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Foraging tactics in alternative heterochronic salamander morphs: trophic quality of ponds matters more than water permanency

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SUMMARY

1. In lentic freshwater habitats, the composition of animal assemblages shifts along a gradient from temporary to permanent basins. When habitats with different degrees of permanence are at the scale of the home range of species, they constitute alternatives in terms of energy acquisition through feeding.
2. In this context, previous studies showed an advantage of metamorphic over paedomorphic tiger salamanders (*Ambystoma tigrinum*) in temporary ponds which are only available to metamorphs. The aim of this study was to establish whether salamanders obtain similar benefits in ponds that do not differ in water permanence and whether salamanders shifted from detrimental to advantageous ponds. To this end, we determined the feeding habits, body condition and movement patterns of the two morphs in a complex of four permanent and four temporary ponds.
3. Consistent with previous studies, metamorphs consumed higher-quality diets than paedomorphs in term of energy intake. However, these differences occurred because metamorphs consumed fairy shrimp in a single temporary pond. Individual movement patterns confirmed that most of the metamorphs used different aquatic habitats both within and between years and that most of them moved from permanent ponds for breeding towards the most profitable temporary pond in terms of foraging.
4. These results indicate that habitat selection by salamanders is optimal in term of energy intake in metamorphs that use high quality ponds independently of hydroperiod. It seems that both spatial and temporal variation can influence the relative foraging success of each morph.

Keywords: alternative developmental pathways, energy intake, habitat selection, optimal foraging, salamander

Introduction

Landscape heterogeneity is a key element in determining species distribution (Schoener, 1974; Kerr & Packer, 1997; Tokeshi, 1999). An important gradient in freshwater habitats is hydroperiod: vernal ponds retain water for a few days to weeks, temporary ponds (semi-permanent) dry after weeks to months, but occasionally remain permanent for one or more years, and permanent waterbodies consistently retain

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water across years. In nearly all vertebrate and invertebrate freshwater taxa, there are shifts in species composition along this gradient (Batzer & Wissinger, 1996; Welborn, Skelly & Werner, 1996). Although some species are restricted to one habitat or another, some can exploit both. For example, cyclic colonizers such as beetles and water bugs can exploit the more abundant food and low predation pressure often found in temporary habitats for several generations, then disperse to permanent habitats before pond drying to circumvent the risk of desiccation (Wissinger, 1997). In contrast, other species, including some amphibians, switch habitats within generations (Wilbur, 1980; Joly, 1997; Wissinger, 1997) and can vary in their ability to exploit different hydroperiod gradients depending on life stage (Whiteman, Wissinger & Bohonak, 1994).

To complete such movements, species often rely on complex life cycles (Wilbur, 1980; Joly, 1997; Wissinger, 1999). As with cyclic colonizers such as water beetles and waterbugs that have an aquatic adult stage, amphibians often have the option to remain in the native aquatic habitat after metamorphosis, to metamorphose into a terrestrial morph or to skip metamorphosis and become sexually mature paedomorphic (aquatic) adults (Breuil, 1992; Denoël & Joly, 2001; Denoël, Whiteman & Joly, 2005). This habitat choice is associated with the costs and benefits of dispersal between habitats and the level of competition, predation, and foraging opportunities within each habitat (Wassersug, 1975; Wilbur, 1980; Denoël, 2004; Denoël *et al.*, 2005).

Although most studies have assumed that metamorphic amphibians are philopatric to one pond during the breeding season and the terrestrial habitat for the rest of the year (e.g. Grant, Anderson & Twitty, 1968; Gill, 1979; Joly & Miaud, 1989), recent studies have shown this is not always the case (Miaud, 1990; Whiteman *et al.*, 1994; Perret *et al.*, 2003). Amphibians can occupy different aquatic habitats from one reproductive season to another (Miaud, 1990), but can also move within the same year among aquatic habitats (Miaud, 1990; Whiteman *et al.*, 1994), sometimes along a hydroperiod gradient with the use of both temporary and permanent waters (Whiteman *et al.*, 1994; Whiteman, Wissinger & Brown, 1996; Denoël, 2003).

Drying constraints can also prevent individuals from using the entire range of habitats along hydroperiod gradients (Semlitsch & Wilbur, 1989; Whiteman *et al.*, 1994; Denoël *et al.*, 2005). For example, paedomorphs are usually not able to use temporary waters (Whiteman *et al.*, 1994), except in exceptional circumstances when they can move briefly on land to reach nearby permanent waters before their pond dries (Denoël, 2003), or when the pond does not dry every year, allowing the persistence of paedomorphs as long as water is present (Scott, 1993; Denoël, 2006). In contrast, metamorphs are able to move from pond to pond while crossing terrestrial landscapes (Whiteman *et al.*, 1994). As a consequence of these different life histories, the payoffs can differ considerably between morphs (Whiteman, 1994; Denoël *et al.*, 2002; Denoël *et al.*, 2005). By moving out of permanent ponds after breeding, metamorphs can experience higher fitness benefits than paedomorphs by foraging in temporary ponds, which are rich in high-energy prey (Whiteman *et al.*, 1994, 1996). However, the precise intra-year dynamics and per-pond foraging benefits of such systems remain unknown.

