Mixed-species social aggregations in Madagascan tadpoles—determinants and species composition

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Abstract
The frequency, species composition, and determinants of mixed-species tadpole aggregations were analysed under natural conditions in a dry forest of western Madagascar. Most aggregations (73%) were formed by more than one species, with up to four species per individual aggregation. Dyscophus insularis (Microhylidae) and Aglyptodactylus securifer (Mantellidae) were the most abundant species in these aggregations. Using a logistic regression model we analysed to what extent the presence and absence of aggregations in a pond can be predicted by its biotic and abiotic habitat variables. Aggregations are more likely in deep, clear ponds with little leaf litter cover on the bottom, while the overall density of invertebrate predators in the pond seems to play a minor role. Our observations suggest that the formation of mixed-species aggregations in tadpoles of the Kirindy Forest in our system is primarily a reaction to vertebrate predators. Therefore, aggregation behaviour may play a key role in the ability of several anuran species to utilize these spawning waters that are unpredictable in regard to the presence of fish and other vertebrates.

Keywords: Anura, Aglyptodactylus securifer, Dyscophus insularis, Madagascar, Kirindy Forest, predation, tadpoles

Introduction
Temporary animal groups are found in many taxa. Groups are termed social when “individuals actively seek the proximity of each other instead of co-occurring in the same spot because of an attraction to the same environmental condition” (the latter is termed non-social aggregation) (Krause and Ruxton 2002). Different benefits can accrue from forming social aggregations. Among others, animals may become more efficient in foraging (Foster 1985), save water via reduced evaporation (Cook 1981) and energy by reduced investment in thermoregulation (Arnold 1988), reduce the energetic costs of movement (Abrahams and Colgan 1985), have higher reproductive success (Alatalo et al. 1992), or be
better protected from predators (Riipi et al. 2001). In tadpoles, social aggregative behaviour is found in several anuran families from different geographic regions, e.g. Microhylidae (Africa), Bufonidae (Africa, North America, Europe), Hylidae (South America), Pipidae (Africa), Pelobatidae (North America), Ranidae (Europe, North America), and Leptodactylidae (South America). It is mainly seen as a means of reducing the high predation pressures most species are confronted with in their diverse habitats. In the field, there is a good correlation between the formation of tadpole aggregations and the direct presence of predators (Rödel and Linsenmair 1997; Watt et al. 1997) and/or chemical compounds released by the predators or by injured tadpoles (Kats and Dill 1998; Spieler and Linsenmair 1999). However, abiotic variables are also thought to promote and to modulate the formation of tadpole aggregations, e.g. water transparency (Spieler 2001), temperature (Brattstrom 1962), and daylight (Beiswenger 1977; Spieler 2001).

Studies on tadpole aggregative behaviour have so far focused on single-species aggregations, and in addition often on aggregations consisting of related individuals (e.g. Waldman 1991). However, further intriguing questions on the reason for their existence and on costs and benefits for the single group members arise when investigating mixed-species aggregation, as in this study. This is in particular true when group members are ecologically dissimilar with respect to feeding and microhabitat preferences.

The Kirindy dry forest in western Madagascar represents a highly dynamic and heterogeneous habitat for amphibians in relation to pond persistence and predator presence. Fifteen amphibian species breed in forest ponds and in rock-pools of the riverbed when the river is not running at the beginning of the wet season. A maximum of eight tadpole species can be found syntopically in the same pond (Glos 2003). Within these water bodies, temporary, mobile tadpole aggregations can be regularly observed.

In this study, we aim to present an extensive analysis of mixed-species tadpole aggregations in the stagnant, ephemeral waters of this forest. We examined the frequency of aggregations under natural conditions and their species composition. Furthermore, we analysed to what extent the presence of aggregations in a pond can be predicted by its biotic and abiotic habitat variables using a logistic regression model.

