



# Social and reproductive behaviour in the Madagascan poison frog, *Mantella laevisgata*, with comparisons to the dendrobatids

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I present the first behavioural study of natural populations of a Madagascan poison frog. Focal watches of marked individuals were conducted for 925 h, in five populations, across two seasons. Like the New World dendrobatids, these diurnal anurans eat ants and are aposematically coloured. Data are presented that provide additional instances of convergence with the dendrobatids, including (1) extended male–male fights over defended resources necessary for reproductive success of both sexes, (2) stereotyped, highly tactile courtships in which the female may reject initial oviposition sites and (3) complex maternal care. Females return to water-filled phytotelmata, or wells, and lay trophic eggs for their tadpoles. *Mantella laevisgata* has the minimum possible clutch size in anurans (usually one) suggesting a high degree of parental investment. Males defend wells, which attract females that oviposit in the wells. Fertilized eggs may hatch and metamorphose, or may be eaten by a tadpole already in that well, of which the territorial male is probably the father. Unfertilized eggs serve as food for tadpoles. Oviposition-site scouting behaviour of both sexes, and the dependency of tadpole presence on the position of eggs laid, provide evidence of context-dependent, and assessment, behaviour. Females leave courtships most often only after visiting potential oviposition sites, while males usually leave to engage other males in aggression, suggesting that territory maintenance may be the most important component of male reproductive success. Two other species of frogs often prevent *M. laevisgata* from using defended oviposition sites, and larval crane flies predate the eggs of all frog species using water-filled wells.

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The poison frogs of Madagascar, genus *Mantella*, have long been of interest to students of anuran behaviour, largely because there are many similarities between species of *Mantella* and the toxic members of the Neotropical family Dendrobatidae, the poison-dart frogs. Many species of dendrobatids, especially those in the genera *Dendrobates* (sensu lato) and *Phylllobates*, are known for their territoriality, stereotyped courtship sequences and complex parental care. Until now, nothing was known of the social system of any species of *Mantella*. This study marks the first behavioural research conducted on *Mantella* in the field.

When Boulenger identified *Mantella* in 1882, he placed the genus in Dendrobatidae. Although he later formalized this taxonomic placement on the basis of their shared lack of teeth (Boulenger 1914), it is clear that he felt that the two groups simply shared a gestalt (Boulenger 1882). Although Boulenger did not know it, the aposematic coloration in both groups arises, in part, from identical

classes of lipophilic alkaloids in the skin, including pumiliotoxins and decahydroquinolines (Daly et al. 1996). Among anurans, these classes of toxins are otherwise known only in two other (unrelated) frog genera, *Melanophryniscus* (Bufonidae) and *Pseudophryne* (Myobatrachidae) (Daly et al. 1984). Other similarities between *Mantella* and the dendrobatids include small size (most species have a snout–vent length of between 20 and 30 mm), diurnality, terrestrial and/or arboreal habit and a diet consisting primarily of ants and mites. Captive dendrobatids lose their toxicity (Daly et al. 1980, 1992), as do captive *Mantella* (Daly et al. 1997), suggesting that the building blocks for the alkaloids are dietary. A high percentage of ants in the diet of dendrobatids is correlated with toxicity (Caldwell 1996), and some ants (genus *Solenopsis*) in the dendrobatid diet produce some of the simpler alkaloids themselves (Spande et al. 1998; Jones et al. 1999).

*Mantella laevisgata*, commonly known as the climbing *Mantella*, has more characters in common with the aposematic dendrobatids than the other 10 species of *Mantella*. It is not fully terrestrial, and has expanded toe-pads. It also breeds in water-filled tree holes or broken bamboo

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(phytotelmata), much like the preferred bromeliads of some dendrobatids. Amplexus is not reliably axillary nor inguinal in *M. laevigata*, which are the two most common mating positions in anurans; *M. laevigata* adopts a variety of positions during mating amplexus (personal observation). In several dendrobatids, amplexus is also unlike that of most anurans, being absent (Crump 1972; Limerick 1980), or cephalic, a highly derived form in which the male grasps the female by the head (Myers et al. 1978; Wells 1980). Finally, the larval morphology of *M. laevigata* resembles that of the oophagous dendrobatid tadpoles, having reduced labial denticles and a large, keratinized horny beak (Glaw & Vences 1994).

Several other taxa are known from both South America and Madagascar, but not Africa (e.g. side-neck turtles, Underwood 1976; iguanids, Frost & Etheridge 1989; boas, Kluge 1991). These examples are consistent with reconstructions of Gondwana that suggest that Africa, with South America, broke off to the north and west from the rest of the southern landmass by the late Jurassic, and that by the early Cretaceous, Africa and South America were rifting, leaving a more recent and direct land connection between South America and Madagascar than between Africa and Madagascar (Scotese & Golonka 1992). These observations might lead to a hypothesis of sister-group relationship between the dendrobatids and *Mantella*, but phylogenetic analyses, although not complete with regard to the taxa investigated, provide evidence against such a historical hypothesis (e.g. Hay et al. 1995). Thus, it seems that all similar specializations between the dendrobatids and *Mantella* are independently evolved.

While a dendrobatid–*Mantella* relationship would support the hypothesis of Gondwana reconstruction outlined above, it provides little insight into more general causal chains that may have led to what we observe today. Complex convergences, involving distinct processes, can help identify environmental factors that might lead to similar results in the different organisms. That is, the known existence of several convergences may suggest that others are present.

