

Geographic variation in life-history characteristics of amphibians: a review

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Summary

1. This review examines the intraspecific patterns and differences in life-history traits of amphibian populations living at different altitudes and latitudes. Specifically we examined differences in development and growth (physiological constraints) and reproductive ecology (plasticity in reproductive traits).
2. Research published to date suggests that amphibian populations at higher altitudes and latitudes tend to: (a) have shorter activity periods, and hence shorter breeding seasons; (b) have longer larval periods; (c) are larger at all larval stages including metamorphosis; (d) are larger as adults; (e) reach reproductive maturity at older ages; (f) produce fewer clutches per year; (g) produce larger clutches absolutely and smaller clutches relative to body size; and (h) produce larger eggs.
3. These generalizations must be viewed with caution, due first to the small number of papers supporting them, and secondly to the inconsistent results published to date.
4. The implications of the intraspecific geographical variation in life history traits for general amphibian biology, amphibian population declines and conservation are discussed.

Key-words: age at maturity, altitude, body size, breeding season length, fecundity, growth and development rates, latitude, resilience.

Journal of Animal Ecology (2003) **72**, 270–279

Introduction

Since the late 1970s, at least 25 frog species have declined or disappeared from high-altitude areas around the world (Blaustein & Wake 1990; Richards, McDonald & Alford 1993; Pounds & Crump 1994; Lips 1998; Young *et al.* 2001). The cause(s) of many of these declines remain unknown and consequently an understanding of the relationship between high altitudes and latitudes and the life-history characteristics of amphibians is an important step in the process of evaluating the proposed potential causes of amphibian declines.

An organism's life history is its lifetime pattern of growth, development, storage and reproduction with every life history being, to some extent at least, unique (Begon, Harper & Townsend 1990). The life history of an organism is not immutable. It is fixed within limits by the genotype of the individual but across different environments, the phenotypic expression of the genotype may vary – otherwise known as phenotypic plasticity (Sorci, Clobert & Belichon 1996). Sources of

variation in life-history traits for organisms with broad geographical ranges include proximate (environmental: temperature, rainfall, food supply, predation, competition, etc.) and ultimate (genetic) factors (Sorci *et al.* 1996). While several studies have reviewed the influence of altitude and latitude on the reproductive ecology of reptiles (Fitch 1970, 1985; Niewiarowski 1994), no similar reviews have been carried out on geographical variation in amphibian life histories (with the exception of Bull & Shine 1979). Herein we examine and summarize the patterns in life-history characteristics of amphibian populations living at different altitudes and latitudes. The characteristics examined are: development and growth rates, body size, age at first reproduction, length of breeding season, the number of clutches produced per year and clutch/egg size. Trends in these characters can potentially be used to evaluate whether amphibians at high altitudes and low latitudes are less resilient and therefore more susceptible to extinction processes.

Breeding season length and number of clutches laid per year

The lower environmental temperatures associated with higher altitudes and latitudes restrict the time available

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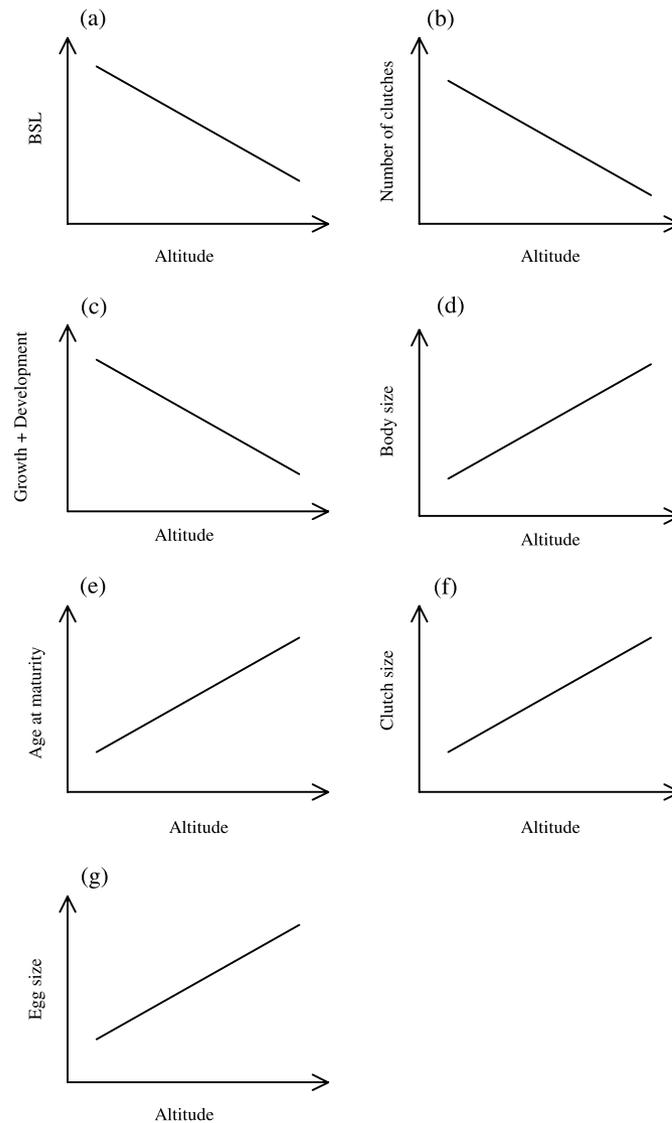


