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Mini Review
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Ecological, Biological, Behavioral and Genetic Adaptation to Xeric Habitats of *Triturus Vittatus Vittatus* (Urodela) on the Southern Border of its Distribution

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Abstract

In the present mini-review, the results and unpublished data that were collected on *Triturus vittatus vittatus* in Israel on the southern border of its distribution, and on its adaptation to the Mediterranean semi-arid climate and to arid climate environments on the southern border of its distribution were presented. The contribution of the present paper is in building a model based on the results collected on the distribution, life cycle, behaviour and genetic variations among different populations in northern Israel down to the central coastal plains and near the desert of this species. More specifically, this model is based on the morphology, biology, behaviour and life cycle of *T. v. vittatus* adaptation. By considering these many parameters, one hypothesis was raised and is supported. The adaptation to and selection of habitats depends mainly on the terrestrial phase and less on the aquatic phases. There are various breeding places in all of the habitats, however, the newts are mainly used to winter ponds, many of which dry up in summer where the larvae can grow and complete metamorphosis. The adaptation of the breeding ponds is not under ecological conditions during larvae growth and complete metamorphosis, but the time of adult breeding and larvae growth occur year-round. The molecular genetic variation in the different areas support our hypothesis that climate is affected by altitude and proximity to the desert. During the life cycle the newts have two habitats aquatic and terrestrial and the adaption to terrestrial habitats is more affected on the newts distribution than the aquatic habitat. The quality model of fitness *T. v. vittatus* to extreme conditions was suggested.

Keywords: Genetic variation; Urodela; *Triturus vittatus vittatus*

Introduction

Ecology defines the relationships and interactions between organisms and their environment. In order to explain the adaptation of *Triturus vittatus vittatus* to a habitat, as many as possible biological parameters, e.g. physiology, behaviour and life cycle, growth and reproduction parameters that are important to these characteristics, must be studied in understanding adaptation to the natural habitat. The banded newt *Triturus vittatus* [1] is distributed throughout western Caucasus, Turkey, Lebanon, Syria, Israel, Iraq. The banded newt consists of two species, *T. ophryticus* and *T. vittatus*, based on trunk vertebrae count, genome size and allozyme data. The northern taxon, *T. ophryticus*, is subdivided into two geographic fragments:

"western group" populations from western Anatolian Turkey; and "eastern group" populations distributed in the remaining area of Pontic Turkey and Western Caucasus. According to the above criteria, the *T. vittatus* species is found in Israel. The biology of *T. vittatus* in the Mediterranean area has been described by Olgun [2]. As indicated by their data, there are two known subspecies in the genus Triturus: *T. v. vittatus* along the eastern edge of the Mediterranean Sea from Turkey to Israel, where it reaches its southern limit, and T. v. ophryticus in the Caucasus, east and south of the Black Sea. The banded newt, *T. v. vittatus*, is an endangered species in Israel [3] at the southern limit of its distribution. The adaptation of *T. v. vittatus* on the southern border of newt populations in Israel has been scarcely described. The purpose of the present paper is to review the data collected and add some unpublished data in order to enhance our knowledge about the adaptation of this species to extreme conditions.

Distribution in Israel

In Israel, newt populations are found under more extreme conditions than in other geographic area of the distribution of populations belong to *T. vittatus* species. The population in the center near south Israel adapted to more extreme conditions than in northern populations Israel. The Mediterranean climate has about 1,000 mm of rain annually in northern Israel down to the central coastal plains, to about 400 mm of rain annually in close proximity to semi-desert conditions [4-10], where conditions are most extreme (Figure 1 and Table 1). Populations of newts in Israel are found around the breeding places, however, not much information has been published on the adaptation to terrestrial life, which includes physiology and environmental behavior [11-15].

Life Cycle

The life cycle of *T. v. vittatus* in Israel has been described in several studies (Figure 2). In northern Israel and the Upper Galilee, the life cycle has been described by Degani and Mendelssohn [4-17]. In central Israel, the life cycle has been described by Geffen [18]. *T. v. vittatus* in the aquatic phase is reproduced in mainly unpredictable habitats such as winter pools that contain water only until the beginning of the summer, although occasionally these pools contain water throughout the year [5,8-10,16,19-23]. Like other newts, *T. v. vittatus* require water bodies surrounded by an adequate terrestrial habitat to support both terrestrial and aquatic life phases. If either habitat is damaged, a population may be unable to survive.

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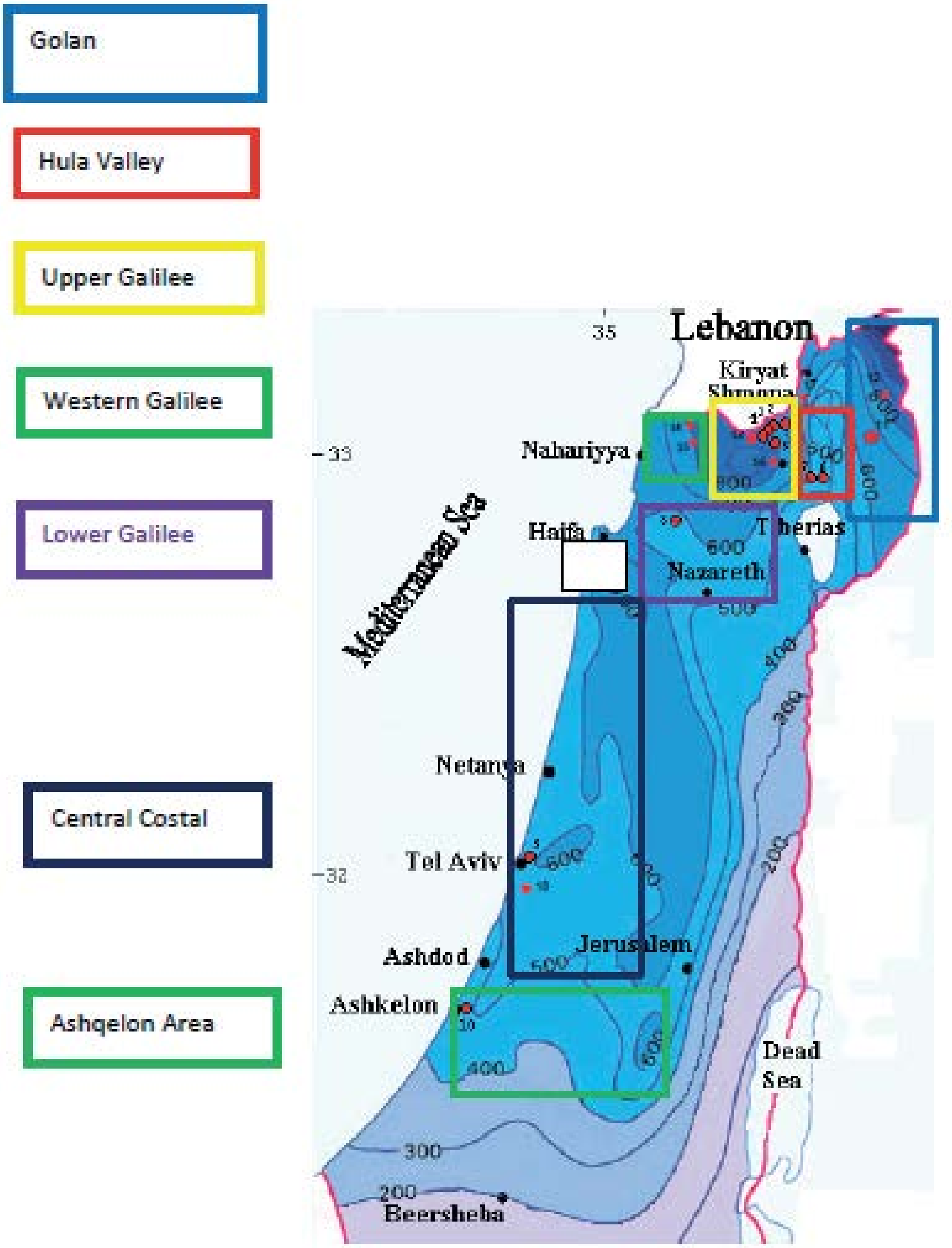