Based on the known similarities described above, my goal was to discover the social system and natural history of *M. laevigata*, with the broad hypothesis that some or all of the behaviours of aposematic dendrobatids would be present in *M. laevigata*. I predicted that male *M. laevigata* would be territorial, defending calling and/or oviposition sites from other males, as observed in several dendrobatids (e.g. *D. granuliferus*, Crump 1972; *D. pumilio*, Bunnell 1973; *Epipedobates femoralis*, Roithmair 1992). I predicted that *M. laevigata* would have a stereotyped courtship sequence similar to that of some dendrobatids, in which a male attracts a female using advertisement calls, changes to a softer courtship call, and through repeated tactile interaction with the female leads her to one or more potential oviposition sites until she accepts one, or abandons the courtship (see review by Wells 1977; also *Colostethus stephens* and *C. marchesianus*, Juncá 1998). I also predicted that *M. laevigata* would have complex maternal care of the type found in the oophagous dendrobatids, in which mothers return to individual

tadpoles repeatedly to feed them trophic (unfertilized) eggs (see reviews by Weygoldt 1987; Crump 1996). This behaviour has also been observed in three unrelated species of anurans, two hylids (*Osteopilus brunneus*, Lannoo et al. 1986; and *Anothea spinosa*, Jungfer 1996; Thompson 1996), and one rhacophorid (*Chirixalus eiffingeri*, Ueda 1986; Kam et al. 1996).

In my 1999 field season, I had already failed to falsify these broadly defined 'hypotheses of convergence', based on the behaviour I had observed in *M. laevigata* in 1997. I then focused on quantifying what variables affect the outcomes of territorial encounters and courtships, and what and how often other organisms in the phytotelmata (well) community interact with *M. laevigata*. With these data it is possible to construct a coherent picture of the selective pressures affecting reproductive success for these frogs.

## METHODS

*Mantella laevigata* was observed during the Malagasy summers of 1997 and 1999 (January–May, and January–April, respectively). The research was conducted on the 510-ha island of Nosy Mangabe, which lies at the northern end of the Bay of Antongil, 5 km south of the town of Maroantsetra, Toamasina province, in northeastern Madagascar (15°30'S, 49°46'E). Nosy Mangabe is a 'Special Reserve' in the Masoala National Park consisting mainly of 100–400-year-old secondary forest. There are two summits, the highest being 332 m, and most of the island is inaccessible by trail. *Mantella laevigata* are found throughout the island, but are densest in coastal bamboo stands. The bamboo on Nosy Mangabe, *Bambusa vulgaris*, was introduced, but in Marojezy, the other region in which *M. laevigata* is found, the frogs are found in association with native bamboo species, including *Ochlandra capitata*.

The goals of the 1997 and 1999 seasons were distinct. Prior to my arrival in 1997, no researchers had observed these frogs in the wild for more than a few hours. As such, my knowledge of the system was based entirely on what I learned anew every day. I therefore made observations in 1997 on an ad libitum basis, in which I changed 'focal' animals any time a more interesting behaviour was observed elsewhere, in order to maximize knowledge about all aspects of the social system of these frogs. In 1999, the intent was to quantify behaviours identified during 1997. The descriptions of behaviours throughout this paper are based on two seasons of observations, while the quantifiable data (e.g. analysis of what percentages of behaviours ended in particular ways) are based entirely on 1999 data.

I conducted ad libitum sampling with continuous recording (Martin & Bateson 1993) on populations of marked frogs in coastal bamboo stands in 1997, while in 1999, I used focal watches with continuous recording (Altmann 1974). Three of the four populations watched in 1997 were in three adjacent bamboo stands, encompassing a total area of approximately 1500 m<sup>2</sup>, although the area taken up by bamboo amounts to only 147 m<sup>2</sup> (stands 4, 5 and 6; Fig. 1). Some females travelled among

