

1 Small-scale spatial and temporal variation of life history traits of common frogs (*Rana temporaria*) in sub-
2 Arctic Finland

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27 **Abstract**

28

29 Small-scale spatial and temporal variation in abiotic and biotic factors can cause variation in several major
30 life history traits in vertebrate ectotherms such as amphibians. However, relatively little is known about
31 small-scale variation in life history traits of sub-Arctic amphibians. We studied the spatio-temporal
32 variation of adult life history traits linked to age and body size in the common frog (*Rana temporaria*)
33 from low (i.e., valley at 480 m a.s.l.) and high (i.e., hill at 530-650 m a.s.l.) altitude sites in the sub-Arctic
34 Kilpisjärvi area (Finland). Data on life history traits of frogs from hill sites collected during a three-year
35 field study were compared with previously published data from the valley sites. The results showed
36 spatio-temporal variation in life-history traits, frogs responding to spatio-temporal variation in the
37 environmental conditions with variation in age, life span, survival rates, body size and mass. Frogs from
38 hill sites had shorter life span, both in terms of mean age (5.6 versus 10.5 years) and longevity (9-10
39 versus 18 years), smaller snout-vent length (63 versus 77 mm) and body mass (24 versus 45 g) than frogs
40 from valley sites. The differences were more pronounced in females than in males indicating some sex-
41 specific responses to environmental differences among sites. The results show that small differences in
42 elevation (or elevation related abiotic and biotic factors) can translate to large differences in mean values
43 of important life history traits in common frogs living at the edge of their distribution range.

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48 **Key words**

49 spatio-temporal variation, life history traits, skeletochronology, age structure

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53 **Introduction**

54
55 Geographic differentiation of life history traits and morphological features are of common occurrence in
56 both plants and animals (Mayr 1963; Endler 1977; Linhart and Grant 1996; Roff 1992). Local populations
57 at the limit of the species' range are thought to be under severe selection pressures to adapt and stay
58 adapted to harsh environmental conditions they face (e.g. Aitken et al. 2008; Hill et al. 2011). This can be
59 accomplished either through phenotypic plasticity, genetic adaptation, or both (Gienapp et al. 2008;
60 Moritz and Agudo 2013). Exploring these mechanisms that allow a species to persist in challenging
61 environments is crucial for understanding how species deal with ecological selection pressures (Merilä
62 and Hendry 2014; Ludwig et al. 2015).

63
64 Widely distributed species can be of particular interest in this context because: i) they experience variation
65 in climate, habitat and resource availability and quality over a wide geographic range; ii) their populations
66 inhabiting distinct locations experience different ecological and climatic pressures and iii) these different
67 selection pressures generate and maintain phenotypic differentiation in their life history traits (Bulgarella
68 et al. 2015; Miaud and Merilä 2001). Ectothermic animals like amphibians are very sensitive to
69 temperature as it influences directly their metabolism and sets limits to their distribution (Ludwig et al.
70 2015). Some temperate zone amphibians, such as the common frog (*Rana temporaria*), are widely
71 distributed and provide excellent models for studying age- and size-related life-history traits (and potential
72 trade-offs among them) across their wide latitudinal and altitudinal distribution range (Morrison and Hero
73 2003; Sinsch et al. 2015).

74
75 The common frog is considered to be a generalist anuran species in its habitat use (Van Buskirk and Arioli
76 2005) although other studies indicated habitat selectivity (Plăiașu et al. 2010; Cogălniceanu et al. 2012). It
77 is a widespread species occurring throughout most of Europe from northern Spain through North Cape to
78 the Urals, and can be found at elevations ranging from sea level to 2,700 m a.s.l. To the south its

79 distribution becomes patchy and increasingly restricted to mountainous regions (Kuzmin et al. 2009). Due
80 to its wide distribution range and high abundance, *R. temporaria* has been used as a model for testing a
81 variety of hypotheses of ecological and evolutionary interest (e.g. Miaud and Merilä 2001; Sinsch et al.
82 2015). Both larval and adult life history traits display extensive geographic variation (Miaud et al. 1999;
83 Miaud and Merilä 2001; Sinsch et al. 2015).