Materials and methods

Study site

The Kirindy Forest is a deciduous dry forest on the west coast of Madagascar, 60 km north of Morondava and about 20 km inland (44°39′E, 20°03′S; 18–40 m above sea level; Sorg and Rohner 1996). The area of the Kirindy Forest lies within the Central Menabe region which has the reputation of containing one of the largest remaining continuous forests in western Madagascar (Nelson and Horning 1993). The forest is intersected by the Kirindy River and is surrounded by a tree-shrub savanna of anthropogenic origin.

The climate is characterized by a marked seasonality. Almost all rain falls in the austral summer from November to March, followed by 8 months of virtually no rain (annual mean rainfall 800 mm; Sorg and Rohner 1996). The study was conducted in the rainy seasons (November to February) of 1999/2000 and 2000/2001.

Breeding sites for amphibians exist in different habitat types: the closed forest, and pools in the bed of the Kirindy river (at the beginning of the wet season). All breeding ponds apart from a few pools in the riverbed dry out completely during the dry season. They are successively filled with the onset of rain in November and December. The first waters that are
used by amphibians for spawning usually form in the rocky parts of the Kirindy riverbed. As a rule, these ponds offer a low risk of desiccation and a low density of invertebrate predators (unpublished data). During the course of the rainy season, these waters eventually merge and fish (mainly *Oreochromis* sp.) immigrate from the few permanent pools in the river bed, then exerting a very high predation pressure on the amphibian larvae. *Oreochromis* is an introduced cichlid species, and is therefore not a native predator in the Menabe region, precluding any long-term adaptation by the tadpoles. Usually in December, the first breeding ponds arise in the closed forest. Depending on the amount and distribution of precipitation and habitat parameters of the ponds themselves, the persistence of these waters varies from 3 days to 5 months. Fish never migrate into these water bodies.

**Frequency and composition of aggregations**

Tadpole aggregations were defined as follows: at least four individuals were not more than 2 cm apart from each other ("dense" aggregations sensu O’Hara and Blaustein 1985), and this grouping behaviour persisted for more than 100 s. Ponds where tadpole density was so high that we could not differentiate between social aggregations and aggregations forced by diminishing water volume due to desiccation were excluded from the analysis.

To examine aggregation frequency under natural conditions, 126 ponds were visually surveyed for the presence (> one aggregation present) and absence of tadpole aggregations, respectively. Depending on pond properties (e.g. bottom substrate, water depth) and the extent of phases with low precipitation, some study ponds dried out during the rainy season. When they were refilled after rainfall, they were repeatedly used for breeding by amphibians, leading to a new composition of tadpoles each time. On account of this, each pond was surveyed for the presence of aggregations after the initial filling of the pond, and additionally after each cycle of drying out and refilling. Each survey was done between 1 and 3 weeks after the filling and each refilling, respectively. In the case of more permanent ponds, i.e. when study ponds did not dry out during the study period, we repeated the surveys each month. Accordingly, each pond was surveyed several times (2.35 ± 1.66; mean ± SD; range 1–10; 296 surveys of 126 ponds). The surveys were conducted in two subsequent seasons (1999/2000 and 2000/2001). We pooled the data from the two seasons because both environmental variables (e.g. pond size, vegetation) and tadpole community composition is very consistent between seasons (Glos 2006). The survey was done by carefully pacing along the margin and observing the pond to a depth of 15 cm below the water surface. In larger ponds, additional observations were made from within the pond by carefully crossing the pond. We did not find any indications that this method affected the aggregation behaviour of the tadpoles in any way. Minimum observation time was 5 min, maximum observation time (for large ponds) was 20 min. Surveys were conducted exclusively during daylight between 09:00 h and 16:00 h. Occasionally, additional observations were conducted during the night-time. This method was chosen because it could be applied in all ponds irrespective of pond size and water clarity.