Fig. 1. General relationships between altitude and (a) breeding season length; (b) number of clutches produced per season; (c) growth and development rates; (d) body size; (e) age at maturity; (f) clutch size; (g) egg size.

for resource or energy accumulation which results in a decrease in activity season length in amphibians (Hemelaar 1988; Elmberg 1991; Ryser 1996). This results in turn in shorter breeding seasons in high-altitude and/or -latitude populations (Fig. 1a; Berven 1981; Howard & Wallace 1985; Elmberg 1991; Ryser 1996). For example, Berven, Gill & Smith-Gill (1979) reported that the breeding season of *Rana clamitans* in lowland localities in Virginia extended from mid-May to mid-September while breeding in montane populations was restricted to a comparatively short 2-month period. Howard & Wallace (1985) found that low elevation populations of *Ambystoma macrodactylum* had longer breeding seasons than mid- and high-altitude populations, while similar patterns were discovered by Elmberg (1991) studying *R. temporaria* populations in Sweden. Shorter breeding seasons have been recorded in high-altitude populations of *Litoria chloris*, *L. lesueuri*, *L. pearsoniana* and *Mixophyes fasciolatus* in mid-eastern Australia (Morrison 2001).

In addition to governing the length of the breeding season, activity period also influences the timing of reproductive bouts and the number of broods or clutches produced in a season. The frequency of reproduction during a breeding season varies between species and individuals, but generally the number of broods or clutches that can be produced during a year or season decreases with a decrease in breeding season length (Fig. 1b; Bull & Shine 1979).

As tropical and subtropical species have longer breeding seasons, they are capable of producing more clutches per season than temperate species restricted to shorter breeding seasons, i.e. at all times of the year some females in the population are in a reproductive state (Crump 1974). Individual *Hyla rosenbergi* can produce as many as six clutches in a single breeding season (Kluge 1981), while individual *Syrhophus marnocki* (Jameson 1955) and *Phyllomedusa trinitatis* females (Kenny 1966) have been reported to produce three clutches per season. Up to four clutches a year

have been reported in *R. kuhlii* in Taiwan (Tsuji & Lue 2000). A study of 81 species of neotropical frogs provided indirect evidence that individual females in all except 17 of these species produced multiple clutches throughout the year (Crump 1974).

Multiple clutches may be common among tropical lowland frogs in nature, but a lengthy breeding season is not necessarily indicative of the production of many clutches per female (Duellman & Trueb 1986). For example, *Coleostethus inguinalis* has a lengthy breeding season spanning several months but individual females only produce two clutches per year (Wells 1980). Species with specialized reproductive modes may also not be able to multiclutch annually, e.g. individual brooding *Gastrotheca riobambae*, although found throughout the year in the Ecuadorian Andes, produce only one clutch per year (del Pino 1980).

Due to the shorter (or cyclic) breeding seasons found in temperate regions, most temperate anurans tend to reproduce annually. In these environments there will be some point in the favourable season at which another reproductive bout, while possible, would contribute very little to the fitness of the female. Although temperate anurans tend to produce single clutches, the production of two clutches per season is known for some temperate species including *R. catesbeiana* in North America (Howard 1978). Perrill & Daniel (1983) found that some *H. cinera* and *H. regilla* produced three clutches in one season.

While most temperate species produce one clutch per season, females in seasonally dry or cold regions may reproduce only biennially or at even longer intervals due to the high energetic requirements of developing and producing eggs and the short activity periods available in which to accumulate the energy needed (Koch & Peterson 1995). For example, individuals in some *Bufo* populations (Blair 1943), *Plethodon glutinosus* and *P. wehrlei* (Bull & Shine 1979) reproduce biennially while *Notophthalmus viridescens* can skip breeding seasons for up to 5 consecutive years (Gill 1985).