Figure 1: Various ponds in Israel where *T. v. vittatus* were identified (Table 1).

Terrestrial adult newts reach the pond area at the beginning of the rainy season before the ponds fill up with water and subsequently enter the ponds in the aquatic phase after they are full. In the Upper Galilee, males inhabit the ponds from January to March, leaving them after mating. Females may remain in the water until May, when they deposit between 18-68 eggs on plant or rock surfaces until they move on to the terrestrial stage [4,8]. Afterwards, the larvae hatch 19-29 days later, depending on water temperature [16].

The period of activity, population parameters and food habits of mature *T. v. vittatus* in central Israel have been studied by Geffen *et al.* [18], who discovered that during November to December, adult newts appear on land and enter the pond after it has filled up, and remain in the water until late February in the Upper Galilee (Tables 2 and 3, Figure 2) [4].

Based on the skeletochronology in two breeding populations of *Triturus vittatus* ophryticus inhabiting altitudes ranging from 300 m (in Gurbulak) to 1,300 m (in Hidirnebi) in northeastern Turkey, the maturation age was between 4 to 8 years but differed between the two populations at the different altitudes [23]. Differences between snout-vent length and sex dimorphismdey were found in Turkey between the populations at different altitudes. In conclusion from the many papers, it seems that the age and size of newts are affected by ecological and climate conditions, which are affected by geographical distribution. In the Upper Galilee in Israel, the males are larger than the females, and differences in body size were significant (Figure 3) [4]. In the aquatic phase, when the females were full of eggs, they were heavier than the males. In the Upper Galilee, spawning occurred from February to May, and different amounts of eggs were deposited, up to 68 eggs per female. The larvae in the pond were also affected by altitude; they were found at the lowest place at the beginning of winter and later at a high altitude at the end of winter (Figure 3) [4,8-10].

Gonadal Cycle of *T. v. vittatus*

The gonadal cycle of the terrestrial and aquatic phases of *T. v. vittatus* has been described in various habitats in the Upper Galilee (Figure 1) for both males and females [6,7,19-23]. In female gonads, different stages were recognized: oogonia, chromatin nucleolus, perinuclear and vitellogenic oocyte maturation (Figure 4). However, there are different oogenesis states of oocytes development among individual females. Moreover, there are differences in oocytes development between aquatic and terrestrial females. In aquatic females, most of the females contained only oocytes at different stages of vitellogenesis. In contrast, ovaries of terrestrial forms had only pre-vitellogenic and atretic oocytes (Figure 4) [19-21].Male gonads consisted of various cells at different stages of development during spermatogenesis: spermatogonia, spermacytes, spermatides and spermatozoa were observed in the gonads of aquatic forms (Figure 4A and 4B), and more developed specimens had lobuli packed with mature spermatozoa. On the other hand, lobuli of testes from terrestrial forms included mainly cells in the early stages: spermatogonia, spermacytes and early spermatids (Figure 5).

T. v. vittatus adults were found in ponds at low temperatures during the winter, but the eggs and larvae developed only when the temperature was above 20ºC [19-22]. The larvae hatched later and remained in the rain pool for 30-75 days. Hatching time and duration in the pool depended on water temperature, with development being slower at higher altitudes.

Breeding Site	Area	Reference	Latitude	Longitude	Altitude
Nahalit Pond 1	Upper Galilee	[3]	776401	243657	665
Matityahu Pond 2	Upper Galilee	[3]	774855	242783	670
Dovev Pond 4	Upper Galilee	[3]	772801	239158	740
Pharaa Pond 3	Upper Galilee	[3]	774580	242784	682
Amiad Water Holes 7	Hula Valley	[3]	757994	251721	212
Jaudha Pond	Hula Valley	[3]	761398	257589	110
Kash Pond 5	Upper Galilee	[3]	770659	246258	815
Leshem Pond 8	Lower Galilee	[3]	750976	225612	300
Afeka Pond 9	Central Costal	[3]	670453	182364	20
Berekhya Pond 10	Ashkelon Area	[3]	618578	166738	15
Katzarin Pond 11	Central Golan	[5]			
Paras Pond 12	Central Golan	[5]	264566	765449	320
Sasa Pond 13	Upper Galilee	[3]	236948	770859	800
Fasuta Pond 14	Western Galilee	[3]	229597	773378	500
Sumara Pond 15	Western Galilee	[3]	227494	776115	540
Beitzan Pond 16	Upper Galilee	[5]			
Raihaniya Pond 17	Upper Galilee	[19-22]	195791	272861	665
Nir Galim Pond 18	Central Coast		169748	536396	20

Table 1: The breeding sites of *T. v. vittatus* on the southern border of its distribution.

Larvae Growth and Complete Metamorphosis

The larvae of *T. v. vittatus* growth and compete metamorphosis have been studied intensively in Israel [4-16]. In Israel, larvae growth at various breeding sites is described in detail on the southern border of its distribution (Figure 6).

Many different water body sites in Israel were examined, and the larvae of newts were found mainly in unpredictable habitats, most of them winter pools where water is available only during part of the year, and the available water varies from one year to the other [9,19-23]. The larval growth period of *T. v. vittatus* differs between the various breeding sites according to the ecological conditions in the ponds [24]. These conditions at the breeding sites are affected by growth and metamorphosis (Figure 7).

The larvae growth period and complete metamorphosis changed according to ecological conditions of the water in the water body; most changed between 1.5 to 3 months (Figure 7). The size of the breeding places, most of them winter ponds where larvae growth varied, was

Breeding Site	2001-2		2002-3		2003-4		2004-5	
	Months	Days	Months	Days	Months	Days	Months	Days
Matitiyahu Pond			May-July	65	April-July	60	April-June	40
Dovev Pond	May-July	60	May-July	65	April-July	75	April-July	75
Pharaa Pond	May-July	60			May-July	50	April-May	50
Amiad Water Hole					June	35		
Nahalit Pond					April-June	60		

Table 2: The duration of larvae found in various breeding places [4,24,46].