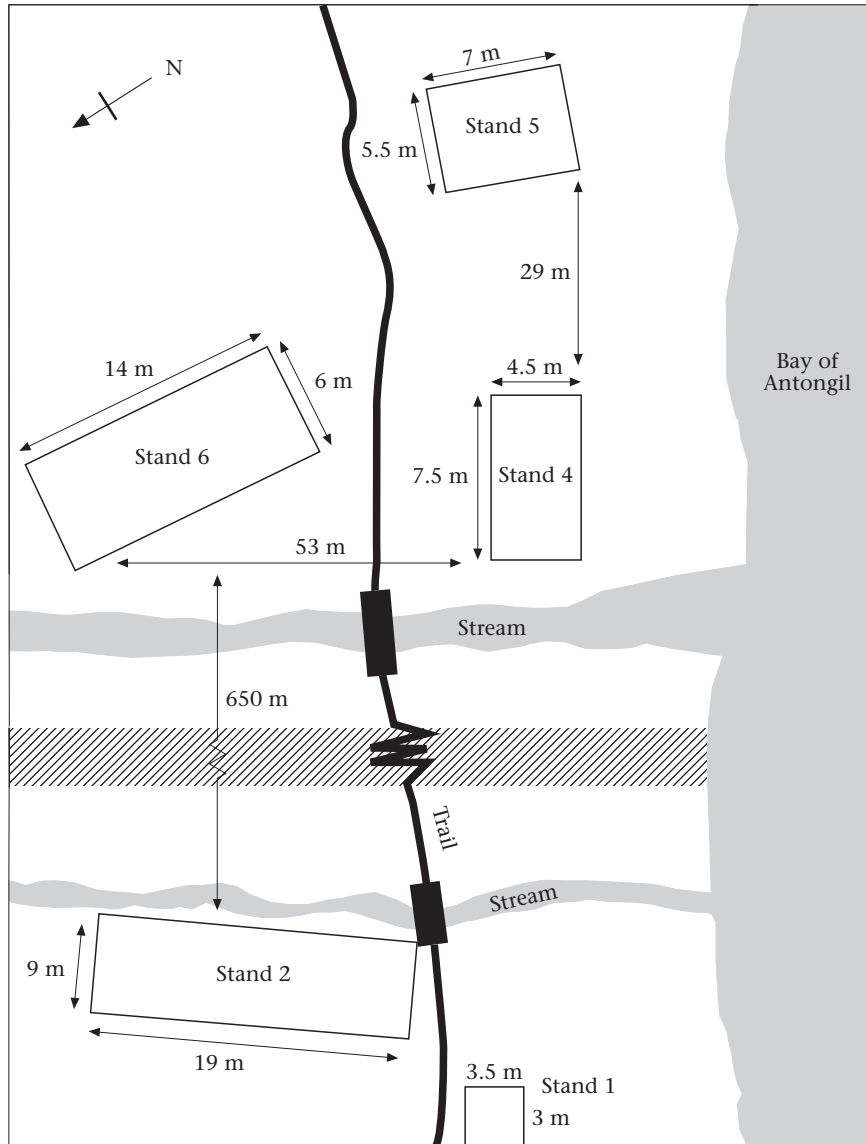


Figure 1. Map of bamboo stands containing focal populations of *M. laevigata* on the island of Nosy Mangabe, Madagascar.

these stands, but males were never observed to do so. The fourth population (bamboo stand 3) was 2.8 km away, and no movement of frogs was recorded between that and the other focal populations. The two populations watched in 1999 were in stands 650 m apart (stands 2 and 4; Fig. 1), and no movement of animals was observed between these populations.

In 1997, I and an assistant (J.M.) observed marked individuals for 509 h. All animals were toe-clipped, in addition to being given a mark that should have enabled us to identify the animals from a distance, including tying small beaded waistbands onto them, and stitching beads directly into the dorsum. None of the marks given in 1997 was reliable for more than 2 weeks. In 1999, I and a second assistant (G.M.F.) conducted 416 h of focal watches on individuals tattooed on the dorsum with a portable battery-operated tattoo machine (Dermo-Marker

Tattoo Machine model 401). These tattoos required reinking every 4–6 weeks, but the animals returned to their territories and resumed calling and territorial defence (if male) immediately upon being returned from tattooing, so the marking technique did not appear to interfere with behaviour. In both 1997 and 1999, I recorded mass and snout-vent length (SVL) for all marked animals ( $N=218$  in 1997,  $N=83$  in 1999; total  $N=301$ ).

We conducted focal watches in 1999 in half-hour intervals. We watched any given animal for as much as 2 h per day, but attempts were made to diversify the animals watched. Dominant, territorial males were the easiest to find, so they were watched more often than other individuals. Individuals that disappeared under the leaf litter or up bamboo during a focal watch were searched for until the next 15-min interval, at which point a new focal animal was found.

The most common behaviour observed and recorded was courtship. Courtship bouts are defined as uninterrupted courtship segments, during which neither participant engages with a third individual, and those courting are within 1 m of each other. When courtships are interrupted, they may resume later. If the same individuals began courting again within 15 min of a courtship bout being interrupted, the ensuing courtship was coded as another bout in the same courtship. The sum total of bouts within one courtship is referred to as a complete courtship.

At the beginning of every day of focal watching, we examined the contents of all water-filled wells in the vicinity of the population with a mini-maglite, and censused *M. laevis* eggs and tadpoles, heterospecific frogs and broods, and egg predators. These observations were repeated after any frog activity was seen around a given well.

During the 1997 season, we conducted 87.8% of the focal watch hours in the morning, primarily between 0530 and 1000 hours, when the frogs are most active. In 1999, we conducted 95.3% of focal watches in the morning. During 416 h of focal watches in 1999, we spent 274.5 h (70.0%) watching adult males, 101 h (24.3%) watching adult females, and the remaining hours watching juveniles or adults of unknown sex.

## Statistics

I used Fisher's exact test to analyse the difference in oviposition location between courtships and incidents of maternal care. Individual females were not clustered in the analysis presented (which would control for the effect of individuals tending to make similar choices repeatedly), but other analyses (including contingency tables using Rao and Scott correction for clustered data) revealed similar significance levels when controlled for non-independence between individuals. I used chi-square goodness-of-fit tests to analyse male discrimination of wells, in which independent observations of the contents of wells in the population were used to calculate 'expected' values, and the contents of wells to which males took females were the 'observed' values. Again, alternate analyses, in which the same males in multiple courtships were treated as nonindependent events, yielded similar results (calculated a 95% confidence interval for the ratio, using clustering). I used logistic regressions with cluster analyses to address the significance of much of the data in which the same animal was engaged in multiple incidences of the measured behaviour, including the analysis of female discrimination of wells, with repeated, individual females clustered as non-independent variables. Therefore, the results presented are as conservative as is possible with the existing data.

I also analysed all of the data described in the preceding paragraph using resampling techniques, which make no a priori assumptions regarding the distribution of the data. The *P* values obtained from resampling statistics were all as or more significant than those generated using more traditional tests.