Salamanders that are facultatively paedomorphic provide an interesting test of the evolution of habitat choice at two levels – the consequences of metamorphosis versus paedomorphosis, and, for metamorphic individuals, the payoffs of choosing habitats of varying hydroperiod. The aim of this study was to explore in a large wetland complex the feeding habits of paedomorphic and metamorphic tiger salamanders within and between ponds that differ in water permanency and trophic quality, and to associate these results with estimates of body condition and long-term mark–recapture data on the history of inter-pond movements. We predicted that metamorphs would have advantages over paedomorphs in being able to cross terrestrial landscapes to colonize temporary ponds, and that movements would be from unproductive to productive habitats. Our goal was to gain insights into how habitat shifts can affect both individual fitness and the maintenance of this unique polyphenism.

Methods

Study sites and species

The study ponds are located in the Mexican Cut Nature Preserve within the White River National Forest in the Elk Mountains of south-central Colorado (Gunnison County, Colorado, U.S.A., 39.02°N/

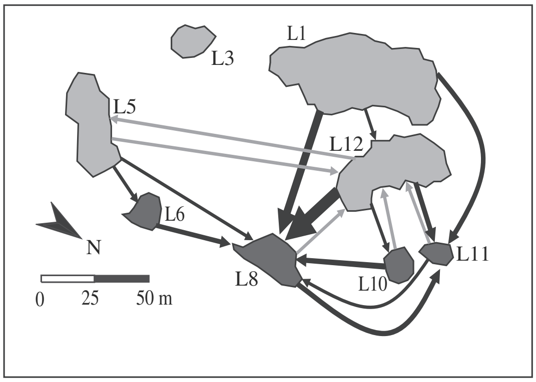

Fig. 1 Schematic map of the studied aquatic habitats in the Mexican Cut Nature Preserve. Dark areas: temporary (semi-permanent) ponds; light grey areas: permanent ponds; dark arrows: intra-annual movements towards temporary ponds; grey arrows: intra-annual movements towards permanent ponds (the thickness of the arrows is proportional to the proportion of individuals making such movements: respectively, 0–5%, 5–10%, 10–15%, more than 15%).

107.06°W). The wetland complex occurs just below tree line at 3400 m elevation on a flat shelf and includes vernal, semi-permanent and permanent ponds, each of which is inhabited by tiger salamanders, *Ambystoma tigrinum nebulosum* Gehlach, 1967 (for a detailed description of this site, see Wissinger *et al*., 1999). The salamander population is composed of two morphs: paedomorphs are restricted to the permanent basins whereas metamorphs utilize all three basin types (Whiteman *et al*., 1994, 1996).

We selected eight ponds containing salamanders (Fig. 1 and Table 1), whose names follow previous descriptions (Wissinger *et al*., 1999). Four of them are permanent (L1, L3, L5, L12), with no drying observed in the past 50 years. The other four ponds are temporary in most years (L6, L8, L10, L11). Their water level decreases during the summer months and they often dry at the end of the summer before being filled again in autumn. Because of the rarity of metamorphs in L1, L3, and L5 and because of the rarity of paedomorphs in L12 during this study, we focus on data of the most common morph in these ponds (i.e. paedomorphs in L1, L3 and L5, and metamorphs in L12).

Sampling and data analyses

This study compared four data sets from the same individuals: historical habitat use, diet, energy intake and body condition. For all statistical tests, values were transformed to approximate normality ($\log_{10}$ for continuous data, square root + 0.5 for counts), alpha was set at 0.05 and all tests were two-tailed (Sokal & Rohlf, 1995).

Capture-mark-recapture analysis. From 1990 until 2003, salamanders in these ponds have been marked each year, approximately 5 days a week from June to August, by toe-clipping (Twitty, 1966) as part of a long-term monitoring programme (Whiteman & Wissinger, 2005). Almost all adult individuals are marked. We used this data set to determine individual history of salamanders, i.e. pond use across time, including within the main study year (2002; see hereafter). This analysis allowed us to determine the directionality of pond change between and within years and to link it with foraging benefits (see below). Chi-square was used to test for an effect of directionality (i.e. to permanent versus to temporary ponds).

Diet analysis. Salamanders were captured by dip-netting between 18 June and 18 July 2002 and identified by their toe clip. Stomach contents of each animal were then collected using a gut-flushing procedure (Joly, 1987). This technique consists of injecting a current of water into the salamander stomach through the oesophagus. The prey items in suspension are expulsed through the mouth and stored in separate vials containing ethanol. Prey items were identified and measured (total length or head

Table 1 Characteristics of the eight ponds during this study. Surface area and depth are maxima for the year, and follow Wissinger *et al.* (1999) or are unpublished data.

