Fly parasitism in Papuan frogs, with a discussion of ecological factors influencing evolution of life-history differences

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Abstract
Dipteran parasitism of frogs in the Papuan region is described and aspects of the ecological interaction are detailed. The fly involved, *Batrachomyia krausi*, is the largest known member of an otherwise Australian genus. Larvae of this species develop in the lateral lymph sacs of frogs of the genus *Rana*, feed on host blood tissues, occur with high incidence and moderate intensity, yet exhibit minimal virulence. Minimal virulence and high infestation rate seen in this host–parasite system contrast with those reported for Australian congeners. These differences are hypothesized to derive from interaction of the large size of the Papuan parasite with its phylogenetically constrained life-history. Differences in virulence exhibited between parasitic chloropids versus calliphorids and sarcophagids are discussed as consistent with ecological predictions based on parasite transmission dynamics.

Keywords: **Anura**, *Batrachomyia*, fly parasitism, New Guinea, *Rana*, virulence

Introduction
Parasitism of adult frogs by dipteran larvae has been described in three of approximately 175 families of dipterans, and these flies parasitize 10 families of anuran hosts (Table I). Information on these ecological relationships is largely anecdotal or descriptive and has not yet been examined in a comparative context. Yet the narrow phylogenetic range of dipterans that exhibit this behaviour and the phylogenetically covariant differences in ecological attributes and life-histories among these parasitic flies suggest that these poorly understood host–parasite systems could be a fruitful venue for testing evolutionary theory of parasite virulence (e.g., May and Anderson 1979; Anderson and May 1982; Ewald 1983, 1995). To date, studies of frog–fly parasites have not employed such a conceptual framework, and ecological contrasts among taxa remain rudimentary.

Each of the dipteran families exhibiting adult-frog parasitism [other flies parasitize frog egg masses and will not be considered here, cf. Villa (1979, 1980), although one of these has also been found to parasitize facultatively frogs in pet shops in Europe (Zwart et al. 2005), perhaps as an instance of wound myiasis] has adapted to a modest diversity of host...
taxa, with each parasitizing a number of genera across three to five frog families (Table I). Lack of systematic survey makes it uncertain to what extent each dipteran species is host-specific, but in all instances in which more than two host species have been reported for a parasite species, they include members of different families. This suggests that many fly species may not be narrowly host restricted. However, among chloropids, no member of the genus *Batrachomyia* confidently identified to species has yet been retrieved from more than one species of frog (Table I), and it remains possible that species in this genus are more host specific than are calliphorids and sarcophagids.

Virulence (harm to the host) differs among these dipteran parasites. The relationship of calliphorids and sarcophagids with their hosts is one of slow predation (Pounds and Crump 1987) inasmuch as the maggots feed on structural tissues and the hosts typically die after a few days. Calliphorids usually lay their eggs on the head of a host, larvae burrow into the nasal passages or spaces surrounding the eyes and eat their way into the cranium, resulting in host death (Brumpt 1934a; Dasgupta 1962; Meisterhans and Heusser 1970; Bolek and Coggins 2002; Bolek and Janovy 2004). Sarcophagids frequently lay their eggs on the dorsal surface of the host’s legs. The larvae burrow into the musculature of the leg and then eat their way into the body cavity (Crump and Pounds 1985). In contrast to these families, chloropids lay their eggs on favourable substrate, larvae come into contact with passing hosts, burrow into their lymphatic sacs, and feed on blood prior to exiting the host to pupate (McAlpine 1955; Elkan 1965; Zumpt 1965). Unlike calliphorids and sarcophagids, parasitism by chloropids does not appear to result typically in host death, although such can occur (Lemckert 2000). Ecological variation in host–parasite relationships within families or genera has received scant attention.