## RESULTS

### Behavioural Descriptions

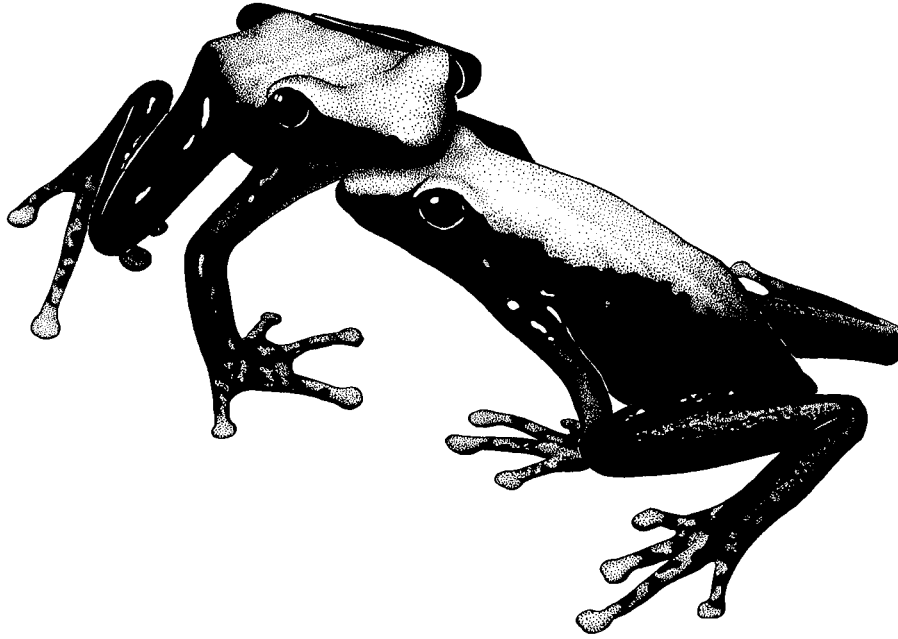
#### *Territorial behaviour*

During 925 h of observations, 215 fights were witnessed between males, in 367 bouts. Fight bouts between males last from 10 s to more than 1.5 h. Fights take place primarily over territories, the best of which include water-filled wells in which mating takes place, and eggs and tadpoles develop. Wells are the limiting resource for these frogs (unpublished data). Males defend these wells, and an area not less than 500 cm in diameter around them, with advertisement calls and fights.

Males are described using two distinct forms of territorial defence, and an additional category of male does not defend territories at all. Among the territorial males, some defend resources, other appear not to. I define males in possession of territories with wells in them 'resource-defence territorial', or RD-territorial. I define males in possession of territories without wells as 'no-resource territorial', or NR-territorial. As wells are known to be limiting (unpublished data), and other parameters such as food are not, territories without wells in them were defined as without resource, and therefore of low quality. Both NR-territorial and RD-territorial males scout in other males' territories, usually without advertisement calls, when they are not defending their own territory. Finally, there are 'aterritorial' males, which do not appear to defend any area, but do spend time in territorial males' territories and try to attract females therein. These 'aterritorial' males may in fact be NR-territorial, with defended territories outside the range of my observations. When either NR-territorial or aterritorial males were in territories with wells, I refer to them as nonresidents, and the territory holder as the resident.

Both NR-territorial and aterritorial males sometimes successfully lead females into matings in wells in territories not their own. Often these nonresident males are seen by the resident (territory holder) and attacked, at which point they respond in one of two ways. Nonresident males may fight back, often repeatedly (several bouts); or they may be docile, not call, and submit to being amplexed by the male resident. Resident males do not amplex, or try to court, nonresponsive animals of either sex for more than 5 min, and leave the nonresident after a short time.

RD-territorial males can usually be found in a given territory, not larger than 2 m square, which contains at least one water-filled well, usually broken bamboo. RD-territorial males call frequently from their territories. NR-territorial males have a high rate of site fidelity as well, but the sites they call from do not have wells in them. These males call and attract females to these low-quality territories, after which they lead females into other males' (high-quality) territories. Territory borders, and even interiors, are repeatedly fought over by the same males. Fights include male-male amplexus, belly-to-belly wrestling, tumbling, leaping onto one another, and chasing. Aterritorial males have home ranges that they do not defend against other males.



**Figure 2.** Chinning behaviour of male *M. laevis* during courtship. During both initiation and continuation of courtship, the male repeatedly makes contact with the female by resting his throat on either the top of her head, or her back, while softly uttering a courtship call. The relative position of the courting animals is variable, but usually the male is facing the female, or perpendicular to her.

#### Courtship behaviour

During 925 h of observations, 348 courtships were witnessed in 521 bouts. Courtships involve stereotyped sequences that begin when the male gives an advertisement call, often from a raised perch, such as a palm axil or the well he defends, and a female responds by approaching. When a male sees a female approaching, he moves towards her and makes initial contact by putting his throat either on the top of her head or on her dorsum (behaviour hereafter referred to as 'chinning'). The male often faces the female during chinning, and less often has his body perpendicular to hers (see Fig. 2). His vocalizations change at this point from the louder, two-note advertisement call to the softer, often single-note courtship call. The male chins the female for up to 5 min before beginning to lead her to a potential oviposition site. He hops not more than 10 cm in front of the female, uttering courtship calls, sporadically returning to chin her again. During some courtships, the male alternates chinning of the female with nonreproductive axillary amplexus. For up to 30 min (although occasionally much longer), the male leads the female to a potential oviposition site, then climbs to the top of it, and chins her again before allowing her to enter. She then enters, goes into the water, and the male follows, uttering continuous courtship vocalizations. If she accepts the well by remaining inside, the male amplexes her on the inside of the well, and a single egg is laid (see clutch size below). This is the first time that amplexus occurs during the courtship. If the female rejects the well, she hops out while the male calls from inside the well. In most cases, the male then follows and catches the female, chins her again, and begins the repeated chinning, leading and calling while leading her to another potential oviposition site.

Only two pairs of *M. laevis* were observed in reproductive amplexus without first engaging in the stereotyped courtship sequence. These two exceptions occurred when the female entered the well and began ovipositing at the water line, at which point the male followed her in and amplexed her, and an egg was laid. In both cases, the egg was quickly eaten by the resident tadpole, suggesting attempted maternal care (see below) rather than true courtship.