Breeding Site	Sample Size		Male		Female		Period in the ponds
	Male	Female	Weight	Length	Weight	Length	
Matityahu Pond	3	7	4.27 ± 1.75	9.90 ± 1.49	4.07 ± 1.02	9.64 ± 1.14	Jan-March
Dovev Pond	6	11	5.33 ± 0.96	10.87 ± 0.64	3.15 ± 0.4	9.09 ± 0.6	Jan-March
Pharaa Pond	1	4	6.4	10	3.93 ± 0.4	8.67 ± 0.58	Jan-March
Amiad Water Holes	3	2	4.27 ± 1.85	10.17 ± 0.29	3.35 ± 1.06	8.50 ± 0.71	Dec-April
Nahalit Pond	2	2	5.35 ± 0.21	10	3.20 ± 1.41	8.25 ± 1.06	Jan-March

Table 3: Size of adult newts at the breeding sites studied [4].

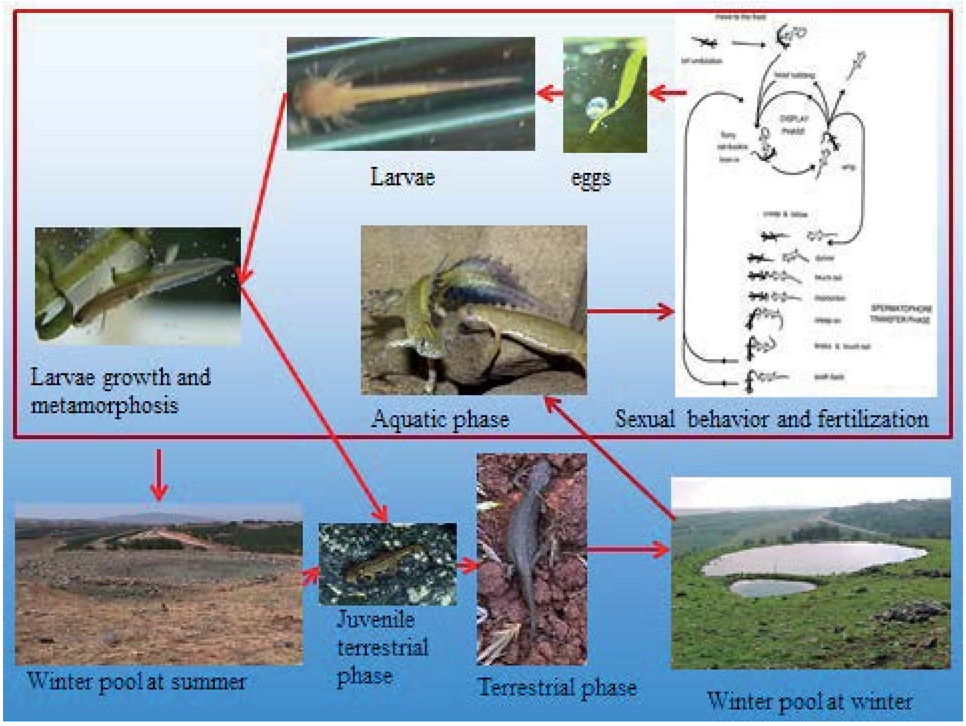

Figure 2: *T. v. vittatus* life cycle [8-10,16,17,19-22,31,50,52].

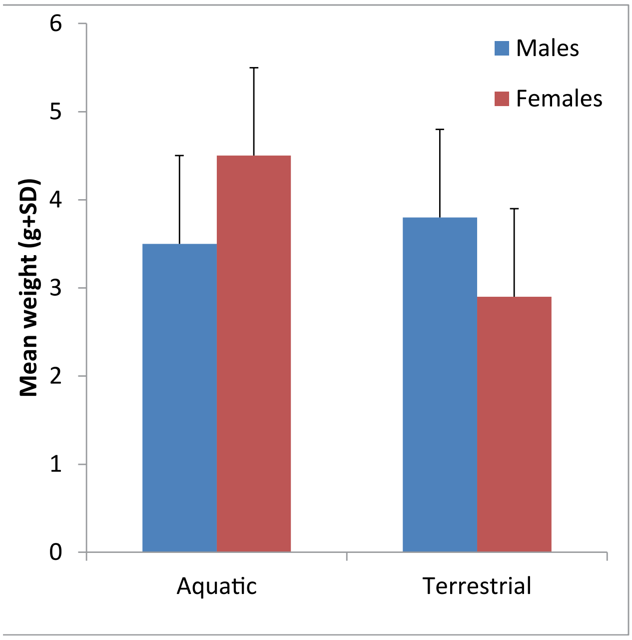

Figure 3: Size of males and females in Upper Galilee [4].

between 78 and 1,017 m^2 and the depth reached 2.5 m. The water quality at the various breeding places in Israel has been described by Pearlson and Degani (Figure 8) [24].

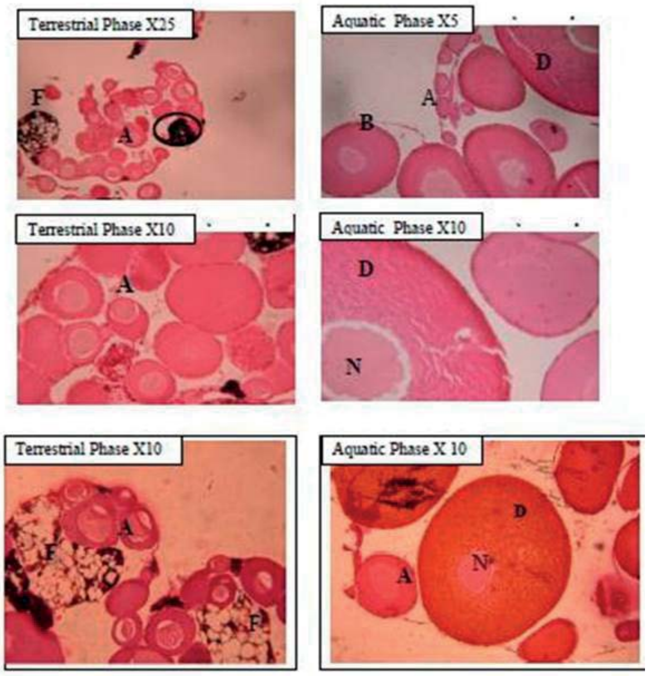

Figure 4: Ovaries of terrestrial and aquatic female newts. A: oocytes in oogenia, B and D: different sized oocytes in vitellogenesis. F: oocytes in artesia. N: nucleus [19-22].

Temperatures vary between 5 and 34°C, dissolved oxygen varies between 0.6 and 27 mg/L, pH varies between 6.5 and 10.4, conductivity varies between 130 and 1,210 and ammonium is less than 1 mg/L (Figure 8) [24].