To date, parasitic fly–frog relationships have been reported from temperate Europe, North America, and Australia, as well as tropical India, Central America, and South America (Table I). Such relationships have not been described for anurans in the Papuan region, comprising New Guinea and surrounding islands. In the course of herpetological surveys on Fergusson Island, off the southeastern coast of Papua New Guinea, a population of frogs heavily parasitized by large fly larvae was discovered. This report provides details on that ecological relationship—which expands the range of ecological variation known for parasitic chloropids—and explains ecological differences between Papuan *Batrachomyia* and their Australian congeners in terms of evolutionary and ecological constraints. These contrasts raise more general questions about the ecological determinants of alternative lifestyles exhibited by this and other parasitic frog–fly families. These issues are discussed within the theoretical framework for evolution of parasite virulence presented by Ewald (1983, 1994, 1995).

**Materials and methods**

Anuran hosts were collected under relevant national and provincial permits, anaesthetized, fixed in 10% buffered formalin, and transferred to 70% ethanol for storage. These specimens consisted of a series of 16 adult and large subadult frogs of the species *Rana supragrisea* from a forested stream at 900–1000 m elevation on the east slope of Oya Tabu, Fergusson Island, D’Entrecasteaux Islands, Papua New Guinea, collected during 20–24 August 2002. Size measurements were made to the nearest 0.1 mm with digital calipers on preserved material; mass measurements were taken in the field to the nearest 0.1 g with a Pesola scale on freshly killed specimens. Fly larvae were preserved incidental to their hosts, and their numbers, sizes, and positions determined. Specimens of the hosts and parasites
| Dipteran Family | Species | Family | Frog | Species | Locality | References |
|---------------|---------|--------|------|---------|----------|------------|
| Calliphoridae | Bufolucilia elongata (Shannon) | Bufonidae | Bufo americana Holbrook | USA | Briggs (1975) |
| Ranidae       | Bufolucilia silvarum (Meigen) | Bufonidae | Bufo bufo (Linnaeus) | Germany | Duncker (1891), Stadler (1930) |
| Hylidae       | Lucilia bufonivora Moniez | Alytidae | Alytes obstetricans (Laurenti) | Frace | Brumpt (1934a) |
| Ranidae       | Lucilia illustris (Meigen) | Hylidae | Hyla arborea (Linnaeus) | Switzerland | Spence (1954) |
|               | Lucilia porphyrina (Walker) | Bufonidae | Bufo melanostictus Schneider | India | Dasgupta (1962) |
|               | Lucilia sp. | Bufonidae | Bufo bufo (Linnaeus) | Germany | Gerber (1950) |
|               | Phaenicia sericata (Meigen) | Bufonidae | Bufo sp. | USA | Stewart and Foote (1974) |
| Dipteran Family | Species | Frog Family | Species | Locality | References |
|----------------|---------|-------------|---------|----------|------------|
| Chloropidae    | *Batrachomyia krausi* | *Rana supragrisea* | Menzies | Papua New Guinea | Evenhuis (2006), this paper |
| *Batrachomyia mertensi* | Lindner | *Litoria caerulea* | (White) | Australia | Lindner (1958), Elkan (1965), Vogelnest (1994) |
| *Batrachomyia nigritarsis* | Skuse | *Litoria phyllochroa* | (Günther) | Australia | Skuse (1889), McAlpine (1955), Elkan (1965) |
| *Batrachomyia quadrimaculata* | Skuse | *Pseudophryne bibronii* | Günther | Australia | Skuse (1889), Elkan (1965) |
| *Batrachomyia striipes* | Malloch | *Uperoleia laevigata* | Keferstein | Australia | McAlpine (1955), Schell and Burgin (2001) |
| *Batrachomyia sp.* | Hylidae | *Litoria citropa* | (Tschochi) | Australia | Krefft (1864), McAlpine (1955), Elkan (1965) |