Within a climatic region, breeding seasons at high altitudes are shorter and consequently the number of clutches that can be produced each year are restricted. Individual *A. gracile* (Eagleson 1976), *Salamandra salamandra* (Joly 1961; from Duellman & Trueb 1986) and *Triturus alpestris* (Vilter & Vilter 1963) occurring at high altitudes reproduce either annually or biennially and tend to breed more frequently at low altitudes. *Rana pretiosa* breed once every 1–3 years in North America but tend to reproduce annually at low altitudes (Licht 1975).

Development and growth

The growth and development rates of amphibians are influenced by a number of intrinsic and extrinsic factors (Duellman & Trueb 1986). Extrinsic factors include: temperature (Volpe 1957; Berven *et al.* 1979; Kaplan 1980; Berven 1982b), density and competition

(Licht 1975; Kaplan 1980; Berven 1982b), food supply and quality (Berven 1982b; Berven & Chadra 1988), predation (Crump 1974, 1984), breeding habitat (Crump 1974; Kaplan 1980; Duellman & Trueb 1986) and inhibitory compounds (Duellman & Trueb 1986; Berven & Chadra 1988). Intrinsic factors include body size or egg size (McLaren & Cooley 1972; Kuramoto 1975; Berven *et al.* 1979) and yolk reserves (Duellman & Trueb 1986). These factors act in synergy to increase or decrease the growth and development rates occurring within and between each life stage in amphibians. The combination of these effects ultimately influences the time taken to progress from eggs to sexually mature adults.

EMBRYOGENESIS

Of the numerous extrinsic and intrinsic factors influencing intraspecific differences in development and growth of amphibian embryos, temperature has been found to be the most important factor with rates increasing with temperature within the thermal limits of the eggs (Fig. 1c; Moore 1939; Voss 1993). Increased development rates and shorter times to hatching with increased temperature have been reported in a number of amphibian species including *R. pipiens*, *R. sylvatica* and *R. palustris* (Moore 1939), *A. maculatum* (Voss 1993), *A. opacum* (Kaplan 1980), *Scaphiopus couchii* and *S. bombifrons* (Justus *et al.* 1977).

Temperature is the factor affecting intraspecific differences in embryonic rates that is most influenced by geographical variation. To date, however, there have been very few intraspecific studies carried out on the effects of altitude and/or latitude on embryonic development rates. Those that have been conducted report longer times to hatching at high altitudes as a result of the colder water temperatures associated with those areas (e.g. Berven 1982b; Howard & Wallace 1985).

FEEDING LARVAE TO METAMORPH

Temperature has differential effects on larval growth and development rates, with differentiation ceasing at low temperatures (as in winter), but growth continuing (at an absolute rate slower than during warmer, summer months) until temperatures eventually become too low and both cease (Smith-Gill & Berven 1979). Consequently, anurans and urodeles grown at low temperatures tend to have prolonged larval periods and higher stage-specific growth than those growing in warmer regions (Smith-Gill & Berven 1979). Voss (1993) reported longer larval periods and larger individuals in *A. maculatum* at lower temperatures. Similar results were found in *A. maculatum*, *A. t. tigrinum* and *A. opacum* (Kaplan 1980) and in *Geocrinia victoriana* (Gollman & Gollman 1996).

As amphibians at high latitudes and elevations experience lower environmental temperatures than those found in tropical lowlands, correlations of development

patterns with temperature between high and low elevation occur for either genetic or environmental reasons (Berven *et al.* 1979). In colder high-altitude and -latitude areas individuals generally have longer larval periods and are larger at metamorphic climax than those in warmer areas (Ruibal 1955; Berven *et al.* 1979; Berven 1982b; Howard & Wallace 1985).

Longer larval periods can, in some species, result in overwintering by larvae. Overwintering has been found to be more prevalent in montane populations of the salamanders *A. macrodactylum* (Howard & Wallace 1985), *A. gracile* (Eagleson (1976) and *A. tigrinum* (Bizer 1978). Lowland tadpoles of green frog, *R. clamitans* in Virginia, North America were found to overwinter no more than once while montane tadpoles had to overwinter at least once and more often twice before being able to metamorphose (Berven *et al.* 1979). These montane larvae were also consistently larger at any given development stage than lowland ones and it was concluded that larval size was inversely correlated with the average monthly temperature of the water (Berven *et al.* 1979). Similar results were reported for temperate species *R. pipiens* (Ruibal 1955), *R. sylvatica* (Berven 1982b), *Ascaphus truei* (Noble & Putnam 1931), *Heleophryne purcelli* (Wager 1965), *Plectrohyla glandulosa* (Duellman 1970) and *R. septentrionalis* (Leclair & Laurin 1996). Morrison & Hero (2003) found that high-altitude tadpoles developed slower than low-altitude tadpoles in two species of subtropical anurans, *L. chloris* and *L. pearsoniana* in eastern Australia.