Pond	Permanency	Area (m^2)	Depth (m)	Metamorphs	Paedomorphs
L1	Permanent	4632	3	Rare	Abundant
L3	Permanent	175	1.5	Rare	Rare
L5	Permanent	1267	1.5	Rare	Abundant
L6	Temporary	206	1.2	Common	Absent
L8	Temporary	928	1.3	Abundant	Absent
L10	Temporary	283	1.0	Common	Absent
L11	Temporary	213	1.0	Abundant	Absent
L12	Permanent	1688	2.5	Common	Rare

width depending on the taxa) under a stereoscopic microscope. Each salamander was included in the analysis only once. Prey items were grouped in ten functional categories: Diptera larvae (DL), Diptera pupae (DP), *Chaoborus* larvae (CL), other Insecta larvae (IL), Hemipteroida (HE), Hirudinae (HI), Microcrustaceans (MC), fairy shrimp (FS), other miscellaneous aquatic prey (MS) and terrestrial insects (TI). A multivariate analysis of variance (MANOVA) was used to determine whether the diets (i.e. these 10 prey categories) were similar across ponds. Additional MANOVAS and ANOVAS were computed to test for an effect of morph on the diet in ponds where paedomorphs and metamorphs coexist.

Energy analysis. The size of stomach-flushed prey allowed us to determine their dry mass by using relationships between biomass and length for each prey type that had previously been obtained from invertebrates in the Mexican Cut Nature Preserve (Wissinger *et al.*, 1999). Energy values of the stomach contents were calculated using a regression between dry mass and joules for each prey type (Cummins & Wuycheck, 1971). The aim of this analysis was to quantify the benefit of foraging on the different prey categories in temporary and permanent ponds. A MANOVA was used to determine whether the energy intake was similar across ponds. Tukey's *post hoc* tests allowed us to determine which ponds provided the highest energy gains. *t*-Tests were used to determine whether water permanence affected energy intake.

Body condition analysis. Each salamander was measured [snout–vent length (SVL), in mm] and weighed (in g) to determine the body condition (i.e. the residuals of the regression of weight on SVL: see Denoël *et al.*, 2002). An ANOVA and a *t*-test were used respectively to test for an effect of pond and water permanency on body condition. Tukey's *post hoc* tests allowed us to determine the ponds in which salamanders had the highest body condition

Results

Movement history

Capture-mark-recapture analysis from 1990 to 2002 of the salamanders used in the feeding analysis revealed that 40% of these metamorphic salamanders were found in more than one of the eight ponds during their adult stage, with up to five ponds visited (mean ± SE = 1.6 ± 0.1, $n = 90$). Across 40 detected intra-annual pond movements, 57.5% were from a permanent to temporary pond whereas only 7.5% were in the opposite direction; 27.5% were between temporary ponds, and 7.5% were between permanent ponds. Metamorphs moved more from permanent to temporary ponds than from temporary to permanent ponds ($\chi^2 = 15.435$, 1 d.f., $P < 0.001$). Fourteen out of the 26 detected intra-year changes, all of which were from permanent to temporary ponds, occurred with L8 as the final destination ($\chi^2 = 24.0$, 1 d.f., $P < 0.001$; Fig. 1).

Feeding habits

The diet of salamanders differed between paedomorphs occupying permanent ponds and metamorphs present in temporary ponds ($\lambda = 0.045$, $F_{100,1272} = 6.872$, $P < 0.001$; Fig. 2). Microcrustaceans dominated in the paedomorphic salamander guts from four permanent ponds (L1, L3, L5, and L12), and in the metamorphic guts in two temporary ponds (L10 and L11). In L8, metamorphs foraged mainly on fairy shrimp (*Branchinecta coloradensis* Packard, 1874), and in L6, salamander stomachs were nearly empty. Terrestrial invertebrates were also abundant in stomach samples of paedomorphs from L1 and L5. Diptera larvae and pupae were caught principally in the four permanent ponds by paedomorphs (L1, L3, L5, L12). In L11, fairy shrimp were the second most common type of prey consumed by the metamorphs, just after the microcrustaceans. Insect larvae (Coleoptera and Odonata) were consumed in all ponds, but mainly in L1, L3, L5, L6 and L12 (Fig. 2).

Coexisting morphs had similar dietary habits in two out of three ponds (L_1: $\lambda = 0.844$, $F_{9,65} = 1.844$, $P = 0.24$; L5: $\lambda = 0.632$, $F_{8,14} = 1.020$, $P = 0.46$; L_{12}: $\lambda = 0.193$, $F_{9,14} = 6.499$, $P < 0.05$). However, in pond L12, paedomorphs ingested more Diptera larvae ($F_{1,22} = 7.206$, $P < 0.05$) and pupae ($F_{1,22} = 9.228$, $P < 0.01$), Insecta ($F_{1,22} = 10.160$, $P < 0.01$) and *Chaoborus* larvae ($F_{1,22} = 10.239$, $P < 0.01$), Hemipteroidea ($F_{1,22} = 14.149$, $P < 0.01$), and microcrustaceans ($F_{1,22} = 31.365$, $P < 0.001$) than metamorphs.