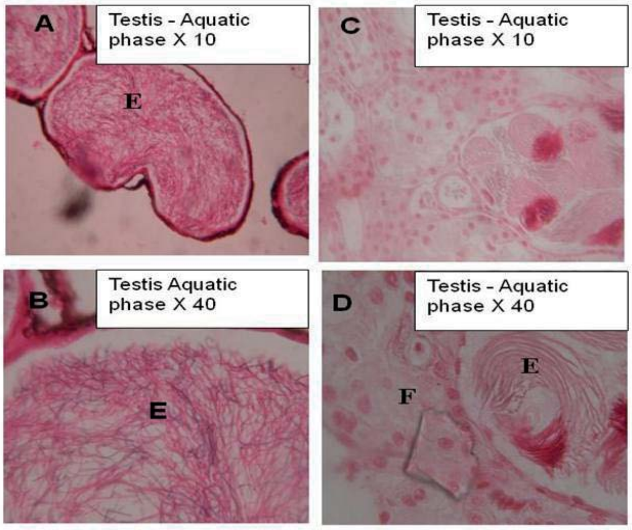

Figure 5: A: Early stage spermatocytes (ES) exist in testes of males in the terrestrial phase (TP). Spermatogenesis takes place before the newts enter the water while they are passing into the aquatic phase (AP); seminiferous lobules are packed with many mature spermatozoids (MS). Fertilization takes place a short time after males and females have entered the pond. B: Testes in the aquatic phase. A and B are spermatophores in the testis, and C and D are different stages of cells in spermatogenesis. E: various cells in the testis during spermatogenesis, F: sperm [19-22].

Environmental Behaviour of *T. t. vittatus*

At the end of metamorphosis, the newts become terrestrial animals and are in danger of dehydration, especially at the southern border of their distribution in Israel [11]. The adaptation to terrestrial metamorphosed newts has been studied less compared to the aquatic phase and larvae growth [15]. Environmental behaviour and the ability to find hiding places to prevent dehydration are crucial for newts to survive in semi-arid habitats on the southern border of their distribution [12,13].

Metamorphosed *T. t. vittatus* are active at night and during the day in selected hiding places in holes and under shelters such as stones to prevent dehydration. The parameters affecting the selection of hiding places, which are very important for adaptation to terrestrial life, particularly at the southern border of its distribution where the newts are found in relatively extreme conditions, are very important. The hypothesis examined by Degani [12,13] showed that the selection of hiding places by newts is affected significantly by soil moisture and negative light (negative photo taxis) (Figure 9) [15]. Post -metamorphosis newts selected only moist soil in the hiding places and under stones and holes in the ground [4,12,13], and the effect of light in hiding places is negative photo taxis (Figure 9). This behavior might help the newts in preventing dehydration and survive the long, dry summer in natural terrestrial habitats.

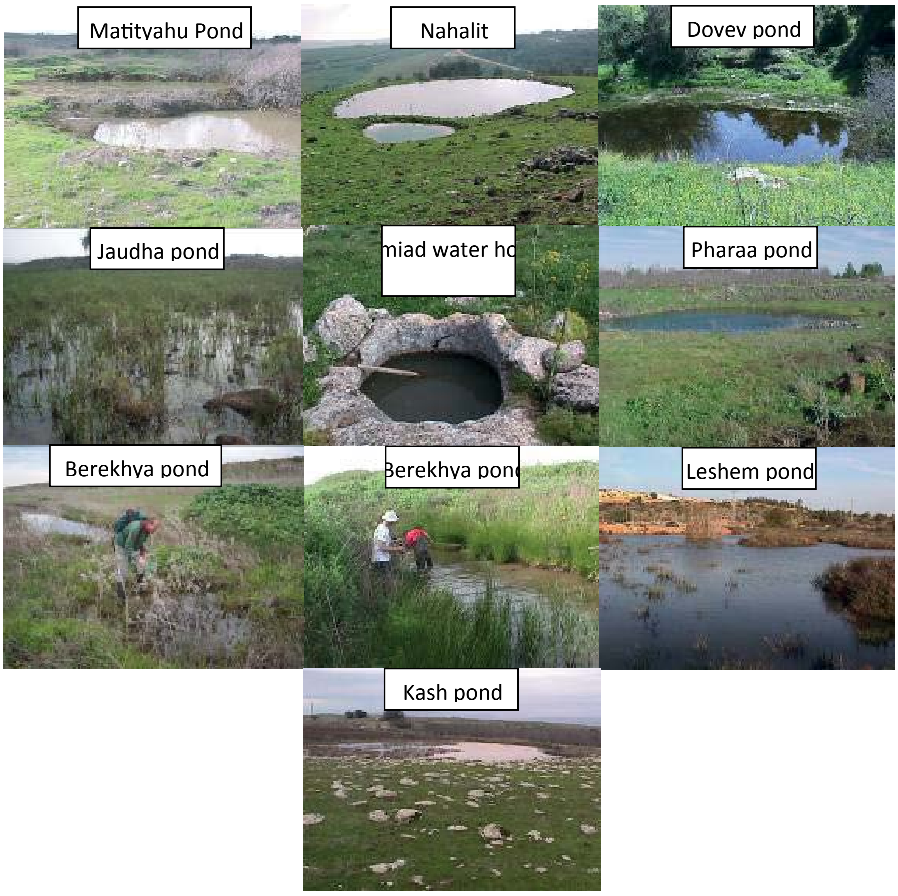

Figure 6: The 10 breeding sites of *T. v. vittatus* in various places in Israel (Table 1) [24,46].