To determine species composition and aggregation size in the field, aggregations were dip-netted in 27 selected breeding waters of the riverbed. Each aggregation was taken from a different pond. Tadpole number in small aggregations was determined by dip-netting the complete swarm in one dip-net stroke (dip-net dimensions: 30 × 30 × 30 cm). In large aggregations, not all individual tadpoles of the aggregation could be captured in one dip-net stroke. In such cases, one dip-net stroke was performed and the tadpoles captured therein were counted, the relative proportion of this dip-net stroke on total aggregation volume was
estimated, and subsequently total aggregation size was extrapolated from these two numbers. Captured tadpoles were taken to the field camp and determined using existing literature (Blommers-Schloesser and Blanc 1991; Glaw and Vences 1994; Glos and Linsenmair 2004, 2005; Glos et al. 2005) and a reference collection. Additionally, the developmental stage according to Gosner (1960) was determined. Species affiliation of each tadpole of the 27 randomly selected aggregations (i.e. of 3995 individual tadpoles) was determined and tadpole number of 12 of these aggregations could be reliably identified.

Predictability of aggregations by habitat variables

In order to extract the key (biotic and abiotic) habitat factors that predict the presence of aggregations in the field we constructed habitat models using multiple logistic regression (Hosmer and Lemeshow 1989). By a preliminary data survey, we eliminated high collinearity within the environmental variables (exclusion of variables in cases of Spearman rho > 0.7, see suggestions by Fielding and Haworth 1997). Using a backward stepwise logistic regression (LR method) we included binary presence/absence (of aggregations) data, coded as 1 and 0, as the dependent variable. In order to measure classification accuracy of the models irrespective of threshold criteria, Receiver Operating Characteristics (ROC) plots were constructed, and Area Under Curve (AUC) values were calculated providing a single quantitative index of the diagnostic accuracy of the model (Zweig and Campbell 1993). We included eight habitat variables as independent variables in the initial model (Table I). Habitat variables were recorded immediately after the surveys for the presence of aggregations. When a pond was surveyed for aggregations more than once and tadpole aggregations were never found, we calculated the second-order mean of the habitat variables measured during all subsequent surveys. When a pond was surveyed for aggregations more than once and we did find tadpole aggregations, we calculated the second-order mean of the habitat variables of only the surveys when aggregations were present. We included 70 breedings ponds in this analysis, i.e. all ponds where we obtained data on all habitat variables and that were situated around a 3 km² area around the field camp.

Results

Frequency and composition of aggregations

In 23.9% of all visual surveys (n=296) at least one tadpole aggregation was found. Considering individual ponds, in 49 (39%) of 126 study ponds tadpole aggregations were present at least once.

The aggregations varied in size and species composition. The number of individuals in one tadpole swarm ranged from 200 to more than 5000 individuals (1060.0 ± 1386.1; mean ± SD; n=12). Tadpoles of six different anuran species were found aggregating, with a maximum of four different species within one particular aggregation. A species was defined as being present in an aggregation when at least one individual of that species was found in the aggregation: 27% of the aggregations consisted of one species, 37% of two species, 22% of three species, and 15% of four species (n=27). The tadpoles found aggregating are members of two anuran families: Mantellidae and Microhylidae. Among those, Aglyptodactylus securifer (Mantellidae) and Dyscophus insularis (Microhylidae) were present in most of the aggregations and were by far the most abundant species (Table IIa).
Laliostoma labrosum (Mantellidae) was present in 40% of all aggregations. All combinations of these three species in the aggregations were found (Table IIb). However, most aggregations consisted either of all three species, or *A. securifer* was associated with *D. insularis* or was found as the only species in the aggregation.

Other species known to occur in the riverbed ponds of Kirindy Forest (Glos 2003) were not found in the aggregations although they were present in these ponds (*Mantella betsileo*, *Mangetanymys*).