Some would-be courtships turn into fights, when silent aterritorial or NR-territorial males enter a calling RD-territorial male's territory, and are chinned by the resident male. It is difficult for humans, and perhaps frogs, to distinguish between the sexes without behavioural cues. This is true despite statistically significant sexual dimorphism for both SVL and mass in this species ( $N=44$  females, 70 males; range, mean  $\pm$  SD: female SVL (mm): 25.0–31.0,  $28.06 \pm 0.18$ ; male SVL (mm) 24.0–30.0,  $26.79 \pm 0.14$ ; female mass (g): 1.15–2.05,  $1.72 \pm 0.03$ ; male mass (g): 1.10–1.90,  $1.53 \pm 0.02$ ; independent samples  $t$  test:  $t=5.54$  for mass,  $t=5.50$  for SVL,  $P<0.0001$  for both variables).

Females were often observed in scouting behaviour, in which they investigate several wells in succession, climb them, look in, and go into the water. While scouting, females ignore the advertisement calls of nearby males, and retreat when males approach them. Males using all of the three territorial categories were also seen scouting potential oviposition sites, never calling while doing so.

#### Maternal care

During 925 h of observations, 10 incidences of maternal care of tadpoles were witnessed. Females were observed climbing wells alone, ignoring the

**Table 1.** How courtship bouts end ( $N=160$ )

Reason for courtship termination	Total frequency (percentage of total bouts)	Percentage of subset (female left, or male left)*
Female left	52 (32.5)	
After being inside a well	31 (19.4)	59.6
For another male	3 (1.9)	5.8
Male left	61 (38.1)	
To initiate territorial defence	27 (16.9)	44.3
To defend against another male	14 (8.8)	23.0
For another female	3 (1.9)	4.9
Competitor interference ( <i>P. notostica</i> , crab)	6 (3.8)	
Success (oviposition)	21 (13.1)	

\*The final column is a measure of the conditions under which males and females left courtships (e.g. of those females that left courtships, 59.6% (31/52) left only after being inside a well, while only 5.8% (3/52) left for another male).

advertisement calls of nearby males, backing into these wells, and depositing single eggs at or below the water line. In all 10 cases, a resident tadpole was observed eating the egg within 30 min of deposition. In five of these cases, the females that returned alone had previously been seen in mating amplexus with males in those same wells. I do not, however, have more direct evidence that the tadpoles in these wells belonged to these females, as viable wells often have eggs from several ovipositions and from different mating pairs at the same time.

Furthermore, two of the successful 'courtships' observed appear to have been attempted maternal care in which a territorial male followed the female into the well and amplexed her while she was already positioned at the water line, which is otherwise never seen in mating pairs. These eggs were also promptly eaten by tadpoles. On five occasions, an egg deposited by a single or amplexed female was completely gone within 5 min of the female or mating pair depositing the egg and leaving the well. This suggests that both maternal care and oophagy generally may be more common than these data suggest, as the evidence is quickly erased, rendering the behaviour invisible to the researcher. Tadpoles were never observed eating anything but conspecific eggs, and wells with tadpoles in them were not free of mosquito or other small arthropod larvae or detritus.

### Quantification of Observed Behaviours

Resident territorial males fought nonresidents in 82.4% of total fights observed (total  $N=131$ ), of which the residents won 88.9%. Of the remaining 17.6% of fights ( $N=23$ ), nine maintained territory boundaries between two resident males, and 14 were fought between nonresident males when the resident was absent. Individual males were predictably winners or losers in successive fights. Eleven males were observed to participate in five or more fight bouts (range 7–45), of which five won less than 23% of fights (range 0–22.2%), while the other six won more than 69% of fights (range 69.2–85.7%). In addition, an initiator's advantage was apparent, as only

17 of 131 fight bouts (12.9%) were won by noninitiators, 10 of which were won by residents that were attacked by nonresidents.

Apparently, territory is the primary reason for fighting. Ninety-six of 131 fight bouts were fought over territory, in which no female was within 1 m of either male participant; 31 fight bouts were fought over territory while a female was within 1 m of the males; and four fights appeared to be entirely over the theft of a female from a courting male by another male.

Courtships ended for a variety of reasons (Table 1). These included females leaving after being inside the well a male had taken her to, males leaving to engage in territorial activities, interference of other species, and success. Of 160 courtship bouts witnessed in 1999, 128 were 'terminal', 32 'nonterminal'. Terminal courtship bouts were those not resumed within 15 min of interruption. Males left nonterminal courtship bouts more often than terminal courtship bouts to engage in territorial activities. Females, however, were equally likely to leave terminal and nonterminal bouts after being led inside a well by a male (Table 2).

In all instances in which a competitor species interrupted a courtship, the interruption terminated that courtship. The only heterospecific frog species seen to interfere directly with the courtships of *M. laevis* was *Plethodontohyla notostica*. However, two other microhylids (*Anodonthyla boulengeri* and *Platypelis grandis*) also used wells, and prevented *M. laevis* from using them.

Females oviposited in wells at different heights relative to the water line when they were engaged in courtship, versus when they were performing maternal care by depositing single eggs for tadpoles. During courtships, females oviposited above the water line 18 of 21 times, while during instances of maternal care, they deposited at or below the water line four out of five times (Fisher's exact test:  $N=26$ ,  $P\leq 0.01$ ). These data include only those ovipositions for which there was no ambiguity about the number or placement of resultant eggs. Of those same 21 nonambiguous courtships observed in 1999, mean clutch size was  $1.29 \pm 0.12$ , with a range of 1–3.