**Sarcophagidae**

| Family | Species | Frog Family | Species | Locality | References |
|--------|---------|-------------|---------|----------|------------|
| Lepidodexia *bufonivora* | (Lopes and Vogelsang) | *Bufo granulosus* | Spix | Venezuela | Lopes and Vogelsang (1953) |
| *Lepidodexia sp.* | Cyclorrhapha | *Eleutherodactylus* | sp. | Panama | Dodge (1968) |
| *Sarcodexia lambins* | (Wiedemann) | *Epipedobates trivittatus* | (Spix) | Peru | Hagman et al. (2005) |
| *Sarcophaga ruficornis* | (Fabricius) | *Bufo melanosticus* | Schneider | India | Roy and Dasgupta (1977) |
| *Wohlfsartia vigil* | (Walker) | *Bufo bufo* | (Linnaeus) | Czechoslovakia | Cepelak (1952), Povolný and Verves (1997) |
| Gen. undetermined | Ranidae | *Rana dybowskii* | Günther | Russia | Povolný and Verves (1997) |
| | | *Epipedobates hassleri* | (Melin) | Peru | Hagman et al. (2005) |
| | | *Epipedobates caninarachi* | Schulte | Peru | Hagman et al. (2005) |

Original citations for *Lucilia bufonivora* in Denmark, Russia, and Sweden, for which I could not obtain references, are provided in Zumpt (1965) and Zavadil et al. (1997); original citations for *Wohlfsartia meigeni* in Russia are available in Povolný and Verves (1997).
are deposited in the Bernice P. Bishop Museum, Honolulu (BPBM). Statistical tests were performed with Minitab 14. Frog sexes were analysed separately to avoid confounding results due to the average greater than twofold mass disparity of females over males in the host species.

Results

The host

*Rana supragrisea* is a large, sexually size-dimorphic (males to 84 mm and 50.8 g, females to 110 mm and 110.0 g), highly active, nocturnal, terrestrial species whose primary habitat is the forested environs of montane streams throughout New Guinea and adjacent islands (Menzies 1987; F. Kraus, personal observation). Adult frogs are typically found at night perched on the banks of high-energy streams; they are wary, agile, and fast. Adults of this species have skins lacking obvious concentrations of granular glands.

Parasites

Individuals of *Rana supragrisea* captured on Oya Tabu were heavily parasitized by final-instar fly larvae of the newly described chloropid species *Batrachomyia krausi* (Evenhuis, 2006). Larvae were 12–16 mm in length. Infested frogs were obvious because of the large, unsightly bulges formed by the larvae (Figure 1). No larvae of earlier instars were found infesting the same frogs.

Site of infestation

Larvae were located in the subcutaneous lateral lymph sacs (sensu Carter 1979) but outside the lateral musculature; they were never located on the dorsum, ventrum, or limbs. Larvae

Figure 1. Preserved specimen of *Rana supragrisea* showing enlarged swellings caused by three (two on right side, one on left) infesting larvae of *Batrachomyia krausi*. Apertures in the skin used to maintain larval access to air are clear on the right; larval respiratory spiracles project from the aperture on left.
maintained connection to the outside of the host via a small aperture in the host’s skin through which they would occasionally protrude their respiratory spiracles (Figure 1). These apertures always faced dorsally, and larvae were aligned vertically within the host, although alignment was usually somewhat less than a strictly 90° orientation. Host tissues medial to the larvae were hypercellularized, isolating the infestation from the lateral musculature of the frogs. As judged by examination with a dissecting microscope, in no case was there evidence of parasite penetration into the peritoneal cavity, and internal organs adjacent to the sites of infestation, including gonads, appeared normal and undamaged.

**Incidence**

Infestation rate was 13 of 16 (81%) collected adult *Rana supragrisea*. Average intensity of infestation was 2.6 larvae per frog, with infested frogs carrying from one to four larvae per side and one to six larvae per animal. All seven collected females carried larvae, as did six of nine collected males. Parasitism rates did not appear to vary importantly by sex, but frog sample size is small, making conclusive statistical testing impossible. Numbers of larvae per frog did not differ between the sexes (Mann–Whitney test, \( W = 47.0, P = 0.503 \)). The three uninfested males do not appear to differ from the six infested males in size (for body length, uninfested males range from 70.6 to 81.2 mm and average 76.3 mm, infested males range from 68.6 to 82.9 mm and average 76.1 mm; for body mass, uninfested males range from 26.7 to 45.8 g and average 36.6 g, infested males range from 28.0 to 44.1 g and average 35.6 g). Thus, there is no evidence that flies targeted larger animals.