Table I. Definition and data acquisition of independent habitat variables.

| Variable name         | Variable definition                                                                 | Unit          | Methods                                                                 |
|-----------------------|--------------------------------------------------------------------------------------|---------------|------------------------------------------------------------------------|
| Pond size             | Absolute surface area of pond when maximum water-filled                               | m²            | Calculated from pond length, width, and shape                          |
| Pond depth            | Maximum pond depth when pond maximum water-filled                                     | cm            | Measured at the deepest point in the pond                              |
| Water transparency    | Transparency of the pond water influenced by dissolved and suspended matters         | Five categories. I (high) to V (low) | The visibility of a metal stick was estimated at a depth of 15 cm at three points within the pond and averaged |
| Leaf litter           | Relative area of pond bottom covered with dead leaves                                 | Five categories. I: 0%, II: 1–20%, III: 21–40%, IV: 41–60%, V: 61–80%, VI: 81–100% | Measured in 12 plots of 0.25 m² within the pond and averaged |
| Surface water plants  | Relative area of pond surface covered with plants (mainly *Nymphaea lotus, Salvinia* sp.) | Five categories. See Leaf litter | Estimated                                                              |
| Submersed plants      | Relative volume of pond filled with submersed water plants (mainly *Lagarosiphon madagascariensis, Najas* sp.) | Five categories. See Leaf litter | Measured in 12 plots of 0.25 m² within the pond and averaged |
| Invertebrate predators| Density of invertebrate predators, including: dytiscid beetles >0.5 cm, larval dytiscid beetles >1 cm, water bugs (Belostomatidae) >0.5 cm, water scorpions (Nepidae) >1 cm, larval dragonflies (Anisoptera) >0.5 cm, larval damselflies (Zygoptera) >2 cm | Five categories. I (low) to V (high) | Measured in 12 plots of 0.25 m² within the pond using dip-netting and the box-method (Heyer et al. 1994) and averaged; determined to higher taxonomic levels in the field and subsequently released |
| Fish                  | Presence of fish (mainly *Oreochromis* sp.)                                          | 0 = absence, 1 = presence | Observation, dip-netting                                              |

Table IIa. Composition of tadpole aggregations in the field.

| Species                              | Total number | Presence (%) | Frequency (%) |
|--------------------------------------|--------------|--------------|---------------|
| *Aglyptodactylus securifer*<sup>Man</sup> (Glaw, Vences and Böhme, 1998) | 2094         | 88.9         | 56.4          |
| *Dyscophus insularis*<sup>Mic</sup> (Grandidier, 1872) | 1487         | 70.4         | 35.3          |
| *Laliostoma labrosum*<sup>Man</sup> (Cope, 1868) | 397          | 40.7         | 8.0           |
| *Boophis doulioti*<sup>Man</sup> (Angel, 1934) | 4            | 7.4          | 0.2           |
| *Scaphiophryne calcarata*<sup>Mic</sup> (Mocquard, 1895) | 9            | 11.1         | 0.1           |
| *Scaphiophryne brevi*<sup>Mic</sup> (Boulenger, 1896) | 4            | 7.4          | 0.1           |

<sup>Man</sup>, Mantellidae; <sup>Mic</sup>, Microhylidae. *Number of individuals that were captured and determined to species level; proportion of aggregations with the respective species present (n=27); mean frequency of the species in the particular aggregation sample (n=27).
As the species composition of aggregations was only studied in riverbed ponds we cannot exclude the possibility that the aggregations of the forest ponds were also composed of the species that mainly occur in this habitat (*Aglyptodactylus laticeps, Blommersia wittei, Ptychadena mascareniensis, Heterixalus tricolor, H. carbonei, Scaphiophryne menabensis*).

### Predictability of aggregations by habitat variables

A multiple logistic regression model was constructed for the occurrence of tadpole aggregations. The independent variables were tested for normal distribution and six of them (pond size, maximum pond depth, dead leaf cover, underwater vegetation, floating water plants, water transparency) were BoxCox-transformed (Box and Cox 1964). The parameters of the initial and of the final model are listed in Table III. Their importance for the model predictions is reflected by the correlation coefficient ($r$).