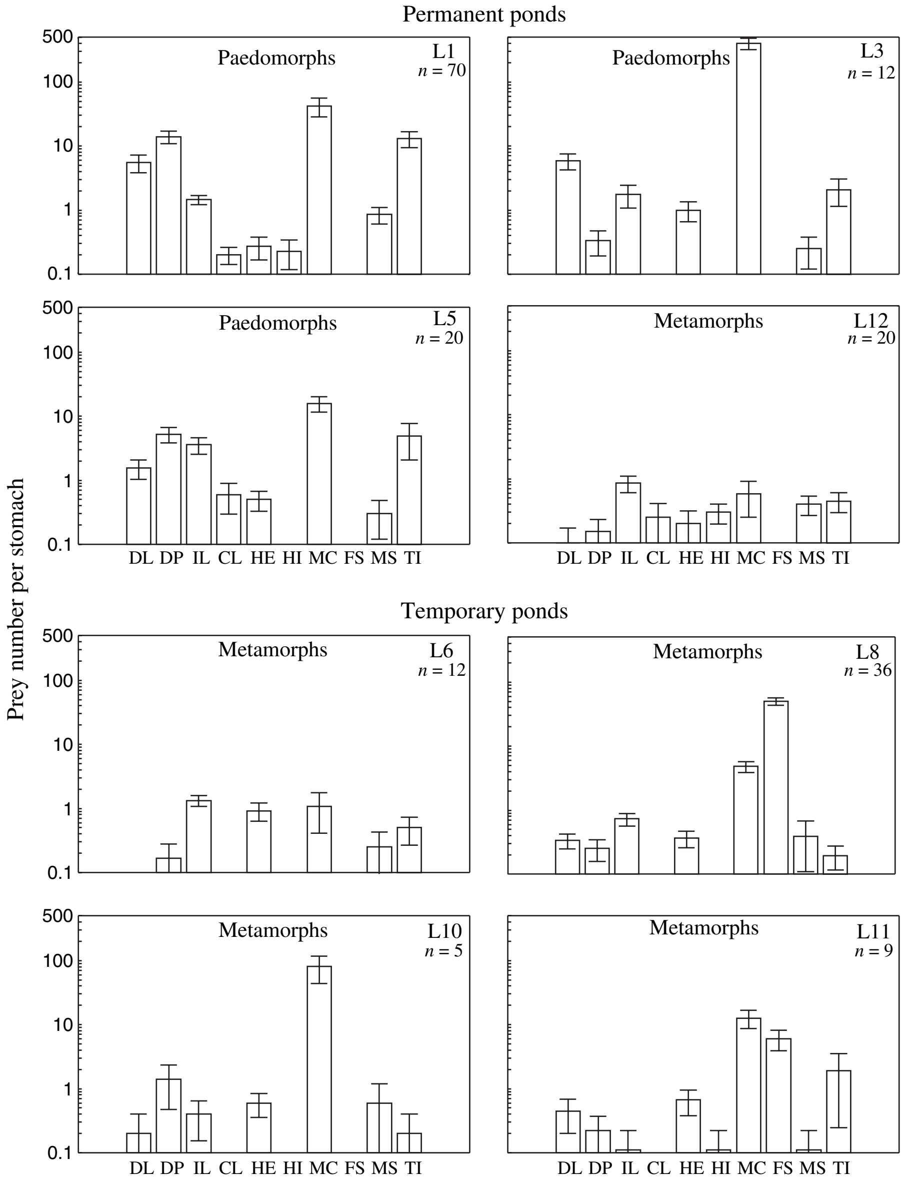

Fig. 2 Mean prey number (±SE) per salamander stomach in the different ponds (log-scale). DL, Diptera larvae; DP, Diptera pupae; IL, other Insecta larvae; CL, *Chaoborus* larvae; HE, Hemipteroida; HI, Hirudinae; MC, microcrustaceans; FS, fairy shrimp; MS, other miscellaneous aquatic prey and TI, terrestrial insects.

Energy intake

Pooling data from ponds of similar permanency shows that the energy values of stomach contents were higher in temporary (mean ± SE = 1913 ± 271 J) than permanent (904 ± 86 J) ponds ($t_{182} = 2.822$, $P < 0.01$). However, pond by pond analysis shows that significant differences existed only between temporary pond L8 and all other ponds (Fig. 3 and Table 2). The mean energy values were very high in L8 (2991 J) in comparison with the other ponds (range from 145 and 1355 J on average).

The energy values of stomach contents were directly connected to the kinds of invertebrates consumed by the salamanders. The very high values found in L8 were because of the consumption of a large number of fairy shrimp (Figs 2 & 4). Microcrustaceans provided a relatively small amount of energy. Terrestrial invertebrates made up the highest energetic gain in L1, L3 and L6, but were also