84
85 The common frog populations inhabiting Fennoscandia have been subject to several studies focused on
86 geographic variation along a latitudinal gradient. They have been used in testing Bergmann's rule in adult
87 body size (Laugen et al. 2005), validity of Allen's rule in leg lengths (Alho et al. 2011), as well as in
88 studies of variation in energy storage patterns (Jönsson et al. 2009) and testis weight (Hettyey et al.
89 2005). Furthermore, studies in sex chromosome differentiation (Rodrigues et al. 2014), genome size
90 variation (Matsuba and Merilä 2006), patterns of growth and age structure (Hjernquist et al. 2012),
91 plasticity in age and size at metamorphosis (Merilä et al. 2000), embryonic and larval development and
92 growth (Laugen et al. 2003; Merilä et al. 2004) have been conducted. They have also been subject to
93 studies in genetic variation and differentiation (Palo et al. 2003, 2004), presence of persistent organic
94 pollutants across Fennoscandia (ter Schure et al. 2002), larval nitrate tolerance (Johansson et al. 2001),
95 and effect of UV-B radiation on embryos (Pahkala et al. 2002).

96
97 Many studies have also focused on age structure, longevity and body size variation among common frog
98 populations (reviewed in: Miaud et al. 1999; Sinsch et al. 2015), but only few have focused on the small
99 scale (i.e. at population and metapopulation level) variations in age and size structure (but see: Elmberg
100 1990; Augert and Joly 1993; Ryser 1996). Two recent studies (Alho et al. 2008; Patrelle et al. 2012a) have
101 described the age structure of a common frog population living under extreme environmental conditions at
102 the limit of species distribution range in the sub-Arctic Finland at 480 m a.s.l. Common frogs in this area
103 occur also at altitudes higher than this, and a recent study discovered that microclimatic factors are

104 important determinants of species occurrence in this area (Blank et al. 2014). However, little is known
105 about the life history of the common frogs inhabiting the high altitude sites in this area.

106
107 The aim of the present study was to compare adult life history traits related to age and size of common
108 frogs from low (“valley” at 480 m a.s.l.) and nearby high (“hill” at 530-650 m a.s.l.) altitude sites in the
109 sub-Artic Kilpisjärvi area.

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112 **Materials and methods**

113
114 *Study area*

115 The study area was located at Kilpisjärvi (69⁰03’N, 20⁰50’E), in the northwestern corner of Finland, 270
116 km north of the Arctic Circle and ca 50 km south-east of the Arctic Ocean. The climate in the area lies
117 between the North Atlantic oceanic climate and the Eurasian continental climate, with a mean annual
118 temperature of -2.0°C. The area experiences a large variation in solar radiation: in winter the sun is below
119 the horizon for 55 days, while in summer there is no sunset for 62 days (Kauhanen 2013). The duration of
120 the growth season varies between 69-132 days (mean 101 days;
121 <http://www.helsinki.fi/kilpis/english/Climate/records.htm>; Järvinen 1987). The area resides about 100 km
122 north of the continuous coniferous forest and belongs to the sub-alpine birch forest zone (*Betula*
123 *pubescens*) at low altitudes (480-600 m). Above 600 m, the area is alpine tundra (Järvinen and Partanen
124 2008; Kauhanen 2013). Frogs in the area appear to be free of chytrid fungus (Patrelle et al. 2012b).

125
126 *Data collection in the field*

127 To obtain data for the high elevation sample (henceforth: hill-site), fieldwork was done during the
128 summers of 2003 (9-28 August), 2009 (6-12 July) and 2010 (10-18 August) in the Malla nature reserve
129 and the south-western slope of the Saana Mountain (Fig. 1). Adult animals were collected along transects

130 and data on 134 (81 females and 53 males) individuals were obtained. The captured animals were
131 measured on site: body size was measured as the length from snout to vent (snout-vent length, SVL) to the
132 nearest 0.1 mm using a dial caliper. Body mass was recorded with an electronic balance (Triton T2 400),
133 with a precision of 0.01g. The animals were photographed and the second toe of the left arm was cut
134 below the second phalange and stored in alcohol. The animals were then released at the site of capture.
135 The exact location and altitude of the animals was taken with a hand-held Garmin GPS-tracker. Toes from
136 at least 20 juveniles were also collected each year as they were required for calibration in
137 skeletochronology (see below).

138
139 To obtain data for the low elevation sample (henceforth: valley-site), we re-used data from Patrelle et al.
140 (2012a) which consisted of 169 adult frogs (116 females and 53 males) collected in the valley between the
141 Malla and the Saana mountains (the distance separating the valley site and the hill sites is about 5 km)
142 (Fig. 1). The raw data consisted of 699 individual measures (captures and recaptures) in different years.
143 Excluding multiple recaptures from the same year, there were 397 unique captures during the five study
144 years (1999-2003). Thus, recaptured individuals were considered repeatedly, in all years of capture or
145 recapture, with SVL and body mass measured each time (if multiple recaptures in a single year, the latest
146 date was considered), and age corrected based on the year of measurement. Animals were captured in late
147 summer in the hill-site (i.e. post reproduction season) whereas in valley-site the captures took place in the
148 early spring (i.e. pre-breeding and breeding season).