Four variables were backwards and stepwise eliminated from the model: floating water plants (step 2), underwater vegetation (step 3), pond size (step 4), and invertebrate predators (step 5). In the final model, the observed and predicted presence of tadpole aggregations rises with increasing pond depth and increasing water transparency. It decreases with cover of dead leaves at the bottom of the pond. The overall percentage of

### Table IIb. Frequency of aggregations with different species compositions ($n=27$); only the three most common species in the aggregations are considered.

| Species combinations | %  |
|----------------------|----|
| *A. securifer* + *L. labrosum* + *D. insularis* | 29.6 |
| *A. securifer* + *L. labrosum* | 3.7 |
| *A. securifer* + *D. insularis* | 33.3 |
| *L. labrosum* + *D. insularis* | 3.7 |
| Only *A. securifer* | 22.2 |
| Only *L. labrosum* | 3.7 |
| Only *D. insularis* | 3.7 |

### Table III. Logistic regression analysis of tadpole aggregations.

| Variables | Coefficient | SE  | Wald   | P    | Exp(B) |
|-----------|-------------|-----|--------|------|--------|
| Initial logistic regression model | | | | | |
| Pond size | 0.132 | 0.338 | 0.152 | 0.696 | 1.141 |
| Pond depth | 0.538 | 0.348 | 2.387 | 0.122 | 1.713 |
| Dead leaf cover | −0.453 | 0.214 | 4.481 | 0.034 | 0.636 |
| Underwater vegetation | −0.997 | 3.658 | 0.074 | 0.785 | 0.369 |
| Floating water plants | 0.039 | 3.369 | 0.000 | 0.991 | 1.039 |
| Water transparency | −4.259 | 1.807 | 5.557 | 0.018 | 0.014 |
| Invertebrate predators | −0.178 | 0.290 | 0.377 | 0.539 | 0.837 |
| Constant | −0.584 | 1.480 | 0.156 | 0.693 | 0.557 |
| Final logistic regression model | | | | | |
| Pond depth | 0.588 | 0.276 | 4.533 | 0.033 | 1.801 |
| Dead leaf cover | −0.465 | 0.204 | 5.205 | 0.023 | 0.628 |
| Water transparency | −4.378 | 1.627 | 7.244 | 0.007 | 0.013 |
| Constant | −0.939 | 1.352 | 0.483 | 0.487 | 0.391 |

*Regression coefficient $B$. Initial model: $n=70$, $\chi^2=19.33$, Nagelkerke $r^2=0.35$, $P=0.007$. Final model (stepwise backwards analysis): $n=70$, $\chi^2=18.72$, Nagelkerke $r^2=0.34$, AUC=0.75, $P<0.001$. 
correctly predicted presences and absences is high with 80.0% (for threshold value $P=0.5$). The AUC value of 0.75 indicates a good reliability to give correct predictions for all possible classification thresholds. The binary variable *Fish* was not included in the model because all 70 ponds analysed in the model were fish-free ponds.

**General observations**

Tadpole swarms were found in forest ponds as well as in stagnant rock pools of the riverbed, both around the ponds’ edges and in the ponds’ centres. The aggregations were mobile, three-dimensional swarms with the upper part of the swarm usually just below the water surface (range 5–80 cm, median=5 cm, $n=10$). Tadpoles were not observed to feed at the water surface. Swarm members were observed to face in the same direction while swimming slowly, being 1–3 cm apart from each other. The swarms were temporary, and they persisted for between 30 min and several hours. Additionally, our observations suggest that all aggregations dispersed with the diminishing daylight at dusk. The maximum extent of an aggregation was over 5 m in length, 1.5 m in width, and 0.3 m in height.

In general, tadpoles of all sizes and developmental stages were found aggregating. However, within one aggregation, most tadpoles were about the same size and developmental stage irrespective of species affiliation. This was the case even though tadpoles of different sizes and developmental stages were usually present at the same time in the respective ponds. In *D. insularis*, the majority of tadpoles within 19 aggregations were either in an early (42%) or a late (47%) stage of development (Figure 1). In *A. securifer*, most tadpoles in nine aggregations were at an early stage (78%) in their development. Tadpoles shortly before metamorphosis (Gosner developmental stage 40–44) were not found aggregating.