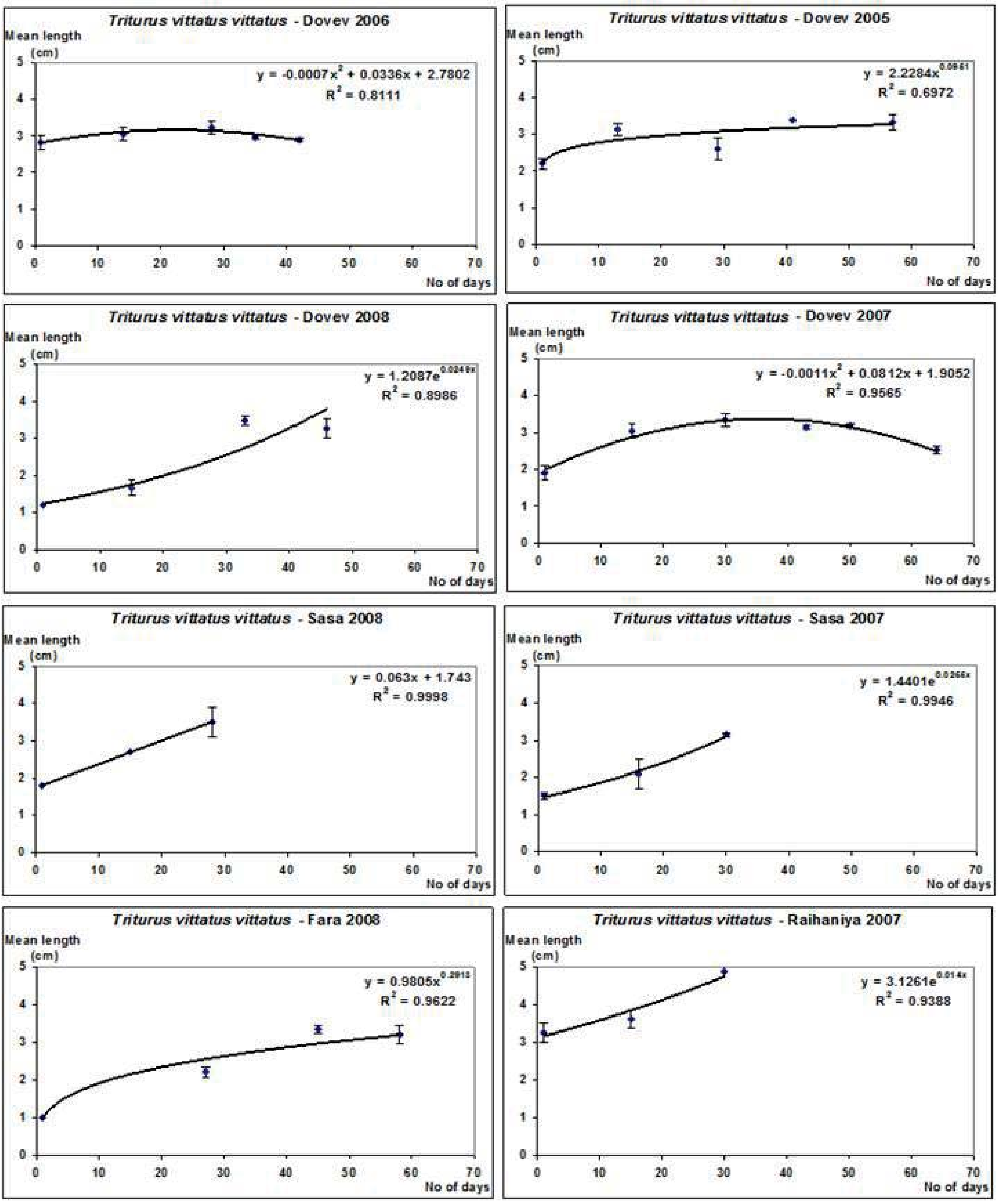

Figure 7: *T. t. vittatus* larvae growth at various breeding sites [19-22].

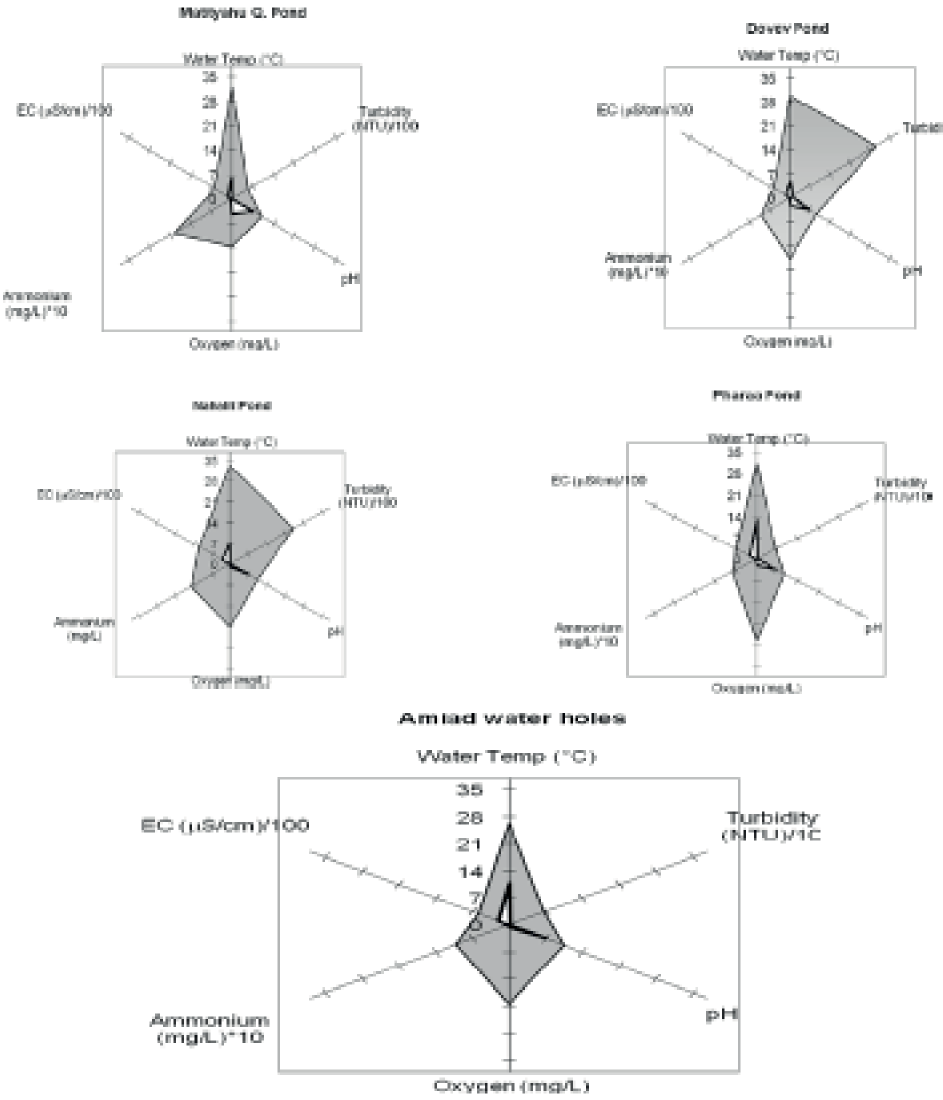

Figure 8: The water quality of *T. t. vittatus* larvae at various breeding sites during the growth period and complete metamorphosis. Oxygen (mg/L), ammonium (mg/L), temperature ºC, conductivity (µS/cm), and pH [24,46].

Effect of Habitat on Genetic Variation of *T. t. vittatus*

A relatively large number of interesting studies have been carried out on the genetic variation of urodelan taxa including the genus *Triturus* regarding various aspects, e.g., systematic, phylogenetic and geographic divergence [25-29]. In order to examine genetic variation among populations, various biochemical and molecular biology methods were used such as serum albumin [17], enzyme isozymes [30], randomly amplified polymorphic DNA chain reaction (RAPD PCR) [31,32], mitochondrial DNA [26,33-35], Amplified Fragment Length Polymorphism (AFLP) [19-22] and sequencing of transcriptome-based genetic markers [36].

The molecular DNA variation of *T. t. vittatus* in different populations in relatively small areas on the southern border of its distribution where the environmental conditions are most extreme were described in several studies and various methods. Using the random RAPD PCR method, variations were found in the larvae population at different breeding sites located at altitudes ranging between 15 and 740 m above sea level (ASL) [6,7] of the 20 primers employed by this method [37], only one was found suitable (OPA-16) to separate among the various populations.

Various bands were found among the different habitats (Figure 10), but high genetic similarity was calculated by band sharing (BS=2x (Nab)/(Na + Nb), where BS=level of band sharing between individuals a and b, Nab=number of bands shard by individuals, a and b, Na=total number of bands of individual a, and Nb=total number of bands of individual b [6,7,38]. High genetic similarity in populations were found between the larvae of newts in the breeding places in ponds at the high altitude (Table 4). A lesser similarity was found between newt larvae from the high altitude to the low altitude (Figure 10).

The Afeka and Amiad Ponds, which are located at relatively low altitudes and at a greater distance from the other breeding sites, differed compared to other high breeding places (Figure 10).