149
150 *Skeletochronology*

151 Age related parameters were estimated through skeletochronology *sensu* Castanet and Smirina (1990),
152 using some modifications following Rozenblut and Ogielska (2005). Skeletochronology allows for the
153 reliable estimation of age of individuals in most populations and species (Sinsch 2015), limited only in the
154 correct assessment of age in old individuals (Wagner et al. 2011). In brief, the second phalange was
155 decalcified for 3 h with 5% HNO₃, followed by inclusion in TissueTek, freezing and sectioning with a

156 Tehsys CR 3000 cryotome at 16 μm . The cross sections were stained with Ehrlich's haematoxylin for 3
157 hrs and photographed thereafter using an Olympus CX 31 microscope and Quick Photo Micro 2.3
158 software. We estimated age from the Lines of Arrested Growth (LAGs), after correction for resorption in
159 older individuals by using cross sections from juveniles and subadults as recommended by Hemelaar
160 (1985), Castanet and Smirina (1990), and Rozenblut and Ogielska (2005). Three independent observers
161 (RP, DR and DC) counted the lines of arrested growth (LAGs) in 2–6 sections per individual.

162
163 The distance between two LAGs is an indicator of individual growth in a given age, and a pattern of
164 decreasing intervals between LAGs after a few years is thought to indicate the onset of sexual maturity,
165 with resources being reallocated from growth to reproduction (Smirina 1994). We inferred the age of
166 sexual maturity from the bone growth pattern as indicated by Smirina (1994), and in addition compared
167 with the youngest adult age class in our sample, considered as the minimal age of sexual maturity. Age
168 was assessed in a similar way in the valley site (Patrelle et al. 2012a), except for endosteal resorption that
169 was based on a method developed by Alho (2004). Since frogs in the valley were collected from breeding
170 sites, all individuals were mature and age of sexual maturity was estimated as the minimum age in the
171 sample (Patrelle et al. 2012a). Although slightly different approaches were used to account for endosteal
172 resorption in hill and valley datasets, this is unlikely to have influenced age assessment.

173
174 *Data analyses*
175 We analyzed data from both the valley sites collected during five consecutive years (1999-2003; Patrelle
176 et al. 2012a), and from the hill sites at three different time points (2003, 2009 and 2010). We computed a
177 sexual dimorphism index (SDI) for SVL, body mass and average age, with the results arbitrarily defined
178 as positive when females are the larger sex and negative in the converse situation (Lovich and Gibbons
179 1992) despite criticisms on using this method (see Ranta et al. 1994) since it allows to compare all three
180 parameters:

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$$SDI = \frac{Mean\ size_{larger\ sex}}{Mean\ size_{smaller\ sex}}$$

The average (minimum) age of maturation (A_{mat}) is the average number of growing seasons experienced before size at sexual maturity is reached. Longevity (A_{max}) is the highest recorded age.

We fitted growth curves based on the von Bertalanffy growth function

$$L_t = L_\infty(1 - e^{-k(t-t_0)})$$

with the FSA package in R (Ogle 2010), where L_t is the body size at age t (or after t growing seasons experienced), L_∞ is the estimated asymptotic body size, k is a growth coefficient relating the rate of decline in growth as individuals attain maximum body size (units are year⁻¹), and t_0 is the age at metamorphosis. Differences between sites and sex-specific growth rates were tested using a likelihood ratio test (Kimura 1980) using package fishmethods in R (Nelson 2014).

Adult survival rate was calculated according to Robson and Chapman's (1961, in Krebs 1989) formula: $S = T/\sum N + T - 1$ with the fishmethods package. Here, S is the average finite survival rate, T is the sum of the coded ages times their frequencies when age is found by setting the youngest included age-class to 0, the next age to 1 and so forth $T = 0N_x + 1N_{x+1} + 2N_{x+2} + \dots + iN_{x+i}$; $\sum N$ is the number of animals from age-class x to $x+1 = N_x + N_{x+1} + N_{x+2} + \dots + N_{x+i}$; and N_x is the number of individuals in age-class x . This formula is only valid for stationary populations in which recruitment and survival are relatively constant. As these assumptions are rarely met in nature, calculated values should be seen as relative estimates allowing only for comparisons between sexes and sites (Schabetsberger and Goldschmid 1994). We note that for the valley site, the assumption about similar survival rates between sexes has been verified (Alho et al. 2008).