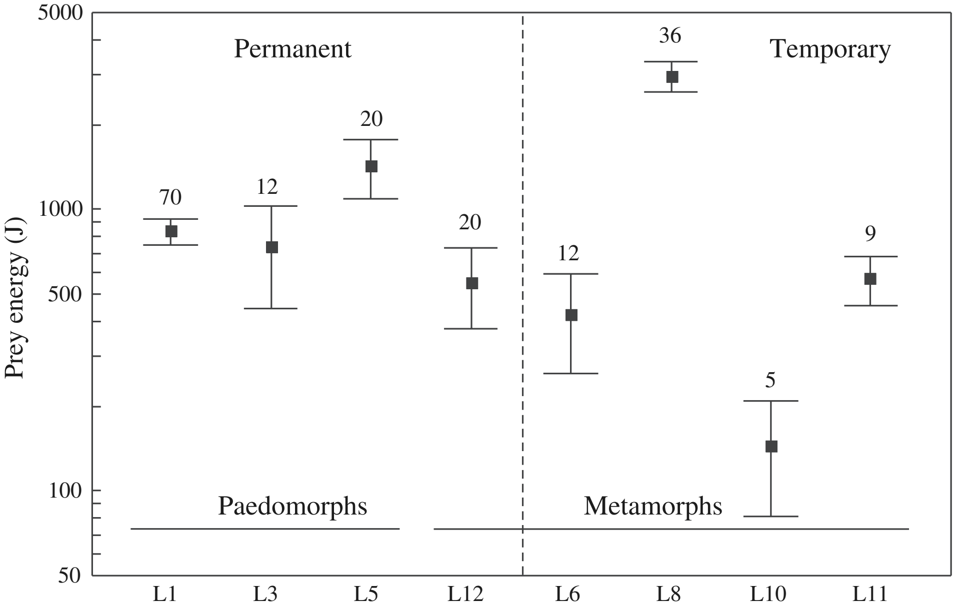

Fig. 3 Mean energy value (±SE) of the salamander stomach contents from each pond (log-scale).

Table 2 *P*-values from Tukey's *post hoc* comparisons testing for the inter-pond differences in log energy intake (below the diagonal) and residuals of the regression of log weight against log SVL (above the diagonal)

	L01	L03	L05	L06	L08	L10	L11	L12
L01	–	<0.01	1	<0.001	<0.001	<0.05	0.70	<0.001
L03	1	–	<0.05	<0.001	1	<0.001	<0.001	<0.001
L05	0.59	0.81	–	<0.001	<0.01	<0.05	0.80	<0.01
L06	0.97	1	0.37	–	<0.001	1	0.56	1
L08	<0.001	<0.001	<0.001	<0.001	–	<0.001	<0.001	<0.001
L10	0.94	0.99	0.47	1	<0.001	–	0.68	1
L11	1	1	0.69	1	<0.001	1	–	0.70
L12	0.99	1	0.36	1	<0.001	1	1	–

important in L5 and L11. Non-dipteran insect larvae constituted an important resource, particularly in the four permanent ponds, but also in L6 and L8. Hirudinae provided a high energy value in L1, L11 and L12.

Coexisting morphs had similar energy gains in all ponds where they were found together (L1: $t_{73} = 0.779$, $P = 0.66$, L5: $t_{21} = 0.632$, $P = 0.53$; L12: $t_{22} = 1.256$, $P = 0.22$).

Body condition

Residuals of the regression of weight on snout–vent length differed significantly between ponds ($F_{7,176} = 19{,}531$, $P < 0.001$), but there was no effect of permanence ($t_{182} = -1.370$, $P = 0.17$). Metamorphs from L8 were in better body condition than salamanders from any other ponds except L3, where body condition was similar (Table 2 and Fig. 5). However, metamorphs from the other ponds, both permanent and temporary, were in poorer body condition than paedomorphs (Table 2 and Fig. 5). Additionally, there was a significant effect of energy intake on body condition ($R_2 = 0.077$, $F_{1,182} = 15.078$, $P < 0.001$); in other words, individuals having a high energy intake had a high body condition.

Coexisting morphs had similar body condition in two out of three ponds (L1: $t_{73} = 0.431$, $P = 0.67$, L5: $t_{21} = 0.282$, $P = 0.78$; L12: $t_{22} = 3.079$, $P < 0.01$), with paedomorphs having a higher body condition than metamorphs in L12.

Discussion

We found that the two alternative morphs of the tiger salamander (paedomorphs and metamorphs)