Out of a total of 126 ponds in the area only three contained fish. These ponds were exclusively situated in the Kirindy riverbed. Fish, in particular cichlids (*Oreochromis* sp.), are obviously causing tadpoles to aggregate. In two instances we observed fish newly immigrating into formerly fish-free pools using a small water bridge that had formed after a heavy rainfall. Within less than 30 s, the majority of the tadpoles that had been randomly distributed previously formed dense aggregations (J. Glos and G. Erdmann, personal observation). Our observations suggest that these aggregations were formed before the fish

![Figure 1](image_url)

Figure 1. Relative frequency of aggregations with *Dyscophus insularis* (grey bars, $N=19$, $n=1487$) and *Aglyptodactylus securifer* (black bars, $N=9$, $n=737$) tadpoles in four developmental stage classes (after Gosner 1960). An aggregation was assigned to a stage class when $>50\%$ of tadpoles had been in that stage class. $N$, number of aggregations; $n$, number of tadpoles.
actually fed on the tadpoles, and therefore before an alarm substance ("Schreckstoff") could have been released. Further observations and unpublished data strongly suggest that predation pressure by fish is very high, e.g. we observed single individual cichlids (*Oreochromis* sp.) that consumed more than 20 individual tadpoles in less than 3 min. Additionally, turtles (*Pelomedusa subrufa*) are common in ponds of the Kirindy riverbed. We observed that juveniles of this species regularly preyed on tadpoles; however, we have no data on their absolute effect on tadpole mortality.

**Discussion**

Surprisingly few studies have so far addressed questions on the range and frequency of conspecific and heterospecific group sizes under natural conditions (Krause and Ruxton 2002). The available data are mainly restricted to fish (Seghers 1981; Bonabeau and Dagorn 1995) and large mammals (Lott and Minta 1983; Wirtz and Lösch 1983). In the Kirindy Forest, mobile, social aggregations of tadpoles were frequently observed. The tadpole aggregations consisted of up to several thousand individuals, and thus are paralleled in size only by large *Bufo* aggregations (Beiswenger 1975; Wassersug et al. 1981; Waldman 1991), and are much larger than those of, for example, the microhylid *Phrynomantis microps* Peters, 1875 (range 6–580; Spieler 2003) or north American ranids (e.g. 4–40 in *Rana cascadae* Slater, 1939; O’Hara and Blaustein 1985). The aggregations resembled “true schools”, in the sense ichthyologists use this term, as they not only aggregated but also exhibited parallel orientation and preferential bearing to their nearest neighbours (Wassersug et al. 1981). Tadpoles of a broad range of sizes and developmental stages were found in aggregations, although within one aggregation most tadpoles were about the same size and developmental stage. Accordingly, we found aggregations of different size classes simultaneously in one pond. Associations of size-matched individuals are known from numerous studies, mainly on fish, and both in conspecific and heterospecific groups (reviewed by Ranta et al. 1994), but also in tadpoles (e.g. Breden et al. 1982; Branch 1983). There, size-assorted shoaling is explained by fitness gains of individual group members, either in the context of predation (e.g. through the “oddity effect”; Landeau and Terborgh 1986) or foraging (Ranta et al. 1994). In contrast to these active mechanisms based on the decisions of individuals, size-assortment in fish, as in tadpoles, might be the result of passive sorting mechanisms based, for example, on differential swimming speeds (Gueron et al. 1996) or differential habitat preferences between different-sized individuals. Further experimental studies are needed to disentangle the mechanisms that are responsible for the observed pattern.