206 Growth rate (R) can be calculated with the following equation: $R = dL/dt = k \times (L_{\infty} - L_t)$, which is
207 maximal when L_t is minimal.

208
209 SVL and body mass were modeled as a function of site, sex, year and age using general additive Mixed
210 Models (GAMMs) which enable individual effects to be accommodated in analyses, thus accounting for
211 non-independence among individuals at the same site or year. The ‘mgcv’ package (Wood 2006) was used
212 to fit the models to the data in R. Pairwise comparisons between site, sexes and years were made using the
213 R multcomp package (Hothorn et al. 2008).

214

215

216 **Results**

217

218 All the age, size and growth related parameters are summarized in Table 1. There were significant
219 differences in body size between sites, sexes and years (Table 2). Frogs were significantly larger and
220 heavier in the valley as compared to the hill site (Table 3, Appendix 1). Females were significantly
221 heavier, but not significantly larger in SVL than males (Table 4). Significant differences in body size were
222 observed also among years (Table 2, Appendix 1).

223

224 Females from the hill site were significantly smaller and lighter compared to females from the valley site
225 (Table 3, Fig. 2A, B): on average females from the hill-site had 78% and 47% of the SVL and body mass
226 of the valley females, respectively. Likewise, males from the hill site were smaller and lighter compared
227 with males from the valley site (Table 3, Fig. 2A, B, Appendix 1): on average, the hill-site males had 90%
228 and 66% of the SVL and body mass of valley males, respectively. In both sexes, SVL and body mass were
229 significantly correlated within each of the sites (Table 4). The regression equations for females had very
230 similar slopes but different intercept values, indicating the females from the hill site had a smaller body
231 mass compared with females from the valley site for the same body length value (Table 4).

232
233 The degree of SDI for SVL and body mass varied between the sexes in both sites: in the valley site
234 females were larger ($SDI_{SVL} = 1.08$) and heavier ($SDI_{body\ mass} = 1.23$), while in the hill site males were
235 larger ($SDI_{SVL} = -1.05$) and heavier ($SDI_{body\ mass} = -1.14$). The sex ratio was biased in both sites, with
236 females being more abundant. The sex ratio (males: females) in the hill site was 0.65 (53:81), significantly
237 higher as compared to the valley site 0.45 (53:116) (*chi-square* = 3.942, *d.f.* = 1, *p* = 0.047). The SDI for
238 mean age showed that females were older in both sites, but the differences between sexes were much
239 larger in the valley population (valley: $SDI_{mean\ age} = 1.39$; hill: $SDI_{mean\ age} = 1.08$).

240
241 Both females and males from the valley site were significantly older than individuals from the hill site
242 (Table 3, Fig. 2C, Appendix 1). Individuals from the hill site had an average age of only 50% in the case
243 of females and 64% for males, compared to those in the valley site.

244
245 The growth curves were significantly different between the hill and valley sites (Table 5, Fig. 3) although
246 there were no significant differences between any of the Von Bertalanffy parameters. Females and males
247 showed significantly different growth curves (Table 5, Fig. 4) driven by significant differences in t_0 (*p*
248 <0.001) and growth coefficient (*p* = 0.039). Differences in L_{∞} were substantial, but not significant (*p* =
249 0.89). In both hill and valley sites frogs showed an evident increase in body length and body mass (Table
250 2, Fig. 2A - C) but frogs reached an asymptote in length and body mass only in hill site (Fig. 4A, B).

251
252 Age structure differed between sites and sexes (Fig. 5, Appendix 1). For the hill site the most abundant
253 age class for both females and males was 6 years old (48% of females and 34% of males). There are
254 differences among years in the age structure, with a decrease in age composition in 2009 compared to
255 2003, followed by an increase from 2009 to 2010 (Fig. 6). For valley site, the proportion of females 10
256 years old (23%) was the highest, whereas the highest proportion (28%) of males were five year old (Fig.
257 5).

258 The lower average age of the frogs on the hill site is supported by the fact that none of the 258 individuals
259 toe-clipped in 2003 were recaptured in 2009. In 2010 19% of the individuals marked in 2009 were
260 recaptured (14 individuals out of 143 captures, not including the 25 freshly metamorphosed individuals).