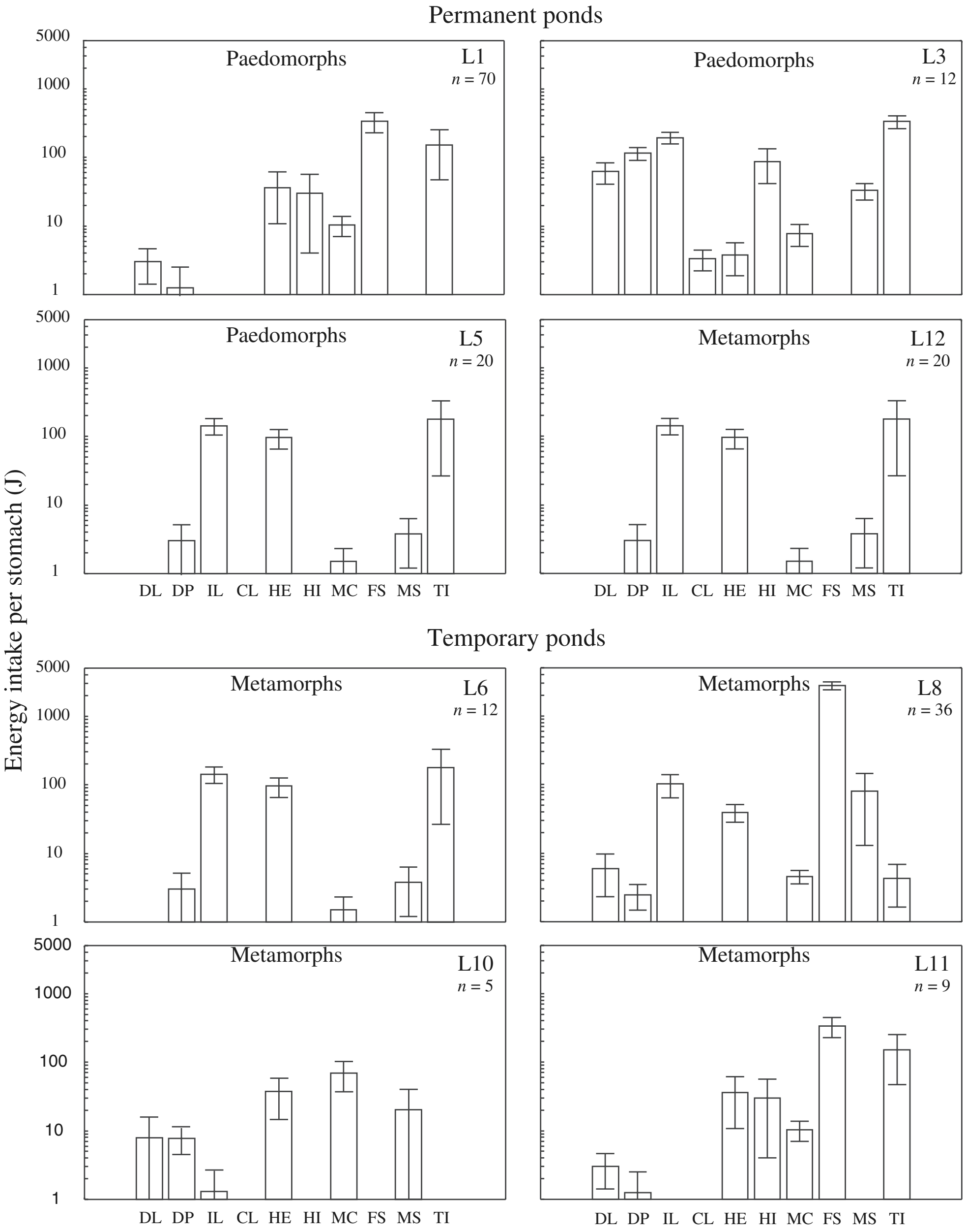

Fig. 4 Mean energy value (±SE) of the different prey categories found in salamander stomachs in the different ponds (log-scale). DL, Diptera larvae; DP, Diptera pupae; IL, other Insecta larvae; CL, *Chaoborus* larvae; HE, Hemipteroida; HI, Hirudinae; MC, micro-crustaceans; FS, fairy shrimp; MS other miscellaneous aquatic prey and TI, terrestrial insects.

had different feeding habits and energy intake as a consequence of their habitat use. Because metamorphs are able to move between ponds within the same year, they can take advantage of transient resources in some ponds that are unavailable to fully aquatic paedomorphs. These results support previous studies (Whiteman *et al.*, 1994, 1996) that showed the advantage to metamorphs of exploiting productive temporary waters. The present study extends this work by integrating individual pond analyses and long-term data on movement patterns to show that trophic quality, rather than hydroperiod, appears to be the primary factor driving habitat use among metamorphs. These findings open new perspectives in the understanding of the optimal selection of habitat in dimorphic salamanders.

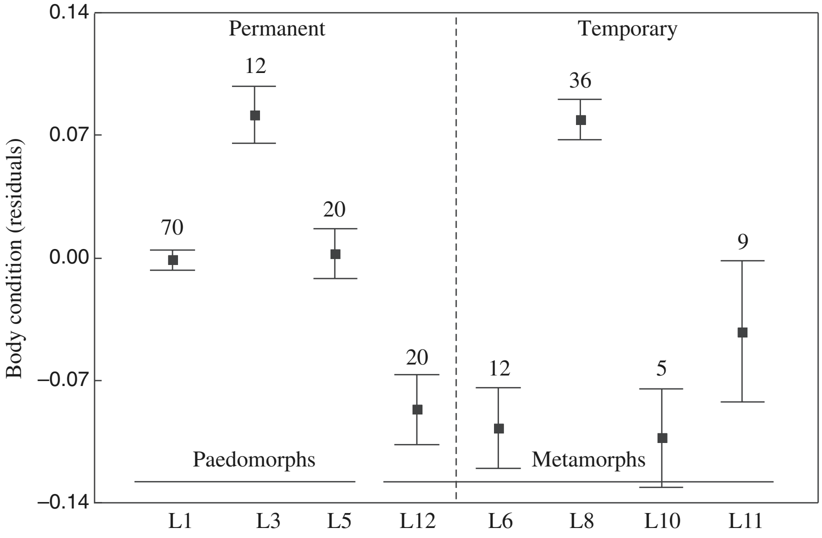

Fig. 5 Body condition (residuals of log body weight against log snout-vent length) of the salamanders in the different ponds.