**Host breadth**

Among 160 specimens of nine other frog species collected syntopically with the host *Rana supragrisea*, only one specimen of the largely arboreal hydrid genus *Nyctimystes* contained a single early-instar larva. These treefrogs are much smaller in size than *R. supragrisea* (4–8 g in *Nyctimystes* versus an average of 36 g in male *R. supragrisea* and 80 g in females) and the absence of late-instar larvae in *Nyctimystes* may be because the small size of *Nyctimystes* makes them incapable of maintaining a larva the size of *B. krausi* to full term. None of the terrestrial microhylids in the surrounding forest contained parasitic flies.

Similar fly larvae were present in *Rana supragrisea* from one population in Central Province (four of nine specimens infested), in a population of *Rana* sp. from Morobe Province (one of nine specimens infested), and from *R. volkerjane* from West Sepik Province (one of 15 specimens infested), all within Papua New Guinea. In these instances, parasitism rates were not as high as on Fergusson Island and it is uncertain if the same species of *Batrachomyia* was involved, although size of larvae was similar in all instances. Flies were not observed infesting any other *Rana* populations in New Guinea, including 66 specimens of *R. supragrisea* from four other areas in Milne Bay Province and 282 specimens of eight additional *Rana* species from 35 other populations in Papua New Guinea. Nor has *Batrachomyia* parasitism been seen in any of thousands of other collected Papuan frogs, except for the three species of *Rana* mentioned above and one report of parasitism in a specimen of the treefrog *Litoria graminea* (Tyler 1968). Thus *Batrachomyia* larvae appear primarily to parasitize frogs of a single genus across the breadth of Papua New Guinea although treefrogs can occasionally be attacked as well. Parasitism incidence appears, on average, to be low.
Effects

Fly parasitism appeared not to affect the condition of hosts greatly. A general linear ANOVA regressing mass versus snout–vent length for parasitized versus unparasitized females showed no difference between the two groups ($F=0.01$, df=1, $P=0.910$). A similar ANOVA for males showed a statistical difference between parasitized and unparasitized frogs ($F=5.06$, df=1, $P=0.031$), but this effect was due solely to a single parasitized outlier (parasitized frog of SV=82.9; Figure 2) and, if this animal is removed from the analysis, no significant difference between parasitized and unparasitized males remains ($F=0.01$, df=1, $P=0.941$). Regression residuals did not correlate with numbers of flies per individual ($r=0.493$, $P=0.103$), confirming the impression of a general lack of effect of parasitism levels on host condition.

Alternatively, the effect of parasitism on frog condition may be assessed using the approach of Lemckert (2000) in which frog mass is divided by SV and differences in this metric compared between parasitized and non-parasitized frogs. Doing this again showed no effect of parasitism on frog condition. For females, unparasitized frogs had a mean body condition of 0.870 and parasitized frogs a mean body condition of 0.798 ($t=0.89$, df=6, $P=0.406$). For males, unparasitized frogs had a mean body condition of 0.471 and parasitized frogs a mean body condition of 0.467 ($t=0.18$, df=7, $P=0.860$).

Parasitized frogs of reproductive size all appeared to have normally functioning gonads. Mature females had hundreds of yolking eggs, immature females had convoluted oviducts and hundreds of follicles, and all mature males save one had swollen testes. One male had testes of normal but unswollen appearance. The animal was of large size and so may have been sexually recrudescent.

![Figure 2. Regressions of weight versus snout–vent length (SV) for male Rana supragrisea. Larger frogs infested with fly larvae (closed squares, dashed line) exhibit lower weights compared to uninfested frogs (open circles, solid line), but this difference in regressions is determined solely by the largest infested specimen.](image)
Discussion

The mode of development of *B. krausi* closely resembles that of Australian *Batrachomyia* in that flies develop in subcutaneous lymph spaces (McAlpine 1955; Lemckert 2000). The lack of gross tissue damage, signs of secondary infection, or penetration into the body cavity are also consistent with evidence from Australian congeners indicating that *Batrachomyia* larvae restrict their feeding to host blood tissues (Elkan 1965; Zumpt 1965).