In contrast to the above, some species of amphibians in temperate regions have reportedly been found to develop faster at high altitudes and latitudes than those from lowland regions. Licht (1975) reported that *R. pretiosa* tadpoles at low altitudes had longer larval periods and transformed at twice the body size of high-altitude species. As the lowland tadpoles were in habitats that were prone to desiccation, the increase in larval body size was thought to lead to faster post-metamorphic growth and a shorter time to reproductive maturity. This is, however, the only exception as larvae living in temporary habitats generally develop faster than do those in more permanent habitats (e.g. Crump 1974; Duellman & Trueb 1986).

Gollman & Gollman (1996) studied *G. victoriana* in southern Australia and found that only a few tadpoles from high-altitude populations reached metamorphic climax and no lowland tadpoles metamorphosed before the termination of their study. These results were thought to be the result of countergradient selection, where the high-altitude tadpoles had faster growth and development rates than the low-altitude larvae to compensate for the differences in environmental temperatures between the different altitudes. Pettus & Angleton (1967) also suggested that the larger size (resulting from larger eggs) of highland tadpoles of *Pseudacris triseriata* in Colorado, North America could potentially shorten the time to metamorphosis and the metamorphic process itself. As their study is, however, restricted to

early development, this claim is entirely unsupported by data.

In summary, the low environmental temperatures at high altitudes tend to decrease amphibian growth and development rates below that of low-altitude individuals resulting in longer larval periods and larger body sizes of individuals in these areas. There are, however, several exceptions in temperate regions leading us to conclude that differences in other factors, besides temperature, including body size, habitat permanency, food availability, predation and growing season length are also responsible for observed differences in the rates of growth and development at high and low latitudes and altitudes. Genetic contributions to larval development and growth can have a significant impact on rates of development and growth but tend to be masked by differences resulting from variation in environmental conditions. The paucity of studies on latitudinal variation in amphibian growth and development rates makes it essentially impossible to determine the influence of latitude on amphibian growth and development rates.

Body size

The influence of cold temperatures on amphibian larval and juvenile growth and development rates has follow-on effects on the timing of maturity and subsequently, the size of adults. As a result of these effects, high-altitude and -latitude amphibians are generally larger than low-altitude and tropical individuals (Fig. 1d; Kozłowska 1971; Bizer 1978; Berven 1982a; Hemelaar 1988; Elmberg 1991; Ryser 1996; Miaud, Guyétant & Faber 1999). There are exceptions to this trend with low- or mid-altitude individuals being significantly larger than high-altitude individuals in some species (Howard & Wallace 1985) or no significant difference in body size being detected in populations from different altitudes (Licht 1975; Ryser 1996; Morrison & Hero 2002). Reasons for these exceptions include the effects of habitat quality and predation pressure on age at maturity (Licht 1975; Howard & Wallace 1985; Ryser 1996) and limited altitudinal gradients (Morrison & Hero 2002). The relationship between body size and maturity will be covered in more detail in the next section.

Age at first reproduction

The length of time required from birth or hatching to sexual maturity is an important aspect of population dynamics. Age at first reproduction is determined by juvenile growth rates and body size of mature individuals (Ryser 1996), both of which are influenced by factors such as length of growing season and level of metabolism (Fitch 1970). As reproductive maturity is dependent on body size, species with faster growth rates will reach the minimum size required for reproduction sooner than those with slower growth rates and thus will be able to begin breeding at a younger age.

Precocity or early reproduction has obvious benefits. Precocious species have a shorter generation length than species that delay reproduction and their rate of population increase is therefore greater (Begon *et al.* 1990). Precocity tends to be favoured in species with short adult life expectancies. The benefits of delayed reproduction are less obvious and generally relate to advantages associated with larger body size. As growth rates of ectotherms decrease greatly after the attainment of sexual maturity (Hemelaar 1988), organisms that delay reproduction are able to achieve larger body sizes than precocious individuals. This results not only in increased success at holding breeding territories (Hemelaar 1988), but also in greater survivorship of parents and the production of larger clutches, or larger offspring which may have higher survival rates than smaller offspring (Berven 1982a; Begon *et al.* 1990).