Aggregation size varied between ponds. Group size is therefore not fixed, but varies with biotic and/or abiotic factors (Spieler 2003), or might be directly related to the total number of tadpoles within a respective pond. Furthermore, the result that aggregations differed in the size of their individual members indicates that there is no clear-cut ontogenetic shift in sociality, as found by Butler (1999) and Ratchford and Eggleston (1998) in lobsters. However, our data indicate that the readiness to shoal might decrease with ongoing development in *Aglyptodactylus securifer*, in contrast to *Dyscophus insularis* where we found as many aggregations consisting of tadpoles in later stages as in younger stages. However, in neither species did we find aggregating tadpoles that were close to metamorphosis.

The ultimate reason for the tadpoles to aggregate might be predator avoidance, as is generally assumed (e.g. Rödel and Linsenmair 1997; Watt et al. 1997; Kats and Dill 1998). This is supported by the observation that tadpoles instantly aggregate when predatory fish
enter formerly fish-free ponds, even before the first tadpoles were eaten by the fish and alarm substances could possibly have been released. This situation is often observed in Kirindy when ongoing rainfall leads to an increase in the water level of the breeding ponds. Subsequently, fish-free ponds eventually merge with those that contain fish, leading then to a high predation threat. Aggregation behaviour might therefore play a key role in the ability of amphibians to utilize predator-rich spawning waters (Spieler and Linsenmair 1999). The density of invertebrate predators seems to be less important for the probability of aggregation formation. However, the logistic regression model shows that the threshold of aggregation formation seems also to be influenced by abiotic factors (Pond depth), structures inside the ponds (Leaf litter), and water characteristics (Water transparency). Aggregations were more likely to be found in deeper ponds, with low cover of leaf litter, and high water transparency. Animals tend to prefer structurally complex microhabitats as a reaction to high predation risk, often combined with a reduction in activity (Kats et al. 1988; Magurran and Higham 1988). Therefore, the absence of sufficient cover against potential predators by leaf litter on the ground might facilitate the change of strategy of tadpoles to seek protection in large, conspicuous groups. Furthermore, low visibility in the water, either caused by water muddiness or by diminishing daylight, is known to negatively affect aggregation size and density, and will eventually lead to its dissolution (Beiswenger 1977; Branch 1983; Rödel and Linsenmair 1997; Spieler 2001), as found in our study. The majority of the most important predators of tadpoles are known to hunt visually (Rödel and Linsenmair 1997; Rödel 1999). Therefore, predation risk most likely decreases when prey detectability is low.

The fact that the aggregations were temporary indicates that there are costs involved in this behaviour. Spieler and Linsenmair (1999) showed that these costs involve both decreased growth and retarded development. These costs are no longer justified when the muddiness of the water increases above a certain level and the benefits of aggregating vanish (Siegfried and Underhill 1975; Watt et al. 1997). Thus for tadpoles in muddy water high costs with respect to growth and development might outweigh decreasing benefits of being in an aggregation as soon as a critical level of turbidity is reached. Since the water transparency in ponds often changes quickly due to disturbance by animals or recent rainfall, the flexible behaviour of aggregation formation seems to be an excellent adaptation to the heterogeneous environment of this habitat.