Although paedomorphs were restricted to four out of the eight ponds that we studied, metamorphs used both temporary and permanent ponds. Amphibians are often considered to be highly philopatric in most (Grant *et al.*, 1968; Gill, 1979; Hershey & Forester, 1979), but not all cases (Miaud, 1990; Perret *et al.*, 2003). Capture-mark-recapture analyses in our study site revealed that at least 40% of metamorphs were not faithful to a particular pond, but rather moved between ponds. Changes in pond occupancy occurred both between years and within the same year, with metamorphs breeding in permanent waters and feeding afterwards in temporary waters (particularly L8; see also Whiteman *et al.*, 1994). Thus, changing ponds is not the result of orientation mistakes during spring migration, but the result of decisions to leave one pond for another pond.

The Mexican Cut Nature Preserve ponds differ in both their invertebrate and salamander communities, and thus in their attractiveness for metamorphs (Wissinger *et al.*, 1999). Another study suggested that drying ponds were more attractive to metamorphs than permanent ponds because of the presence of fairy shrimp, a valuable prey type (Whiteman *et al.*, 1996). Our study is consistent with this conclusion, but we found that the diet of metamorphs was more important than the drying regime of a pond. Metamorphic adults encountered fairy shrimp in several temporary ponds, but this taxon was the dominant prey item only in the one pond where it was in highest density (L8). In L8, metamorphs had an average of about 50 fairy shrimp in their stomachs, whereas those in the other temporary ponds had only 0–10 per stomach. These differences allowed salamanders in L8 to obtain higher energetic values per stomach than any other pond, temporary or permanent.

In contrast to the situation occurring in isolated lakes and ponds (Denoël *et al.*, 2002; Denoël & Andreone, 2003; Denoël, Schabetsberger & Joly, 2004), the feeding tactic of metamorphs at the cluster of ponds at Mexican Cut appears to be particularly adaptive and advantageous over the paedomorphic tactic in the same population. Although both morphs have access to the predictable food resources in the permanent ponds, only metamorphs can take advantage of prey in the adjacent temporary habitats. The switching from permanent breeding habitats to temporary feeding habitats by the metamorphs is consistent with predictions from optimal foraging theory (e.g. Stephens & Krebs, 1986). Indeed, energy intake is similar between morphs when they coexist but higher in metamorphs when they shift habitats. The positive impact of this habitat selection is also supported by the body condition of metamorphs, with morph differences in the main two ponds where they coexist (L1 and L5); paedomorphs from those ponds had substantially lower body conditions when compared with metamorphs from L8. Body condition is an estimate of fat reserves (Denoël *et al.*, 2002) and is explained partly by energy intake.

One might predict that individuals foraging in L8 should have higher fecundities than those that forage in other ponds since size is correlated with fecundity in salamanders (Semlitsch, 1985), although this remains to be determined in the Mexican Cut population. The low body condition found in temporary ponds in which fairy shrimp are rare suggests that patch selection may be based on prey composition rather than pond hydroperiod.

Our study revealed that foraging gains to metamorphs varied considerably from pond to pond, but most metamorphs optimized their foraging by moving to more productive ponds regardless of hydroperiod. Ponds also vary in fairy shrimp density from year to year; thus, both spatial and temporal variation will be important in the relative foraging success, and subsequent fitness payoffs, of the two morphs (Whiteman *et al.*, 1996; Denoël *et al.*, 2002). Clearly, long-term monitoring is necessary to better understand the fitness consequences of these behavioural patterns (Whiteman & Wissinger, 2005). Because wetland complexes with varied hydroperiod and associated faunas may be critical to the persistence of animal populations via metapopulation effects (e.g. Lannoo, 1998; Wissinger, 1999), a better understanding of the movement and foraging patterns of this species may also provide insights into amphibian population dynamics and conservation.

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References

Batzer D.P. & Wissinger S.A. (1996) Ecology of insect communities in nontidal wetlands. *Annual Review of Entomology*, **41**, 75–100.

Breuil M. (1992) La néoténie dans le genre *Triturus*: mythes et réalités. *Bulletin de la Société Herpétologique de France*, **61**, 11–44.

Cummins K.W. & Wuycheck J.C. (1971) Caloric equivalents for investigations in ecological energetics. *Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie*, **18**, 1–158.

Denoël M. (2003) How do paedomorphic newts cope with lake drying? *Ecography*, **26**, 405–410.

Denoël M. (2004) Terrestrial versus aquatic foraging in juvenile Alpine newts (*Triturus alpestris*). *Ecoscience*, **11**, 404–409.

Denoël M. (2006) Seasonal variation of morph ratio in facultatively paedomorphic populations of the palmate newt *Triturus helveticus*. *Acta oecologica*, **29**, 165–170.

Denoël M. & Andreone F. (2003) Trophic habits and aquatic microhabitat use in gilled immature, paedomorphic and metamorphic Alpine newts (*Triturus alpestris apuanus*) in a pond in central Italy. *Belgian Journal of Zoology*, **133**, 95–102.

Denoël M. & Joly P. (2001) Adaptive significance of facultative paedomorphosis in *Triturus alpestris* (Amphibia, Caudata): resource partitioning in an alpine lake. *Freshwater Biology*, **46**, 1387–1396.

Denoël M., Schabetsberger R. & Joly P. (2004) Trophic specializations in alternative heterochronic morphs. *Naturwissenschaften*, **91**, 81–84.

Denoël M., Whiteman H.H. & Joly P. (2005) Evolutionary ecology of facultative paedomorphosis in newts and salamanders. *Biological Reviews*, **80**, 663–671.