**Table 2.** Differences in courtship termination between terminal and nonterminal bouts

Termination reason	Nonterminal bouts (%)	Terminal bouts (%)	Difference ( <i>P</i> value)
A Female leaves after being inside well	7/32 (21.9)	24/128 (18.75)	0.65
B Male leaves to initiate territorial defence	10/32 (31.3)	17/128 (13.3)	0.02
C Male leaves to defend himself against another male	6/32 (18.8)	8/128 (6.3)	<0.0001
D Male leaves to engage in territorial activity (B+C)	16/32 (50.0)	25/128 (19.6)	0.001

*P* values generated using logistic regression with clustering of females (A) or males (B–D).

**Table 3.** Male discrimination of wells in bamboo stand 4

Type of well	Number (percentage) of wells containing other organisms			
	Eggs	Tadpoles	Tipulids	Other frog species*
Average well ( <i>N</i> =238)†	71 (29.8)	90 (37.8)	43 (29.8)	71 (29.8)
Wells males take females to ( <i>N</i> =31)	13 (41.9)	15 (48.4)	1 (3.2)	0 (0)
Difference (chi-square goodness-of-fit <i>P</i> value)	0.11	0.27	0.02	0.0004

\*Other frog species include only *Plethodontohyla notostica* and *Anodonthyla Boulengeri*.

†Average wells include all data from wells in stand 4, which were surveyed every 3 days independent of focal watches. Each well was included in the survey only if, at some point during the 3.5 months of survey, evidence of *M. laevisgata* reproductive activity was observed in that well (eggs, tadpoles, or courting adults directly observed).

A larval crane fly (*Limonia renaudi* Alexander, Tipulidae) was observed eating the eggs of *M. laevisgata*, as well as those of one of the other two species of frogs that breed in bamboo wells on Nosy Mangabe, *P. notostica*. The tipulid larvae attach their mouth parts to the gelatinous capsule, and suck out the ovum. Embryos in later stages of development stop moving during egg predation, and are then eaten.

Tadpoles were never observed to engage in cannibalism of other tadpoles. Up to four tadpoles of different developmental stages were observed coexisting in wells, and smaller tadpoles did not disappear from wells with larger tadpoles in them more often than they disappeared from wells in which they were the only inhabitants.

Males discriminated between wells on the basis of tipulid and heterospecific frog presence (Table 3). Wells to which males took females during courtships did not differ significantly from average viable wells with regard to tadpole presence. Wells to which males led females tended to have more conspecific eggs in them than did random wells, but this difference was nonsignificant (Table 3). Females are not left with the option to discriminate between wells on the basis of heterospecific frog presence, as males never took them to these wells. A female rejected the one tipulid-filled well that a male took her to. Furthermore, there was a significant tendency for courted females to reject wells with tadpoles in them. As with wells that males chose, wells that females accepted had a nonsignificant tendency to contain more eggs than the average (Table 4).

*Mantella laevisgata* avoided most heterospecific frog species when choosing oviposition sites, including the

**Table 4.** Female discrimination of wells during courtships

Type of well	Egg occupied (%)	Tadpole occupied (%)
Wells males take females to ( <i>N</i> =31)	13 (41.9)	15 (48.4)
Wells females accept ( <i>N</i> =18)	9 (50.0)	6 (33.3)
Difference (logistic regression two-tailed <i>P</i> values)	0.12	0.02

Females rejected wells for oviposition if they contained tadpoles. They did not discriminate against egg presence in wells; rather, there was a nonsignificant tendency for females to favour wells that contained eggs.

microhylids *A. Boulengeri*, *P. notostica* and *P. grandis*. *Platypelis grandis* is a large, short-term resident that presents an obstacle for less than 24 h. In contrast, the first two species move in and produce clutches, which the fathers stay with until metamorphosis, effectively removing those wells from use by *M. laevisgata* for a month or more. In one instance, I observed a pre-existing *M. laevisgata* tadpole survive 10 days in the same well with a *P. notostica* father and clutch. For over one month after the *P. notostica* father abandoned the clutch, it decayed in the well while the *M. laevisgata* tadpole was still developing in that well. The *M. laevisgata* tadpole survived to metamorphosis. In several other cases, however, when *P. notostica* mating pairs moved in, and fathers stayed for

over a month with their developing brood, previously existing *M. laevis* eggs or tadpoles were never seen again in those wells. The other paternal-care giving microhylid that usurps wells from *M. laevis*, *A. boulengeri*, is more common in forest than in bamboo stands, where the watched populations of *M. laevis* live. Thus, no direct competition between *A. boulengeri* and *M. laevis* for wells was seen, although *A. boulengeri* was observed occupying wells that *M. laevis* previously had occupied. *Anodonthyla boulengeri* and *M. laevis* were both observed to move into artificial wells that were established in forest plots, suggesting possible competition for wells between these two species as well (unpublished data).

*Mantella laevis* did not discriminate against all heterospecific frog species when choosing oviposition sites. *Platyplepis cowani*, a small (25 mm SVL) microhylid species, was often found in wells, then difficult to locate minutes later when no frogs had been observed to leave. As such, no data were taken on *P. cowani* presence in wells due to suspected inaccuracies. However, in one directly observed *M. laevis* courtship, there were two *P. cowani* easily seen inside the well in which the *M. laevis* mating pair oviposited an egg.