Three out of four aggregations in the ponds of the Kirindy Forest consisted of two or more species, with three species being abundant in those aggregations and a further three species being present only sporadically. The two most abundant species were *Dyscophus insularis* (Microhylidae) and *Aglyptodactylus securifer* (Mantellidae). To our knowledge this is the first detailed study on mixed-species aggregations in tadpoles (see Vences and Glaw (2003) for an observational note). *Dyscophus insularis* and *A. securifer* were frequently found together in one aggregation, despite their ecological dissimilarity. The tadpoles of *Dyscophus insularis* are filter-feeding, and completely microphageous. They are generally found in all vertical positions of the water column and usually float horizontally in midwater (Glaw and Vences 1994). *Aglyptodactylus securifer* tadpoles, on the other hand, feed on plant and/or microbial matter of detritus. They are usually only found on the bottom of the pond (Glos and Linsenmair 2004). It is therefore likely that possible costs of aggregative behaviour are asymmetrical between the two species. As aggregations were usually found right below the water surface, *A. securifer* obviously changed their preferred microhabitat to join these aggregations. Therefore, and because tadpoles were not observed to feed on the water surface film, they presumably bear the costs of a greatly reduced food input, while
D. insularis as a filter feeder can continue feeding. The position of the aggregations beneath
the water surface might be an adaptation to reduce the predation risk by those fish that are
preferably foraging at the bottom or in the middle of the water column. Moreover, only the
bright ventral side of the tadpole is exposed to aquatic predators, when swimming close
to the water surface. This might camouflage the tadpoles against the sunlight gleaming on
the water surface and further reduce predation risk by visual hunters, as are most fish. On
the other hand, this behaviour might render the tadpoles more conspicuous for species
foraging from outside the pond, in particular kingfishers (Alcedo vintsioides: Eydoux and
Gervais, 1836). However, kingfishers only consume a small proportion of the tadpoles
whereas fish usually quantitatively eliminate tadpoles in a pond (personal observation). The
predation pressure by the kingfisher will in any case be smaller than that by fish.

Benefits for group members within a social mixed-species aggregation may differ
(Diamond 1981; Wolters and Zuberbühler 2003). They may have access to resources
within a territory whose owner would expel solitary competitors (“gang theory”; Diamond
1981). Group members may facilitate feeding of other group members in the course of their
own foraging (“beater theory”). Group members may seize food that another group
member has caught (“pirate theory”). Group members benefit in terms of foraging from
being in a large group, even when all species have similar diets, by raising the probability of
finding a good feeding patch or by learning new foraging techniques from heterospecifics
(“feeding efficiency theory”).

These theories all predict that one or more species within a mixed-species group can
increase their food input by the presence of other species. However, in tadpole aggregations
of Kirindy Forest, this is not very likely. First, competing for food in these tadpoles is
exploitative rather than direct (excluding gang and pirate theory). Second, as their feeding
ecology is very different, it is most unlikely that they profit from the presence of other
species as the beater theory and the feeding efficiency theory suggest. However, the
formation of large, temporal aggregations including more than one species may be an
adaptation to reduce predation risk (“convoy theory”; Diamond 1981; Gibson et al. 2002).
In several tadpole species, this is seen as the main ultimate cause for social aggregative
behaviour (e.g. Rödel and Linsenmair 1997; Spieler and Linsenmair 1999; Spieler 2003).
Within mixed-species aggregations, all group members may benefit from mere group-size-
related anti-predator benefits, such as the dilution effect (Hamilton 1971), confusion effect
(Heller and Milinski 1979), Trafalgar effect (Siegfried and Underhill 1975), and the
learning effect, when there are unpalatable individuals in the group (Brodie and Formanowicz 1987). In addition, group members may benefit from other species’ abilities
to detect and react to predators, as has been suggested in other vertebrate groups (e.g.
tamarin monkeys; Peres 1993). Different tadpole species are known to react to different
proximate cues that indicate the presence of a predator or a high actual predation risk (e.g.
Rödel and Linsenmair 1997; Kats and Dill 1998; Spieler and Linsenmair 1999). Therefore,
members of a mixed-species group may be better protected than those of single-species groups as a consequence of differential anti-predatory abilities within a
group. Accordingly, members of one species may join an aggregation based solely on the
visual presence of other heterospecific individuals (Wassersug and Hessler 1971).

The formation of mixed-species aggregations of tadpoles in the Kirindy Forest might be
mainly a reaction to vertebrate predators. It is more likely to occur in profound ponds with
low leaf cover and clear water, while the density of invertebrate predators in the pond seems
to play a minor role. Therefore, aggregation behaviour may play a key role in the ability of
several anuran species to utilize spawning waters that are unpredictable in the presence of
fish and other vertebrate predators (e.g. turtles, kingfishers). It is not yet clear what the proximate cues are that lead to the formation of aggregations in the different species and what the fitness costs of this behaviour are. This needs to be investigated further.

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