	Nahalit	Amiad Water	Dovev	Afeka
	Pond	**Hole**	**Pond**	**Pond**
Matityahu Pond	90%	96%	92%	88%
Nahalit Pond		80%	83%	80%
Amiad Water Hole			88%	92%
Dovev Pond				88%

Table 4: Band sharing (%BS) of newts in the various ponds (Figure 6) [6,7].

The variation in nucleotide sequences of the mitochondrial cytochrome gene and control region (D-loop) of *T. v. vittatus* larvae from different habitats along the area of its distribution from northern through central Israel have been described by Pearlson [3]. The results of this study support the analysis of results from RAPD [38]. The nucleotides of the D-loop and cytochrome b gene at the lowest altitude and greatest distance from other habitats are more divergent from the other newt populations (Figure 11). Moreover, the sequence analysis of mitochondrial DNA newts from the same species, *T. vittatus* from Syria (Damascus) and from Turkey (European part,) where the conditions seem to be less extreme or different than in Israel, is very different from Israel populations (Figure 12).

It is difficult to separate between geographical distribution

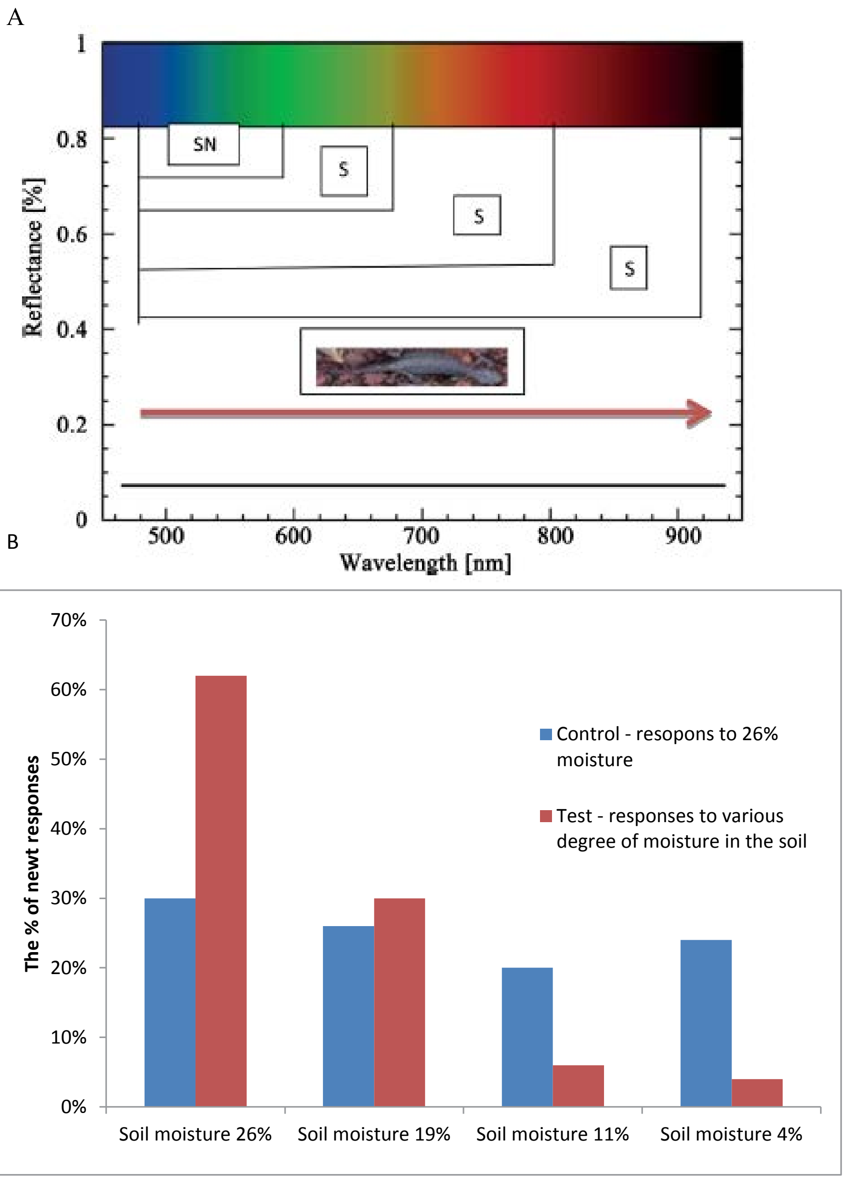

Figure 9: A: Suggested model of the effect of wavelength (WL) on the behavior of metamorphosed *T. t. vittatus*. S=significant differences (X^2-test; $P<0.05$) among the WL, NS=not significant (X^2-test; $P>0.05$) differences among the WL [15]. B: The juveniles selecting various moist soils after metamorphosis compared to the control (X^2-test; $P<0.05$) [12,13].