## DISCUSSION

*Mantella laevis* reveals a surprising number of behavioural convergences with the aposematic dendrobatids. The extended, repeated fights between males over territory, the stereotyped and highly tactile courtship sequences, and the maternal care that is given to tadpoles in the form of unfertilized eggs all resemble behaviours of some dendrobatids. Convergent morphology or behaviour may provide information about the evolution of adaptations by revealing universal rules or causal chains. For instance: toxicity is a prerequisite for aposematic coloration; aposematic coloration leads to diurnality and clumping of individuals due to lower predation pressure; clumping allows for greater complexity of social interactions, which includes males trying to control females through controlling the resources they need access to (Emlen & Oring 1977; Heying 1997; Vences et al. 1998). Perhaps of more biological significance, however, are the differences between the dendrobatids and *Mantella* that emerge on closer inspection, and the specifics of the *M. laevis* system.

Maternal care in *M. laevis* is probably facultative, rather than obligate, given the small number of occurrences observed during this study. The evidence of maternal care may often disappear quickly, as hungry tadpoles eat trophic eggs within minutes of deposition. Most tadpoles were never seen receiving maternal care, which suggests that many tadpoles obtain nutrition from nonmaternal sources. Whereas in most parental care-giving dendrobatids, clutches are laid in one place, allowed to hatch, and the tadpoles are then transported, usually singly, to bromeliads or other wells (reviews in Weygoldt 1987; and Crump 1995; but see Summers 1999 for an exception); in *M. laevis* the eggs and tadpoles develop in the same space. Thus, courted females lay eggs

while amplexed by males in the same phytotelmata used by lone females for maternal care when ovipositing for their already hatched offspring. These spaces are limiting for *M. laevis* (unpublished data), and during courtships, males often take females to wells that already have developing eggs or tadpoles in them. If a male has fathered tadpoles currently developing in a well he actively defends, then the male's potential gain from convincing a female to oviposit in that well is increased. The egg the female lays during courtship may result in another offspring of his, or may go to feed his already existing offspring. Whether prezygotic or postzygotic investment, his effort is parental in nature. This should be considered reproductive parasitism on the part of the male (Weygoldt 1987; Summers 1999).

The 'icebox hypothesis', which postulates that some offspring provide indirect parental investment by providing food for other offspring, is predicted to be in effect in such a system, where future conditions are unpredictable (Mock & Parker 1997). If heavy rains bring the water level in a well up to the level of an egg laid during courtship, that egg will be eaten if the well contains a tadpole. In such a case, however, that egg, left uneaten, would probably die, due to insufficient oxygen (Seymour & Bradford 1995). Females, then, might be expected to return to wells already containing their offspring for future courtships, as egg predation in such a well still furthers the female's reproductive success. It is not clear that females are doing this, but males do lead females to defended wells during courtships that already contain the male's tadpoles. Higher certainty of paternity than maternity in individual wells might have led to this manifestation of the icebox hypothesis, in which males defending oviposition sites are more eager than nonterritorial females to have eggs laid in particular viable sites.

In response to males evolving reproductively parasitic behaviour to further their reproductive success, females are expected to evolve detection mechanisms by which to avoid such parasitism during courtships. In *M. laevis*, the evidence is strong that females actively discriminate against wells with tadpoles during courtships (Table 4). Tadpoles, in turn, are likely to evolve mechanisms by which to hide from females. The scouting behaviour of females serves to give them multiple interactions with possible oviposition sites, such that when a female is taken to a well by a male during courtship, she already has some information about the quality and inhabitants of that well.

When courted females do oviposit into wells with tadpoles in them, the resultant egg (or occasionally eggs) is usually laid above the water line. Tadpoles are unable to reach eggs above the water line, except in rare cases where their forelimbs are well developed but they have not yet dispersed from the well; thus the oviposition location is another mechanism by which females can attempt to protect their offspring from becoming food for another. Because wells are limiting, however, it is rare that *M. laevis* tadpoles exist in wells without conspecific eggs on the walls of those wells. When other courting pairs, or individuals of either sex that are scouting wells,



move around in them, eggs are often dislodged into the water below. Thus, unlike the dendrobatid species with obligately oophagous tadpoles (e.g. *Dendrobates pumilio*, Brust 1993; and the other four species in the *D. pumilio* group, Crump 1995; *D. vanzolinii*, Caldwell & de Oliveira 1999), tadpoles of *M. laevisgata* have sources of conspecific eggs other than from their mothers. However, other species of dendrobatids have also been observed to cannibalize conspecific, fertilized eggs (e.g. *D. ventrimaculatus*, Summers & Amos 1997; Summers 1999). All cases of maternal care observed in *M. laevisgata* involved non-courted females, and were directed at tadpoles in wells in which eggs had not been seen for at least 3 days, suggesting that females monitor the wells in which their tadpoles live. There is no evidence in *M. laevisgata* that tadpoles cannibalize other tadpoles.

In amphibians, small clutch size, large egg size and terrestrial deposition of eggs are often correlated with a high degree of parental care in individual offspring (Crump 1995). *Mantella laevisgata* usually exhibits the minimum possible clutch size, its ova are large, approximately 3–3.5 mm in diameter, and, although not having terrestrial oviposition per se, females oviposit on the sides of wells above the water line, which is presumably a defence against egg predation, like terrestrial oviposition. Given these predictors of parental care, facultative maternal care probably does not describe the extent of care in offspring in *M. laevisgata*. Males may provide parental care that is not immediately identifiable as such. Males defend wells actively, often leaving individual courtships to chase other males away from their territories. Fights between *M. laevisgata* males serve, most often, to maintain the territorial status quo. Initiators win fights most of the time, and initiators are usually resident males. (This is true across taxa in which it has been studied; e.g. Tasmanian hens, *Gallinula mortierii*, Putland & Goldizen 1998.)