Geographic differences in post-metamorphic growth rates are influenced by differences in the physical environment (Duellman & Trueb 1986). Temperatures are higher in tropical areas and many tropical anurans apparently grow throughout the year and thus attain their maximum sizes rapidly (Duellman & Trueb 1986). The large neotropical tree frog *H. rosenbergi* grows at a rate of 0.21 mm per day and reaches adult size in less than a year (Kluge 1981), while the growth rates of *R. erythraea* in the Philippines greatly exceeds that of the temperate populations (Brown & Alcaca 1970).

As species at higher latitude and altitude experience shorter growing seasons than those at lower latitudes and elevations, it takes longer to reach the minimum size required for sexual maturity and the average age at first reproduction is older (Berven 1982a; Hemelaar 1988; Ryser 1996). Among anurans it is found generally that the oldest ages of first reproduction are in species at high latitude and altitude while those in aseasonal, tropical lowlands mature much earlier (Duellman & Trueb 1986). The age at first reproduction in 12 tropical species was found to be 6–15 months (mean = 10.79 months) in males and 8–15 months (mean = 10.99 months) in females, whereas in 25 mid-latitude species the values were 1–2.5 years (mean = 1.54 years) in males and 1–3 years (mean = 1.83 years) in females. By contrast, the ages of eight species in temperate regions were 2–4 years (mean = 3.44 years) in males and 2.5–6 years (mean = 3.69 years) in females (Duellman & Trueb 1986).

Intraspecific comparisons have reported longer growth to maturation in high-altitude populations of a number of species including alpine *R. temporaria* vs. lowland individuals (Elmberg 1991; Ryser 1996) and in *Desmognathus ochrophaeus* (Tilley 1980). Noticeable differences have been found in the life history patterns of lowland vs. highland populations of *R. pretiosa*, where lowland females mature in 1–2 years and reproduce annually, while the higher-elevation females require 5–6 years to mature and breed every 2–3 years (Licht 1975). Similarly, a 2–4-year difference in age at first reproduction occurs between lowland and

highland populations of *R. sylvatica* in Maryland (Berven 1981; Berven 1982a). Hemelaar (1988) found that the age of the youngest breeding males and females varied from 2 to 3 years in a low-elevation population to 6–8 years in a high-altitude population of *B. bufo*. Older ages at maturity and longevity have also been recorded in high-altitude populations of *L. chloris* and *M. fleayi* in south-east Queensland, Australia (Morrison 2001).

Similarly, slower growth rates at higher latitudes have been reported to cause delays in maturity of up to 2 years in *B. calamita* from Switzerland to Sweden and in *R. pipiens* from southern to northern Michigan (Duellman & Trueb 1986). Delays of 1 year have been reported in *R. septentrionalis* from southern to northern Canada (Leclair & Laurin 1996). Slower growth rates to maturity and older ages at maturity have also been reported in northern populations of *B. bufo* in Europe (Hemelaar 1988).

Some of the species that require the longest time to mature have lengthy larval periods (see previous section). The age at first reproduction in *R. catesbeiana* depends on its larval period (one or two overwinterings), as frogs usually reach sexual maturity 1 year after metamorphosis (Duellman & Trueb 1986). Howard & Wallace (1985) found *A. macrodactylum* at high elevations remained in ponds for an extra summer, despite reaching body sizes comparable to the sizes at metamorphosis observed at lower elevation sites. They concluded that some advantage in increased survivorship was likely to result from the additional year of larval life and the larger body size attained before metamorphosis.

In summary, amphibian species and individuals at high latitude and altitude grow slower and consequently tend to be older and larger when breeding for the first time compared to those species and individuals found in tropical lowlands (Fig. 1d,e). These differences are due primarily to environmental constraints on growth and development rates, which in some cases are mediated by genetic factors.

Clutch size and egg size

The size of a clutch or litter represents the number of potential offspring and is regarded as an attribute that populations have evolved through time in adaptation to their general environment and their ecological niche (Crump 1974; Fitch 1985). Factors such as rainfall and temperature can directly affect the availability of food, and may indirectly affect clutch size by reducing the fat stores that are necessary for the development of a complete clutch (Heatwole & Taylor 1987). The length of the adult activity period also influences clutch size as it is during this period that energy required for reproduction and producing clutches is obtained and stored (Bull & Shine 1979).

Egg size is affected by the amount of energy available for reproduction as well as external factors including reproductive mode (Crump 1974) and habitat (Salthe

& Duellman 1973). Egg size affects the survival of offspring by influencing the size, shape, growth and development rates during embryonic development (Kaplan & King 1997). Egg size also determines the number of offspring a parent can produce (Kaplan 1980).