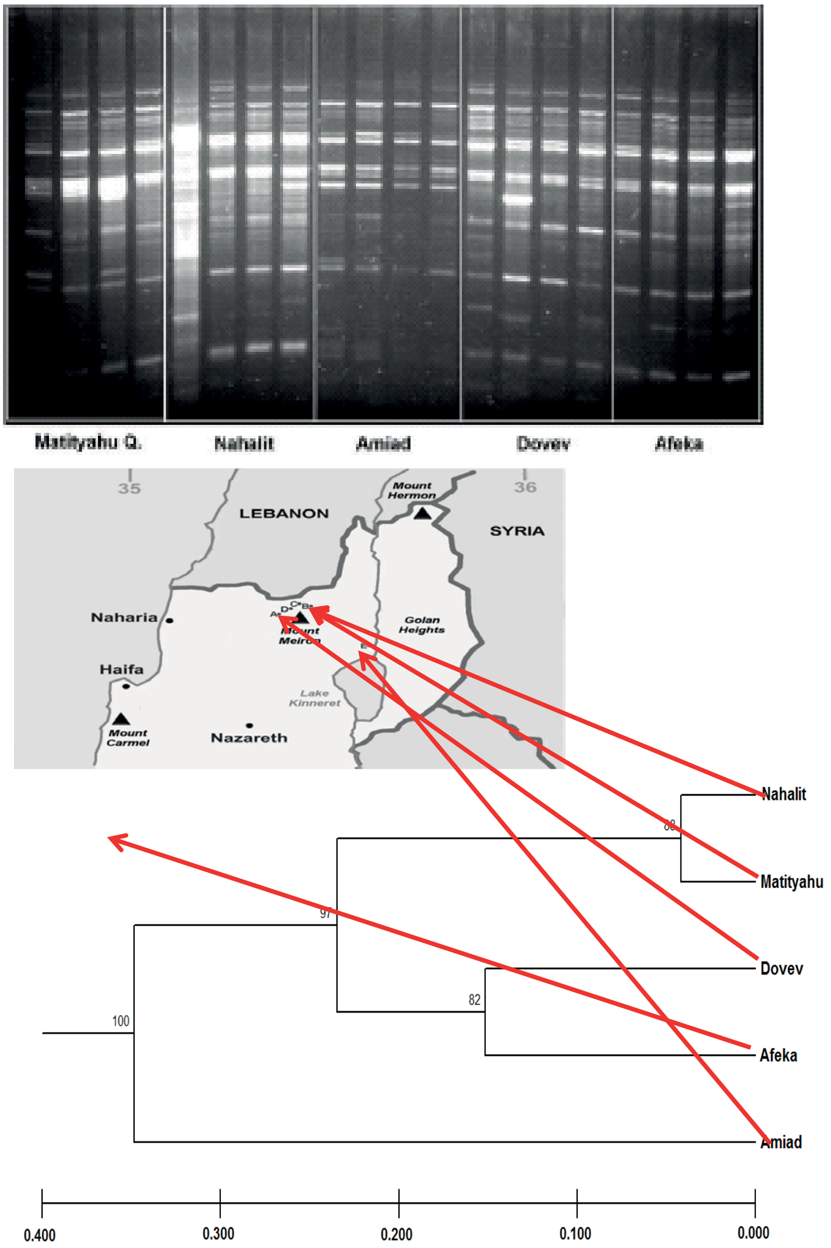

Figure 10: Nei's genetic distance UPGMA topology of five newt populations in Israel based on all 27 Random Amplified Polymorphic DNA loci (RAPD). Bootstrap values (% of 1,000 replicates) are shown above the nodes [6,7].

and variation phenomena to various habitats based on variation in nucleotide sequences collection of *T. v. vittatus* in Israel. The analysis this data by correlation between genetic distances to the geographical distribution (Figure 13) might show if there are genetic differences among those habitats. However, in some cases habitats that found vary close on to another, having different molecular markers as was fond between habitats located far away from each other. The great distance might showed that there is no, or very low, genetic flow among habitats, therefore the newts selected to different ecological conditions.

Amplified Fragment Length Polymorphism (ALFP) methods (unpublished data) support the hypothesis that the southern populations found under more extreme conditions are less variable, however, additional studies are required in order to support this hypothesis (Figure 14).

Discussion

The ecology of the adaptation of *Triturus vittatus vittatus* in natural habitats refers to its study in natural systems, emphasizing the interdependence on the ecological system, other elements and characteristics of the animal. In the present paper, we will consider the relatively many different characteristics from different fields of biology of *T. v. vittatus* to adaptation to various environments under relatively

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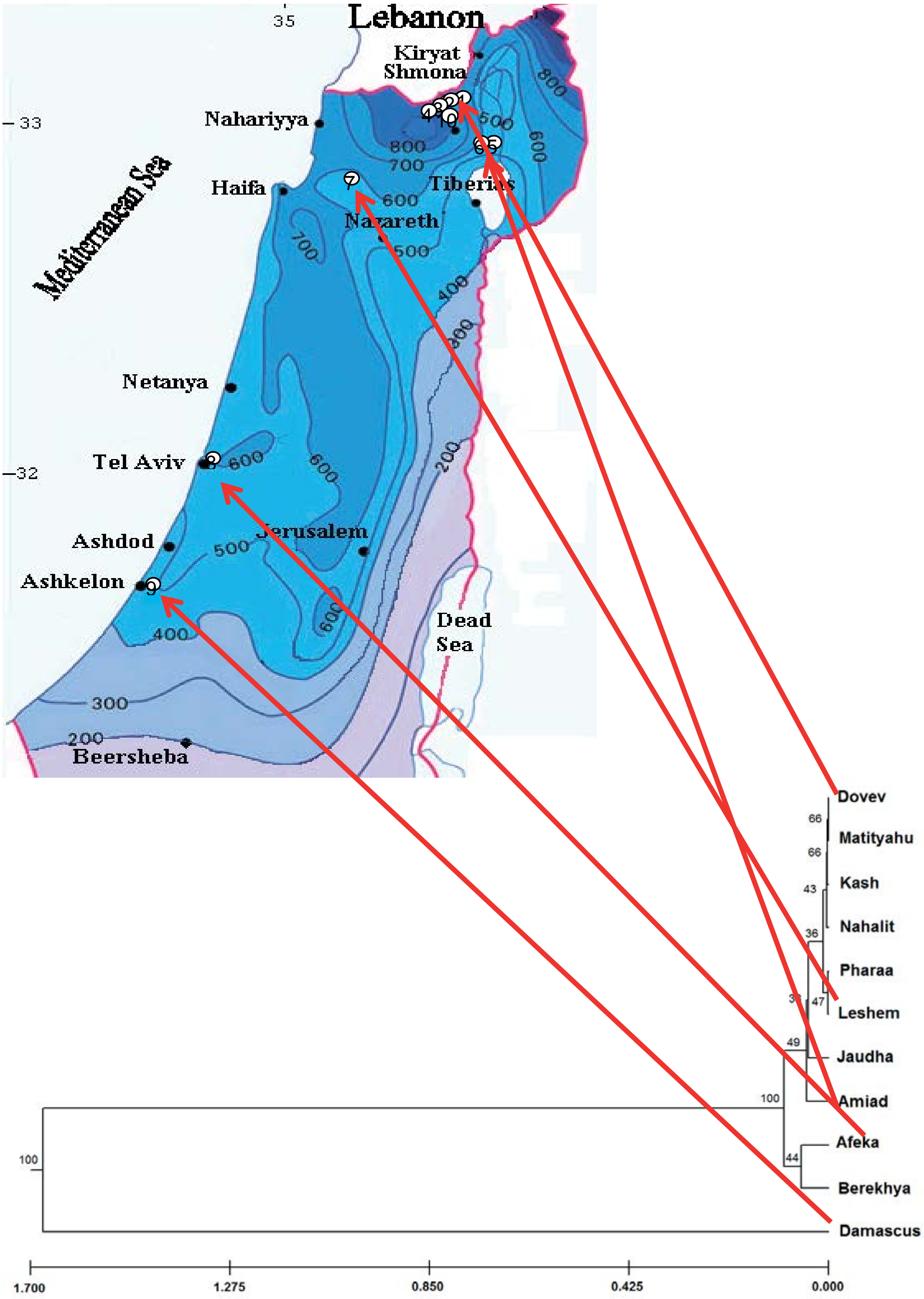

Figure 11: Nei's genetic distance UPGMA topology based on differences in nucleotide sequences of the control region (D-loop) fragment. Bootstrap values (% of 1,000 replicates) are shown above the nodes [3].

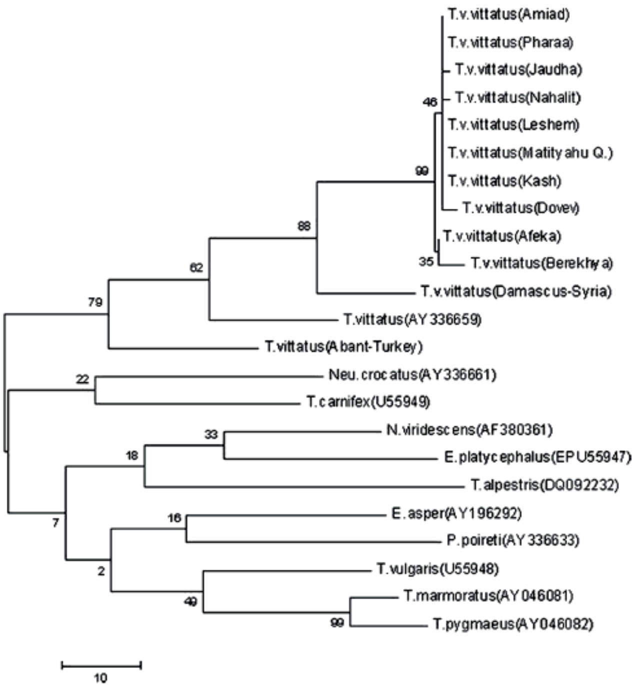

Figure 12: Maximum parsimony tree data of the mitochondrial cytochrome g gene fragment [3] Numerals at each node refer to bootstrap support (%) in 100 replicates. Branch lengths are proportional to the number of changes over the whole sequence. Sources of sequence data from samples other than those obtained in Israel [3] and other countries [47,48].