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262

263 **Discussion**

264

265 Our study revealed significant differences in common frog life-history traits, including life span, survival,
266 body size and mass over short spatial and temporal scales. Individuals from the hill site had shorter life
267 span, both in terms of mean age and longevity, smaller body size and body mass than those from the
268 valley-site. These differences were more pronounced in females as compared to males. Males were larger
269 and heavier than females in the hill than in the valley site indicating that females were more affected by
270 factor(s) associated with higher altitude conditions than males. The individuals from the hill site exhibited
271 strong interannual variation in body mass and length, but mostly in the former, and also in age structure.
272 In the following, we discuss these findings in relation to what is known about common frog life history
273 trait differentiation, in particular, in relation to environmental gradients.

274 Studies of neighboring populations at small spatial scale often are focused on local ecological conditions
275 as the main explanation for the observed differences (Miaud and Merilä 2001). A recent review (Sinsch et
276 al. 2015) found that common frogs at higher altitudes and latitudes (i.e. experiencing adverse conditions)
277 reached reproductive maturity at significantly older ages and enjoyed an increased longevity as well. Our
278 results support this finding only for the valley site frogs. This finding is at odds with Miaud et al. (1999),
279 who showed that under adverse conditions *R. temporaria* grows older and larger, with sexual size
280 dimorphism increasing with climatic harshness, due to slower juvenile growth rate and a delayed maturity
281 in females. One possible explanation for this difference is that conditions at the hill-site are so adverse that
282 common frogs there never reach very old ages and sizes.

283 The hill sites are likely to be harsher environments than the valley sites as ambient temperatures drop with
284 altitude on average 0.9°C with every 100 m increase in altitude (Järvinen 1989), exposure to winds
285 becomes higher, and vegetation cover is reduced (Kauhanen 2013). Because of the latter, also exposure to
286 predation by birds and mammals is likely to increase. Likewise, lower invertebrate prey abundance should
287 make finding food more difficult in the hill as compared valley sites. All these coupled with the slightly
288 shorter growth season in the hill than in valley sites should impose constraints on growth, development
289 and survival (Muir et al. 2014). In contrast, although day length is the most accurate and consistent
290 environmental cue in northernmost seasonal environments (Saikkonen et al. 2012), and has a major
291 influence on mean age, age at first reproduction and longevity in common frog (Hjernquist et al. 2012), it
292 cannot explain the life history trait differentiation between hill and valley sites situated just a few
293 kilometers apart.

294
295 Temperature has a strong effect on the development and growth of most living organisms (Marchand
296 2014). A larger body size and lower growth rates in adults are adaptive in colder environments (Angilletta
297 et al. 2004), and are probably coupled with higher metabolic rates required to sustain activity during the
298 shorter growing season and lower predation risk. To reach the large body size in a cold environment,
299 individuals must prolong growth period and delay reproduction relative to those in warm environments.
300 Such delayed maturation is adaptive when larger body size favors an increase in fecundity and/or survival
301 rates (Stearns 1992; Angilletta et al. 2004). Contrary to Bergmann's rule, body size variation in adult
302 common frogs is not linearly related to latitude (or altitude), but covaries with age as expected for a
303 species that grows indeterminately (Laugen et al. 2005; Sinsch et al. 2015). This indicates that variation in
304 common frog body size mirrors differences in age structure. Thus, the finding that individuals from the
305 hill sites had lower age and smaller body size than those from the valley-sites fits with this idea. However,
306 an alternative explanation for age (and size) differences between hill and valley relates to how the data
307 from the contrasting sites were collected. Since the hill sites were sampled in the late summer and valley
308 sites in early summer, the hill samples may include more subadults than the valley samples which were all

309 breeding adults. However, we believe this is an unlikely explanation for the observed differences because
310 the differences in body size persisted even after controlling for age difference among sites.

311
312 We discovered that the population sex ratio differed significantly between the hill and valley site, with
313 stronger bias towards females in the valley than in the hill site. The strong female bias in the valley
314 population is known since earlier (Alho et al. 2008, 2010), with on average, only one third of breeding
315 individuals being males. The cause of this sex-bias is thought to be environmentally induced sex reversal for
316 which evidence has been accumulating (Perrin 2009; Matsuba et al. 2010; Rodrigues et al. 2016). The
317 reason why the sex bias is less pronounced in the hill site than in the valley site is not obvious, but this
318 difference can be related to differences in environmental conditions experienced by maturing individuals.
319 Likewise, an earlier study has confirmed that males and females in the valley site do not differ in their
320 survival rates (Alho et al. 2008). Hence, the differences in sex ratio among valley and hill sites are
321 unlikely to depend on sex differences in mortality.