Clutch volume is the product of egg size and the number of eggs produced (Duellman 1992), and relates mainly to the size of the female (i.e. larger females tend to have larger clutch volumes: Salthe & Duellman 1973; Kuramoto 1978; Flemming 1994). As clutch volume is the product of egg size and clutch size, species producing large eggs will produce fewer to compensate for the energy put into the large eggs (Pettus & Angleton 1967; Crump 1984). Similarly, species with small eggs will produce greater numbers (Kuramoto 1975).

The trade-off between egg size and clutch size for a given clutch volume influences the fitness of both the female parent and the juvenile (Begon *et al.* 1990). Most studies have concluded that larvae derived from large eggs should enjoy an increase in fitness either because of greater initial size, faster growth rates, development rates or both (Kuramoto 1978; Crump 1984; Kaplan & King 1997). The advantage associated with producing smaller eggs is due to the corresponding

increase in fecundity (Crump 1984). The relative fitness, however, of large and small eggs and consequently the best combination of egg size and egg number may vary with environmental conditions (Berven & Chadra 1988).

Due to the effects of temperature on growth and development on sexual maturity (discussed previously), females in colder parts of their range (high latitude and altitude) are usually larger than their counterparts in warmer parts of the range (Pettus & Angleton 1967; Kozłowska 1971; Berven 1982a). As these individuals are larger, they produce more eggs (Fig. 1f; Kuramoto 1978; Tilley 1980; Cummins 1986; Ryser 1996; Kaplan & King 1997), larger eggs (Fig. 1g; Pettus & Angleton 1967; Licht 1975) or both (Pettus & Angleton 1967).

Studies on the effects of altitude on clutch size in amphibians are often contradictory in that there is no clear overall trend. A summary of the studies and their results is presented in Table 1.

Larger clutches in high-altitude populations have been reported in *R. sylvatica* (Berven 1982a), *R. temporaria* (Cummins 1986), *Pseudacris triseriata* (Pettus & Angleton 1967) and *Desmognathus orochrophaeus*

Table 1. A summary of the results of studies carried out on the effects of altitude on amphibian reproductive characteristics. Female body size, clutch size and egg sizes are presented as ranges or means (± 1 SD). AR = altitudinal range

Species	Latitude	AR (m)	Site Alt.	Body size	Clutch size (mm)	Egg size (mm)	Ref.
<i>Litoria chloris</i> *	Subtrop.	80–600	Low	63.4 \pm 8.83	1787.8 \pm 187.3	1.21 \pm 0.1	1
			High	64.1 \pm 6.42	1810.6 \pm 195.6	1.23 \pm 0.1	
<i>L. lesueuri</i> *	Subtrop.	20–1000	Low	57.8 \pm 3.58	2433.8 \pm 702.3	1.12 \pm 0.20	1
			High	58.5 \pm 4.42	2507.8 \pm 788.3	1.25 \pm 0.25	
<i>L. pearsoniana</i> *	Subtrop.	60–1000	Low	32.1 \pm 1.55	489.3 \pm 177.2	1.15 \pm 0.16	1
			High	33.5 \pm 2.76	551.3 \pm 139.2	1.22 \pm 0.03	
<i>Mixophyes fasciolatus</i> *	Subtrop.	100–7000	Low	74.9 \pm 2.19	976.8 \pm 262.1	1.15 \pm 0.16	1
			High	79.0 \pm 2.34	963.9 \pm 252.2	1.22 \pm 0.03	
<i>M. iteratus</i> *	Subtrop.	40–600	Low	94.5 \pm 6.87	1961.3 \pm 682.1	1.74 \pm 0.06	1
			High	99.2 \pm 6.29	2647.7 \pm 641.3	1.76 \pm 0.02	
<i>Ambystoma macrodactylum</i> * ^a	Temperate	360–2470	Low	69.9 \pm 4.80	166.5 \pm 59.7	2.15 \pm 0.16	2
			Mid	60.8 \pm 4.07	105.3 \pm 31.1	2.09 \pm 0.11	
			High	66.0 \pm 3.39	90.1 \pm 48.8	2.65 \pm 0.05	
<i>Geocrinia victoriana</i> *	Temperate	180–1300	Low	–	< 196	1.9 \pm 0.06	3
			Mid	–	< 218	2.5 \pm 0.05	
			High	–	47–69	–	
<i>Rana sylvatica</i> ^b	Temperate	43–1100	Low	47.7 \pm 3.7	642 \pm 200	1.83 \pm 0.29	4
			High	64.4 \pm 3.5	920 \pm 217	2.28 \pm 0.13	
<i>R. temporaria</i> ^a	Temperate	200–1000	Low	80.5 \pm 1.64	2522 \pm 164	1.75 \pm 0.02	5
			Mid	89.0 \pm 2.01	2340 \pm 125	1.95 \pm 0.02	
			High	87.4 \pm 1.56	1880 \pm 112	1.98 \pm 0.03	
<i>R. temporaria</i> ^b	Temperate	600–1930	Low	81.6	726–1901	1.83–2.35	6
			High	80.6 \pm 4.8	784–1616	1.83–2.19	
<i>R. pretiosa</i> ^c	Temperate	70–2600	Low	62.0	643	–	7
			High	65.0	539	–	
<i>Pseudacris triseriata</i> ^a	Temperate	590–2818	Low	24.1 \pm 0.66	455.5 \pm 46.6	0.80 \pm 0.01	8
			High	31.4 \pm 0.27	443.9 \pm 17.5	1.15 \pm 0.01	
<i>Desmognathus orochrophaeus</i> ^c	Temperate	1024–1048	Low	30	9.25 \pm 0.62	–	9
			High	35	11.27 \pm 1.4	–	