Although nonresident males were seen successfully mating in resident males' wells, this was the exception. A male 'confident' of his paternity, which I could not assess without molecular data, stands to increase his reproductive success through courtship regardless of the future of the egg that is laid. Reproductive parasitism by a male to feed a pre-existing offspring is clearly parental investment on behalf of that offspring. Male defence of wells when tadpoles are inside could also be considered parental investment. If a male *M. laevisgata* drives away individuals of one of the two paternal-care giving microhylid frog species from a well containing his offspring, he has probably saved his tadpole's life. Individuals of both *P. notostica* and *A. Boulengeri* fill a well with their clutch, and then the father remains there with the clutch for more than a month, making it functionally impossible for *M. laevisgata* to coexist in that space. This anuran phytotelm community is ecologically quite similar to a Neotropical phytotelm community, which includes females of *Dendrobates castaneoticus* (which deposit a single tadpole into each phytotelm) and *Bufo castaneoticus* (which oviposit 61–387 eggs into each phytotelm, Caldwell 1993). Other competitors for well space include land crabs, which have, on occasion, been observed to

move into wells and eat *M. laevisgata* eggs. I predict that success of crabs moving into wells is diminished by the presence of an actively defending male, as only crabs already on the inside of a well interacted with adult *M. laevisgata*.

Courtships are the most direct route to reproductive success that these frogs have, but courtships end frequently without an egg being laid (Tables 1, 2). This raises the question: what is more important to long-term reproductive success than the continuation of the present courtship? Females most frequently leave courtships only after investigating the well into which a courting male expects her to oviposit, suggesting that some measure of well quality is a better predictor of offspring success than individual male quality. Sexual selection experiments support this hypothesis (unpublished data).

When males leave courtships, however, more explanation is required. Males rarely leave to court other females, even though the quality of the tadpole in the well a male defends must be critical to the father's reproductive success. Thus, males do not appear to display mate choice in this species, although some parameters of the social system fit predictions of male mate choice: males provide benefits to both females and offspring by defending oviposition sites, but the courtship process is long enough to limit, but not preclude, multiple matings by males (Krupa 1995). Furthermore, the resource provided by the male in this system cannot be used simultaneously by a large number of offspring, as tadpoles will eat younger, conspecific eggs if they can. 'Mate' choice for oviposition sites rather than individuals is consistent with experimental evidence that these sites are limiting for *M. laevisgata* (unpublished data).

Males determine the quality of wells before they begin courting females, which is consistent with focal observations of males scouting the area and investigating various wells. Thus, before females have a chance to reject wells, males have already surveyed wells, and do not take potential mates to wells containing crane fly larvae or members of other frog species (Table 3). This is not due to different habitat requirements for the various species, as the same wells discriminated against by *M. laevisgata* when they contain other frogs or tipulid larvae are used for reproduction when they are free of competitors and predators. In the first reported system in which frogs assess oviposition sites for egg density (*Hyla pseudopuma*, a tropical hylid with known egg cannibalism by tadpoles), females and males are both choosy with regard to the phytotelmata in which they oviposit (Crump 1991). Findings were similar in three dendrobatid systems. Summers (1989) observed male *D. auratus* exploring oviposition sites in succession before taking tadpoles to them. Caldwell (1993) hypothesized that adult *D. castaneoticus* carrying tadpoles detect predatory insect larvae in phytotelmata, and discriminate against wells containing them. Finally, Summers (1999) demonstrated that *D. ventrimaculatus* males do discriminate against pools containing large tadpoles when courting females and when depositing tadpoles.

Although the evidence is strong that *M. laevisgata* discriminate against wells with crane fly larvae in them

(Table 3), *M. laevigata* males cannot prevent adult crane flies from ovipositing in wells that already contain frog eggs. Because clutch size is minimal in *M. laevigata*, the effect of a single voracious crane fly larva on the mating effort of *M. laevigata* will potentially be much greater than that on a clutch of *P. notostica* eggs ( $N > 40$  in all clutches observed). Minimal clutch size may, however, be due in part to a selective response to tipulid presence, such that females scatter their eggs across multiple wells in order to reduce the likelihood of all of their offspring being eaten in a single predation event.

Although *M. laevigata* and *P. notostica* eggs are both at risk from crane fly larvae, tadpoles do not appear to be, as they were frequently seen coexisting in wells with crane fly larvae. In such cases, the crane fly larvae were often positioned above the water line, suggesting a possible reverse predation by tadpoles on the crane flies, although this has not been tested.

Several aspects of the reproductive behaviour of *M. laevigata* are clearly context dependent. Examples include males scouting for oviposition sites, and not taking females to previously favoured wells, which changed for the worse, due to new inhabitants or low water level; females both scouting for wells alone, and discriminating between wells at the time of courtship, depending on the current contents of the well; and females ovipositing at different positions relative to the water line when they are in courtship, versus providing maternal care. The assessment required for all of these choices points to a sophisticated set of standards and rules on which choices are based.

To summarize, males defend water-filled wells that are used as oviposition sites by females. Extremely small clutch size suggests that rare instances of direct maternal provisioning of tadpoles are not the only form of parental care in this species. Males win, reproductively, whenever they court a female that oviposits in a well in which one of the male's offspring already exists. A father's reproductive success is aided whenever his tadpole eats an egg, be it from the tadpole's mother, the result of a courtship involving the father, or the result of a courtship involving neither mother nor father. Males do not take females to wells that contain frog species larger than themselves, nor do they expose courted females to the predatory crane fly larvae that eat frog eggs. Females avoid courtships in wells that already have tadpoles in them, but tadpoles are probably selected to hide from disturbance, so as to increase their chances of being provisioned. The previously unknown social system and well community of *M. laevigata* is as complex and evolutionarily fascinating as that of the better-studied dart-poison frogs.

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