Denoël M., Hervant F., Schabetsberger R. & Joly P. (2002) Short- and long term advantages of an alternative ontogenetic pathway. *Biological Journal of the Linnean Society*, **77**, 105–112.

Gill D.E. (1979) Density dependence and homing behavior in adult red-spotted newts *Notophthalmus viridescens* (Rafinesque). *Ecology*, **60**, 800–813.

Grant D., Anderson O. & Twitty V.C. (1968) Homing orientation by olfaction in newts (*Taricha rivularis*). *Science*, **160**, 1354–1356.

Hershey J.L. & Forester D.C. (1979) Sensory orientation in *Notophthalmus v. viridescens* (Amphibia: Salamandridae). *Canadian Journal of Zoology*, **58**, 266–276.

Joly P. (1987) Le régime alimentaire des amphibiens: méthodes d'étude. *Alytes*, **6**, 11–17.

Joly P. (1997) Ecologie du développement et persistance d'un cycle complexe chez les amphibiens anoures. In: *L'évolution biologique. Science, histoire ou philosophie?*

(Eds J.-M. Exbrayat & J. Flatin), pp. 191–215. Librairie Philosophique J. Vrin, Institut Interdisciplinaire d'Etudes Epistémologiques, Paris, Lyon.

Joly P. & Miaud C. (1989) Fidelity to the breeding site in the Alpine newt *Triturus alpestris*. *Behavioural Processes*, **19**, 47–56.

Kerr J.K. & Packer L. (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, **385**, 252–254.

Lannoo M.J. (1998) Amphibian conservation and wetland management in the Upper Midwest: a catch-22 for the cricket frog? In: *Status and Conservation of Midwestern Amphibians*. pp. 330–339. University of Iowa Press, Iowa City, IA, U.S.A.

Miaud C. (1990) *La dynamique des populations subdivisées: étude comparative chez trois amphibiens urodèles (Triturus alpestris, T. helveticus et T. cristatus)*. Claude Bernard Lyon I University, Villeurbanne.

Perret N., Pradel R., Miaud C., Grolet O. & Joly P. (2003) Transience, dispersal and survival rates in newt patchy populations. *Journal of Animal Ecology*, **72**, 567–575.

Schoener T.W. (1974) Resource partitioning in ecological communities. *Science*, **185**, 27–39.

Scott D.E. (1993) Timing of reproduction of paedomorphic and metamorphic *Ambystoma talpoideum*. *American Midland Naturalist*, **129**, 397–402.

Semlitsch R.D. (1985) Reproductive strategy of a facultatively paedomorphic salamander *Ambystoma talpoideum*. *Oecologia, Berlin*, **65**, 305–313.

Semlitsch R.D. & Wilbur H.M. (1989) Artificial selection for paedomorphosis in the salamander *Ambystoma talpoideum*. *Evolution*, **43**, 105–112.

Sokal R.R. & Rohlf F.J. (1995) *Biometry*. Freeman and Co, New York.

Stephens D.W. & Krebs J.R. (1986) *Foraging Theory. Monographs in Behavior and Ecology*. Princeton University Press, Princeton.

Tokeshi M. (1999) *Species Coexistence. Ecological and Evolutionary Perspectives*. Blackwell Science, Oxford.

Twitty V.C. (1966) *Of Scientists and Salamanders*. Freeman and Co, San Francisco.

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

Welborn G.A., Skelly D.K. & Werner E.E. (1996) Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics*, **27**, 337–363.

Whiteman H.H. (1994) Evolution of facultative paedomorphosis in salamanders. *Quarterly Review of Biology*, **69**, 205–221.

Whiteman H.H. & Wissinger S.A. (2005) Amphibian population cycles and long-term data sets. In: *Status and Conservation of U.S. Amphibians* (Ed M.J. Lannoo), pp. 177–184. California University Press, CA, U.S.A.

Whiteman H.H., Wissinger S.A. & Bohonak A.J. (1994) Seasonal movement patterns in a sub-alpine population of the tiger salamander, *Ambystoma tigrinum nebulosum*. *Canadian Journal of Zoology*, **72**, 1780–1787.

Whiteman H.H., Wissinger S.A. & Brown W.S. (1996) Growth and foraging consequences of facultative paedomorphosis in the tiger salamander, *Ambystoma tigrinum nebulosum*. *Evolutionary Ecology*, **10**, 433–446.

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

Wissinger S.A. (1997) Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. *Biological Control*, **10**, 4–15.

Wissinger S.A. (1999) Ecology of wetland invertebrates: synthesis and applications for conservation and management. In: *Invertebrates in Freshwater Wetlands of North America: Ecology and Management* (Eds D.P Batzer, R.B. Rader & S.A. Wissinger), pp. 1043–1086. Wiley, New York.

Wissinger S.A., Bohonak A.J., Whiteman H.H. & Brown W.S. (1999) Habitat permanence, salamander predation, and invertebrate communities. In: *Invertebrates in Freshwater Wetlands of North America: Ecology and Management* (Eds D.P. Batzer, R.B. Rader & S.A. Wissinger), pp. 757–789. Wiley, New York.

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