*All measurements made in field, ^adissection of dead specimens, ^bfemales oviposit in laboratory, ^cmethod not stated. 1 = Morrison & Hero (2002), 2 = Howard & Wallace (1985), 3 = Gollman & Gollman (1996), 4 = Berven (1982a), 5 = Kozłowska (1971), 6 = Ryser (1996), 7 = Licht (1975), 8 = Pettus & Angleton (1967), 9 = Tilley (1980).

(Tilley 1980). Not all studies, however, reach the same conclusions. In a study of altitudinal variation in clutch size and egg size Morrison & Hero (2002) found no relationship between altitude and clutch size in five anuran species, while Licht (1975) found that fecundity was the same in high- and low-elevation populations of *R. pretiosa*. Ryser (1996) reported no difference in clutch size in populations of *R. temporaria* from different altitudes in Switzerland. In all three of these studies, however, there was no difference in female body size between high- and low-elevation populations. Other studies have reported larger clutch sizes at low altitudes (Kozłowska 1971; Howard & Wallace 1985; Gollman & Gollman 1996). The larger clutch sizes in low-altitude *A. macrodactylum* (Howard & Wallace 1985) and *G. victoriana* (Gollman & Gollman 1996) were due to the larger body size of females occurring at low altitudes. Kozłowska's (1971) study appears to be an exception to the trend that larger females produce larger clutches irrespective of altitude.

As larger females produce larger clutches and females at high altitudes are usually larger, it would follow that high-altitude females lay larger clutches (Tilley 1980). As seen in the previous paragraph however, this is not always the case. Also, when the effect of female body size is removed, high-altitude females have been found to produce relatively smaller clutches and larger eggs than their lowland counterparts (Kozłowska 1971; Berven 1982a). As there is a trade-off between clutch size and egg size for any given clutch volume or female body size, it appears that high-altitude females trade fecundity for higher survival of individual offspring.

Larger ova have been reported in high-altitude populations when compared to lowland populations in a number of species. Pettus & Angleton (1967), while comparing the reproductive biology of montane and piedmont *Pseudacris triseriata*, found that the montane frogs laid significantly larger eggs than the lowland frogs. Similar results have been reported for a number of other amphibians including, *R. temporaria* (Kozłowska 1971; Beattie 1987), *R. sylvatica* (Berven 1982a), *G. victoriana* (Gollman & Gollman 1996), and *A. macrodactylum* (Howard & Wallace 1985).

Although the pattern of increasing egg size with altitude is well documented, there have been studies that report no significant difference between egg sizes found in high- and low-altitude populations. For example, Ryser (1996) found no significant difference in the size of the eggs produced by high and low elevation populations of *R. temporaria*. Morrison & Hero (2002) examined altitudinal variation in clutch size and egg size in five anuran species in mid-eastern Australia and found no relationship between altitude and egg size in any of the species (Table 1).

Very few studies have been carried out on the influence of latitude on clutch and egg size in anurans. Gollman & Gollman (1996) reported an increase in egg size and decrease in clutch size in *G. victoriana* with increasing latitude. Hero (unpublished data) examined interspecific

patterns in Australian anurans and discovered that moving from tropical to subtropical to temperate regions resulted in an increase in average egg size.

In summary, females at high altitudes and latitudes are larger and are therefore able to produce larger clutches and/or eggs. The majority of studies report that high-altitude and -latitude females lay larger eggs than their lowland or more tropical counterparts. The pattern for altitudinal variation in clutch size is not as clear with some studies reporting larger clutches, some smaller clutches and some finding no difference in clutch size between females in populations from different altitudes. Most of this variation in clutch size, however, can be attributed to variation in female body size.