322
323 In conclusion, the results demonstrate marked differences in common frog key life history traits between
324 ecologically contrasting environments in the sub-Arctic. The frogs inhabiting the environmentally more
325 adverse hill sites are younger and smaller than those inhabiting valleys. As these findings go against the
326 large-scale patterns showing that common frogs tend to get older with increasing environmental adversity
327 (Miaud et al. 1999; Sinsch et al. 2015), the results highlight the importance of scale in ecology (Schneider
328 2001): downscaling large scale patterns may be of limited validity.

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330

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332

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571 Figure Captions

572

573 **Fig. 1** Location of the study site in northern Finland (inserted map) and of the valley and hill sites in
574 Kilpisjärvi (larger map).

575

576 **Fig. 2** Mean (A) SVL, (B) body mass and (C) age of female (white) and male (black) in common frogs,
577 *Rana temporaria*, from hill and valley sites

578

579 **Fig. 3** Body size a function of age as estimated by GAMMSs (generalized additive mixed models) for the
580 common frogs, *Rana temporaria* from: hill site, (A) SVL (mm) and (B) body mass (g) and valley site, (C)
581 SVL (mm) and (D) body mass (g); gray shading shows 95% confidence intervals

582

583

584 **Fig. 4** Length-at-age growth curves for the common frogs, *Rana temporaria*, derived with Von
585 Bertalanffy method. (A) Hill (open circle, solid line) and valley (closed circle, dotted line) sites, and (B)
586 females (open circle, solid line) and males (closed circle, dotted line)

587

588 **Fig. 5** Age distribution of female and male common frogs, *Rana temporaria*, from hill ($n = 134$) and
589 valley ($n = 169$) sites

590

591 **Fig. 6** Yearly variation in age distribution of female and male common frogs *Rana temporaria* from the
592 hill site

Table 3 The pairwise comparisons between site and sex on the SVL, body mass and age for the common frogs, *Rana temporaria*

	Estimate	SE	z	p
SVL (mm)				
Valley Female - Hill Female	16.799	0.717	23.443	<0.001
Hill Male - Hill Female	3.675	1.001	3.671	0.001
Valley Male - Hill Female	10.702	0.819	13.067	<0.001
Hill Male - Valley Female	-13.124	0.850	-15.435	<0.001
Valley Male - Valley Female	-6.097	0.626	-9.744	<0.001
Valley Male - Hill Male	7.027	0.938	7.490	<0.001
Body mass (g)				
Valley Female - Hill Female	25.628	1.118	22.914	<0.001
Hill Male - Hill Female	3.216	1.566	2.054	0.162
Valley Male - Hill Female	16.431	1.272	12.916	<0.001
Hill Male- Valley Female	-22.411	1.328	-16.879	<0.001
Valley Male - Valley Female	-9.197	0.965	-9.535	<0.001
Valley Male - Hill Male	13.214	1.460	9.053	<0.001
Age (year)				
Valley Female - Hill Female	5.713	0.263	21.736	<0.001
Hill Male - Hill Female	-0.451	0.368	-1.224	0.603
Valley Male - Hill Female	2.516	0.299	8.411	<0.001
Hill Male- Valley Female	-6.164	0.312	-19.750	<0.001
Valley Male - Valley Female	-3.198	0.227	-14.108	<0.001
Valley Male - Hill Male	2.966	0.343	8.643	<0.001

Table 5. Likelihood ratio test results comparing the von Bertalanffy model parameters between (1) hill and (2) valley sites, as well as between (3) female and (4) male common frog, *Rana temporaria*.

Hypothesis	Chi-sq.	df	p
Site			
$L_{\infty 1} = L_{\infty 2}$	1.92	1	0.166
$k_1 = k_2$	2.5	1	0.114
$t_{01} = t_{02}$	0	1	1
$L_{\infty 1} = L_{\infty 2}, k_1 = k_2, t_{01} = t_{02}$	32.53	3	<0.001
Sex			
$L_{\infty 3} = L_{\infty 4}$	0.02	1	0.888
$k_3 = k_4$	4.28	1	0.039
$t_{03} = t_{04}$	13.23	1	<0.001
$L_{\infty 3} = L_{\infty 4}, k_3 = k_4, t_{03} = t_{04}$	33.84	3	<0.001