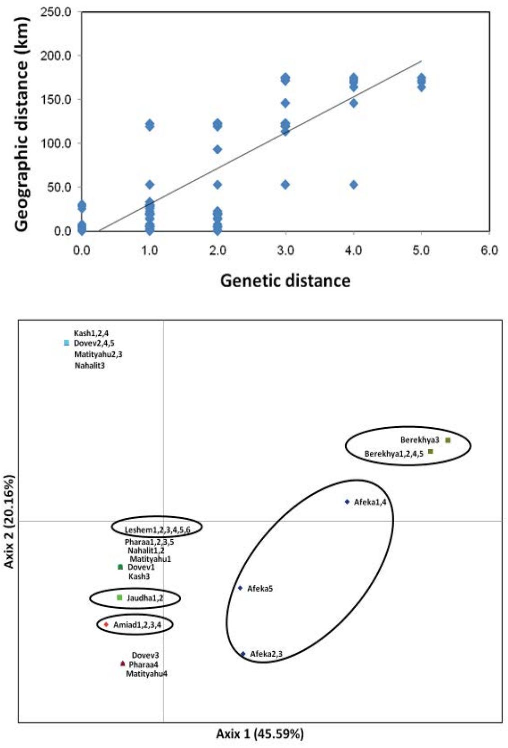

Figure 13: A: Nei's genetic distances based on differences in nucleotide sequences of the control region fragment of *Triturus vittatus vittatus* examined for correlation to geographic distance (km). B: Principal components analysis (PCA) of genetic differences in the control region fragment among 43 individuals from 10 newt populations. The two axes combined accounted for 65.75% of the total genetic variation [51].

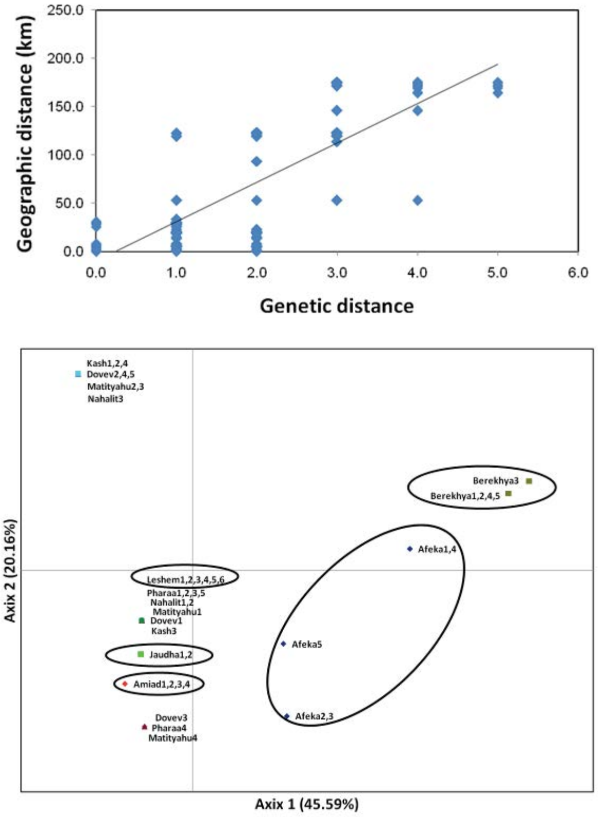

Figure 14: Genetic variation in Triturus vittatus vittatus from different populations at various altitudes and environments, as determined by Amplified Fragment Length Polymorphism (ALFP).

extreme conditions by comparing these characteristics to the various altitudes, habitats and climates in Israel.

Fewer studies on the adaptation of newts *T. v. vittatus* at the southern border of its distribution have been carried out compared to Salamandra infraimmaculata of other Urodela in Israel [39]. The distribution of this species in Israel is much less than newts and does not reach the very extreme conditions like *T. v. vittatus*. *T. v. vittatus* exist in all *S. infraimmaculata* habitats [5,40-42].

The *T. v. vittatus* population in this area is concentrated mainly around rain pools and which are unstable breeding places. *T. v. vittatus* is a relatively small Urodela (Table 2) compared to *S. infraimmaculata*, for example [40,43]. No studies have been carried out on morphological variation among the various population as was done for *S. infraimmaculata* [30]. The genetic consequences of habitat fragmentation are an important component of population extinction risk assessment for threatened and endangered *T. v. vittatus*, similar to what was found in other amphibians in the same area [5,9,10,16,17,39,40,44]. The genetic variation is also described in some Anurans, e.g., tree frog (Hyla savignyi) [45], *Pseudepidalea Viridis* (Syn. *Bufo Viridis*), Spadefoot Toads (*Pelobates syriacus*, Boettger, 1869) [19] and Rana bedreagae [19-22].

In summary, the adaptation of newts (*T. v. vittatus*) to xeric habitats in the proposed model (Figure 15) is based on more than 30 papers (cited here) and unpublished data showing the involvement of ecological ability adaptation of this species under extreme conditions. There is not only a connection between the ecological and biological adaptation of the different parameters, but also between the various biological parameters interacting with one another. However, no significant differences were found in the ecological conditions in the aquatic phase and larvae growth in various habitats [6,7,46] compared to the terrestrial phase of the newts. There are variations in the time of the breeding and spawning periods and larvae growth but not in ecological conditions [8]. Therefore, my hypothesis is that the adaptation and selection among the populations are stronger in the terrestrial phase compared to the aquatic phase in *S. infraimmaculata* [39]. Most of the breeding places of newts were winter ponds, and the larvae growth periods were relatively short [6-10,16,17,31,46-52]. A summary of this paper proposed the suggested model (Figure 15) for understanding the heterogeneity adaptation among *T. v. vittatus* populations on the southern border of its distribution in Israel, different parameters for different biological and ecological aspects are involved. However, greater information on the terrestrial phase will provide us with a better understanding of the adapted of the xeric habitats.

Figure 15: A suggested model for understanding the heterogeneity adaptation of T. v. vittatus on the southern border of its distribution, different parameters for different biological and ecological aspects are involved.

Conclusion

The conclusion to this manuscript, which describes many aspects of the adaptation of *T. v. vittatus* to extreme conditions, is that this sub-species is in danger of annihilation, especially due to its complex life under extreme conditions in habitats at the southern border of its distribution. In order to protect this species, terrestrial and aquatic habitats must be conserved. This paper emphasizes important parameters of *T. v. vittatus* adaptations.

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