Summary and implications of results for declining frogs

Amphibian populations at high latitudes and altitudes experience restricted activity and breeding seasons when compared to low-latitude and -elevation populations resulting in the production of fewer clutches or broods per season. The colder temperatures in these areas affect growth and development rates and usually result in longer larval periods and larger sizes both during and after metamorphosis in high elevation and latitude individuals. There are, however, exceptions, suggesting that other factors including competition, food, habitat permanency and predation also play a role in determining development and growth rates. Due to their slower growth and development rates, high-altitude and -latitude females usually mature at an older age, are larger and consequently tend to produce larger eggs and sometimes larger clutch sizes than their lowland counterparts. When the effect of female body size is removed, high-altitude females lay relatively fewer but larger eggs than females from low altitudes.

The shorter breeding seasons, slower growth and development rates, older age at maturity, larger eggs and fewer clutches seen in high-altitude and -latitude amphibian populations result in increased generation time and lower fecundity in high-altitude populations. In turn, increased generation time and lower fecundity can result in a population being less resilient (i.e. population takes longer to return equilibrium after a disturbance away from equilibrium) and subsequently potentially more prone to decline or extinction (Pimm, Jones & Diamond 1988; Pimm 1991). We hypothesize that the influences of altitude on the reproductive ecology of amphibian populations at high altitudes could make them more vulnerable to processes of extinction, thereby increasing the likelihood of population decline or extinction.

If high-altitude populations are less resilient, we would expect species whose geographical range partially or totally encompasses high altitudes to be more vulnerable to extinction processes. Within eastern Australia, 31 of the 37 frog species listed as vulnerable, endangered or extinct under current IUCN criteria

Table 2. Proportion of high-altitude (geographical range includes altitudes > 400 m) and low-altitude anuran species that have declined or disappeared from eastern Australia (Queensland, New South Wales, Victoria and Tasmania)

	High altitude	Low altitude
Total number of species	75	68
Number of declining species	31	6
% declining species	41.3%	8.8%

(IUCN 2000) have geographical ranges that include altitudes > 400 m (Morrison 2001). Forty-one per cent of all frog species in eastern Australia with ranges including altitudes > 400 m have populations that have declined or disappeared compared to 9% of lowland species (Table 2; Morrison 2001). The causal factors responsible for the declines of many of the high-altitude populations of these species remain unknown. The remaining six species are lowland species threatened by anthropogenic factors, e.g. habitat destruction.

Although the trends reported in this review provide some support for the hypothesis that high-altitude populations of amphibians are less resilient or more vulnerable than their lowland counterparts, they do not explain why more tropical than temperate frog species are declining or disappearing, as we would expect high-latitude or temperate populations to be more vulnerable, based on the trends reported in this review. Many of the tropical populations that have experienced declines or disappearances, however, were situated at high altitudes (Heyer *et al.* 1988; Richards *et al.* 1993; Pounds & Crump 1994; Laurance 1996; Alford & Richards 1999; Young *et al.* 2001) suggesting that although latitude has an effect on amphibian life-history characteristics, the influence of altitude is much greater. Alternatively, the larger number of amphibian declines in tropical areas may simply be an artifact of high species richness in those areas. Tropical areas have higher species richness than temperate areas (Duellman 1999) and therefore the potential for more species to disappear or decline. Comparing the relative number of declines in each region may provide a more realistic picture of the effects of latitude.

Further work on the effects of geographical variation, specifically interactions between altitude and latitude, on amphibian life-history characteristics is needed to enhance our current limited knowledge of geographical life-history patterns and allow us to evaluate better the hypotheses for the causes of these amphibian disappearances and declines. Recent studies have linked amphibian declines to a number of potential factors, including changing weather patterns associated with global warming (Kiesecker, Blaustein & Belden 2001; Pounds 2001), disease (Laurance, McDonald & Speare 1996; Berger *et al.* 1998; Bosch, Martinez-Solano & Garcia-Paris 2001) and UV radiation (Davidson, Shaffer & Jennings 2001; Pounds

2001). We propose that all frog populations are potentially affected by a global cause; however, the impacts are manifested or exacerbated only in populations and/or species that are ecologically susceptible, namely high-altitude populations. A concerted effort is needed to determine the cause of amphibian declines. In the meantime, management and conservation agencies should focus on monitoring and protecting the potentially more vulnerable high-altitude amphibian populations and their habitat from known processes of extinction.

Acknowledgements

We thank Luke Shoo and Vance Vredenburg for critically reviewing our paper. Financial support for the writing of this paper and research on amphibian populations was provided to CM by Griffith University Gold Coast in the form of a Postgraduate Research Scholarship.

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Received 19 April 2002; accepted 5 November 2002