traits are shared characters of all the pipid lines. Swisher (1969) noted that turnovers did not occur when *X. laevis* or *X. mulleri* were kept in aquarium conditions, similar to those used for *X. (S.) tropicalis*. In most laboratory studies, aquaria are not provided with floating vegetation, and thus maintenance conditions may inhibit natural behavior, including turnovers.

There may be advantages to laying eggs in an inverted position near the water surface. This position may have temperature, pH, and dissolved oxygen concentrations favorable to development of the eggs and may make eggs inaccessible to benthic predators. Plants that are free floating, or break away from their stems, may also help distribute eggs to other areas in large water bodies aiding dispersal and reducing cannibalism. Small floating plants, such as *L. minor*, are also reputed to be carried by waterfowl to other wetland areas. In this account, it is shown that, given sufficient water depth and the presence of floating weed in an aquarium, amplexed *X. wittei* exhibits turnovers during which females may lay eggs in an inverted position. The significance of these novel observations warrants further work, both in the laboratory and in the field, into mating behavior of other members of the Pipidae.

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