The fact that flies parasitized both host sexes with similar frequencies confirms that they do not target hosts by use of host advertisement calls (only male frogs call). That flies instead target oviposition sites in favourable streamside habitat is suggested by the fact that parasitism in the present instance was virtually restricted to streamside terrestrial frogs, being extremely rare among syntopic arboreal frogs and absent from terrestrial frogs in the surrounding forest. These observations are consistent with reports in Australia that *Batrachomyia* lay their eggs in substrates frequented by frogs and not on the frogs themselves (McAlpine 1955; Elkan 1965), thereby avoiding the requirement that adult flies and their hosts overlap in activity period. Similarly, oviposition by *Lepidodexia bufonivora* females in Costa Rica has been shown to be non-random with respect to habitat patchiness (Pounds and Crump 1987), although *Lepidodexia* actively search for hosts and preferentially target female frogs.

Of greater interest is that the ecological relationship between *Batrachomyia krausi* and *Rana supragrisea* appears to differ in a number of ways from relationships described between Australian *Batrachomyia* species and their hosts. First, Tyler (1976) noted that all but one reported anuran host in Australia have glandular skin and he suggested that frog species with this attribute may be more attractive to the parasites. Presumably this is because protection is conferred on the hosts by the distasteful or poisonous substances produced by granular glands, which would reduce risk of parasite death by third-party predation on hosts. *Rana supragrisea*, however, does not have an obviously glandular skin and does not produce noticeably noxious secretions.

Second, the invariable distribution of *Batrachomyia krausi* larvae in the lateral lymph sacs differs from that of *Batrachomyia* reported from Australia, which typically infest the dorsal and ventral surfaces of the host (Tyler 1976; Pengilley 1992), frequently sequestering themselves under the poisonous parotoid glands (Schell and Burgin 2001). Hypercellularization of host tissues adjacent to the site of infestation, as seen in the current instance, has also been reported for Australian *Pseudophryne bibronii* infested with *B. quadrilineata* (Elkan 1965), but has not otherwise been noted.

More importantly, some virulence of *Batrachomyia* parasitism on frogs has been demonstrated in Australia (McAlpine 1955; Zumpt 1965; Lemckert 2000; Schell and Burgin 2001) but appears lacking or minimal in *Rana supragrisea*. There was little or no evidence for difference in body mass or condition between parasitized and unparasitized frogs in the present study. Lack of fly penetration into the body cavity, presence of normal-appearing gonads, and presence of large complements of yolked eggs suggest that neither physical nor chemical castration of hosts (Lemckert 2000) is occurring. This lack of effect is true even though *B. krausi* is larger than its Australian congeners. However, relative size of flies to frogs is clearly higher for many Australian host species. As a result, resistance to fly parasitism in *R. supragrisea* is likely conferred by its large size, allowing moderate loss of blood tissues to the parasites without compromising host vitality. Hypercellular compartmentalization of the parasite from the body musculature may also keep the lateral lymph sacs partially functional and/or reduce the risk of secondary infection.
A final difference is that reported prevalences (infestation rates) of *Batrachomyia* in Australian frogs are typically much lower (2.3–5.1%, Lemckert 2000; Schell and Burgin 2001) than those observed in *R. supragrisea*, but can vary importantly by locality, season, and anuran life stage (Pengilley 1992). The high prevalence observed in the present sample could be due to greater ease of human capture of fly-parasitized frogs, but this seems unlikely to be a complete explanation, given the lack of observed effects of parasitism on frog condition. Moreover, it was estimated that approximately 25–50% of all observed *R. supragrisea* at this locality were captured and, even if one were to make the dubious assumption that all escaping frogs were free of fly parasites, this would still leave a parasitism rate (20–40%) equalled by only one *Litoria phyllochroa* population sampled by McAlpine (1955) and some *Pseudophryne corroboree* populations studied by Pengilley (1992). The failure to find early-stage larvae in the frogs may indicate that a single cohort of flies was involved in the sample, raising the possibility that parasitism is seasonal at this locality, as reported among juvenile *Pseudophryne corroboree* in temperate Australia (Pengilley 1992), or at least that parasites occur in non-overlapping generations. If true, it may be that parasitism rates are lower in the study area at other times of year. Whether high prevalence in the sample is seasonal or permanent, it is consistent with modelling that predicts high prevalence to result from low virulence (May and Anderson 1979).

Each of these ecological differences between *Batrachomyia krausi* and its Australian congener, with the exception of lateral placement of larvae on the hosts, conceivably follows from the dual constraints imposed by the fly’s requirement for living hosts and its large size. *Batrachomyia krausi* larvae attain 16 mm in length, making them approximately 5–10 times larger than their Australian congeners. Few frogs in the Australo-Papuan region attain sufficient size to support that amount of maggot biomass to term without inducing host morbidity or death, an outcome intolerable to the dependent parasite. Given that *Batrachomyia* deposits its eggs on soil substrates instead of searching for hosts directly (McAlpine 1955), only terrestrial frogs could serve as reliable hosts for *B. krausi*. The only terrestrial Papuan frogs large enough to accommodate *B. krausi* are some species of the genera *Rana*, *Callulops*, and *Lechriodus*, and the latter two genera are likely too sparsely distributed or sedentary to maintain a parasitic fly population often. In contrast, *Rana* species are common, range widely, and are reliably distributed along water bodies throughout New Guinea. This abundance and reliability may explain why *Rana* is the only Papuan frog genus found to support *Batrachomyia* larvae to late-stage development. This contrasts with the situation in Australia, where the much smaller native *Batrachomyia* species attack a greater diversity of appropriately sized hosts across a number of genera (Table I). Hence, it seems possible that *Batrachomyia krausi* is tightly co-evolved with certain large, streamside-dwelling *Rana* in New Guinea. If true, this host constraint, imposed by the parasite’s own large size and and non-predatory lifestyle, would account for the unique ecological features discussed above: absence of deleterious effects on hosts (allowed for by large host size), high parasite prevalence (allowed for by low parasite virulence), and presence in hosts without obviously glandular skin (a phylogenetic accident of *Rana* being the sole host meeting the ecological requirements of the parasite). Determining whether evolution within *Batrachomyia* progressed toward large size in the Papuan species or toward small size in the Australian species awaits resolution of phylogenetic relationships within that genus. In either case, it is proposed that evolution of fly size was determined by body size of reliably available host species.

Taking a broader phylogenetic view, either or both of two ecological differences may account for the drastic differences in parasite virulence between chloropids, on the one
hand, and calliphorids and sarcophagids, on the other. First, high parasite mobility and durability are expected to select for high parasite virulence, whereas relative immobility and short survival period in the external environment are predicted to select for low virulence (Ewald 1983, 1994, 1995). Ecological differences between chloropids and the other two families are consistent with these theoretical predictions: eggs or first-instar larvae are directly vectored to hosts by highly mobile female calliphorids and sarcophagids, whereas *Batrachomyia* oviposit in favourable substrates where newly hatched larvae wait to attach to passing frogs (McAlpine 1955). Furthermore, limited stores of energy and narrow humidity tolerance of chloropid eggs and larvae (McAlpine 1955) likely limit their durability in the external environment, a constraint that calliphorids and sarcophagids do not suffer. Secondly, calliphorids and sarcophagids can complete their life cycles in dead hosts (Dasgupta 1962; Anderson and Bennett 1963; Meisterhans and Heusser 1970; Koskela et al. 1974; Roy and Dasgupta 1977; Crump and Pounds 1985; Bolek and Coggins 2002; Bolek and Janovy 2004). In contrast, *Batrachomyia* feed on blood tissues that become unavailable to the parasite in the event of host death. Thus, there is no penalty to calliphorids and sarcophagid larvae for causing host death, whereas for chloropids host death leads to their own death, a strong selective pressure favouring low parasite virulence (Ewald 1994).

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