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A shift in reptile diversity and abundance over the last 25 years

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Abstract The south-facing slopes in canyons, oriented along an east-west axis north of the equator, are often hotter and drier than north-facing slopes, promoting differences in the biotic and abiotic characteristics of the opposing slopes. We studied how diversity and abundance patterns have changed in Oren stream (Carmel Mountains, Israel) during the last 25 years. We tested whether temperature and habitat preferences of reptiles affected observation frequencies, to assess potential effects of global warming on the reptiles. We compared the results of a 1993–1994 survey in Oren stream to a survey we conducted during 2017–2018, using similar methods, survey area and effort. Species composition and abundance in Oren stream did not significantly change between studies, but the proportion of observations differed significantly across slopes for four out of the six most abundant species. The number of observations increased monotonically with increasing temperatures on the south-facing slope, but decreased on the north-facing slope above a temperature of 22°C. The major biome species inhabit globally was unrelated to the number of observations across slopes or studies, but species inhabiting warmer ranges were more frequently observed in the current survey. Our results suggest that as global temperatures rise, reptile species which can tolerate higher temperatures, and those which can avoid the hottest temperatures of the day, may be able to cope better. These results however may also derive from better detection ability of some species over others between study teams.

Keywords detectability; global warming; north-facing slope; Oren stream; south-facing slope; survey

Introduction

Global warming predicts rising temperatures over the next few decades (IPCC, 2013), and has the dubious honor of being on the list of major species extinction generators (Gibbons et al., 2000; Thomas et al., 2004; Brook, Sodhi and Bradshaw, 2008; Bellard et al., 2012). The impact of global warming on species is predicted to vary geographically, with a greater risk for species living in higher latitudes, and for species which are physiologically more sensitive to changes in temperature (Van Berkum, 1988; Calosi, Bilton and Spicer, 2007; Sunday et al., 2014; Gunderson, Dillon and Stillman, 2017). As a response to global warming, species can shift their range to cooler areas by moving to higher latitudes or altitudes, adapting by adjusting their behavior or physiology, or they may eventually go locally or globally extinct (Thomas and Lennon, 1999; Parmesan and Yohe, 2003; Thomas et al., 2004; Deutsch et al., 2008; Sinervo et al., 2010; Chen et al., 2011; Bellard et al., 2012). Some species, however, such as heat loving species residing in currently relatively cool habitats, may even benefit from global warming, which may provide them with better conditions (Araújo, Thuiller and Pearson, 2006; Deutsch et al., 2008).

Since the 1990s, the mean annual temperature in Israel increased by 1.1 degrees, mainly as a result of an increase in temperatures of cold years (IMS, 2015a), coinciding with global and regional patterns (Pan, 2013). By the end of the 21st century the mean annual temperatures in Israel are predicted to rise by 1.5°C to 4°C (IMS, 2015b). Research into the impacts of warming on species is rapidly accumulating (e.g. Rodriguez-Trellis and Rodriguez, 1998; Easterling et al., 2000; Thomas et al., 2004; Sinervo et al., 2010) and most projections are grim (e.g. Sinervo et al., 2010; Levy et al., 2015; Gunderson et al., 2017; Telemeco et al., 2017).

The south-facing slopes in E-W oriented canyons north of the equator often receive higher solar radiation than do the opposite, north-facing slopes (Pavlícek et al., 2003). Although the geology, soils and topography are often similar among slopes, the south facing slope is often hotter and drier compared to the cooler and more humid north-facing slopes (in Mediterranean biomes), creating different habitats across slopes, which can be only about 100 m apart (Kutiel and Lavee, 1999; Pavlícek et al., 2003). Nevo (2012) proposed that canyons with contrasting habitats may serve as natural models for testing the effects of global warming. This claim followed a study which found that *Drosophila* migrated 10-fold more from the hotter south-facing slope of a canyon in Israel to the cooler north-facing slope (Pavlíček et al., 2008). In the Mediterranean part of Israel species are often near the southern edge of their distribution (Tchernov and Yom-Tov, 1988), and hence are more likely to favour cooler environments. Conversely, desert species, which are usually nearer the northern edge of their distribution (Tchernov and Yom-Tov, 1988; see also ranges in Roll et al., 2017) may prefer the hotter environments (Nevo, 1995). Nevo (2012) postulated that increasing global temperatures will drive migration from the south-facing slope to the north-facing slope and the local extinction of taxa with more northerly origins on both slopes.

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Between 1993–1994, Nevo, Raz and Beiles (1996) surveyed the reptiles of lower Oren stream in the Carmel Mountains, Israel (32.71N, 34.98E). They found 307 individuals belonging to 13 species from the two slopes and the valley bottom (Nevo et al., 1996). We identified a rare opportunity to study whether diversity and abundance patterns of lizard species have changed during the last 25 years, potentially as a result of rising temperatures. We examined this by repeating the survey done by Nevo et al. (1996) 23–24 years later, comparing the findings of the two studies, and analyzing whether rising temperatures may be the driver behind the variation in the diversity and abundance patterns between studies.

We hypothesized that in the 2017–2018 survey we will find fewer reptiles in the hotter, south-facing slope compared to the 1993–1994 survey. Furthermore, we expected that there will be a shift of abundance towards the cooler north-facing slope, as reptiles will avoid the hotter and drier south-facing slope. We also hypothesized that temperature will differentially affect the number of observations on the opposing slopes. We reasoned that on the more shaded north-facing slope, reptiles may require higher ambient temperatures to reach operating temperatures (Webb and Shine, 1998), and will also be able to remain active for longer in warm days. Thus we expected that abundance will increase with temperature faster on the north-facing slope compared to the south-facing slope.

We further hypothesized that predominantly Mediterranean-biome species will prefer the cooler, more humid north-facing slope. Species ranging widely in both Mediterranean and desert biomes, however, will prefer the hotter, drier, south-facing slope. Following the same logic, we predicted that species for which Oren stream is nearer the southern edge of their global distribution range, will prefer the north-facing slope, while species nearer the northern edge of their range will prefer the south-facing slope. We predicted that species which in Oren stream are at the center of their global distribution range, will occupy an intermediate position between the two extremes. Finally, we hypothesized that, because of warming, hot-adapted species will be more frequently observed in the 2017–2018 compared to the 1993–1994 survey.

Materials and methods

Field survey and data collection

Oren stream is an E-W oriented canyon in the Carmel Mountain range located along the NW coast of Israel, and is situated in the Mediterranean biome, with an average annual precipitation of ~550 mm (Malkinson and Wittenberg, 2007; Fig. 1). Oren stream was formed around 3–5 Mya. Its substrate consists primarily of carbonate rocks, mainly limestone, dolomite, chalk and marl, covered by terra rossa (Malkinson and Wittenberg, 2007). The south-facing slope receives 300% more solar radiation (Kutiel and Sher, 1991), thus the vegetation contrasts across slopes, from 35% to 150% cover of vegetation layers on the north- and south-facing slopes respectively (Nevo et al., 1998; Fig. 1). The vegetation of the north-facing slope is a typical Mediterranean maquis comprised of oak (*Quercus*) and

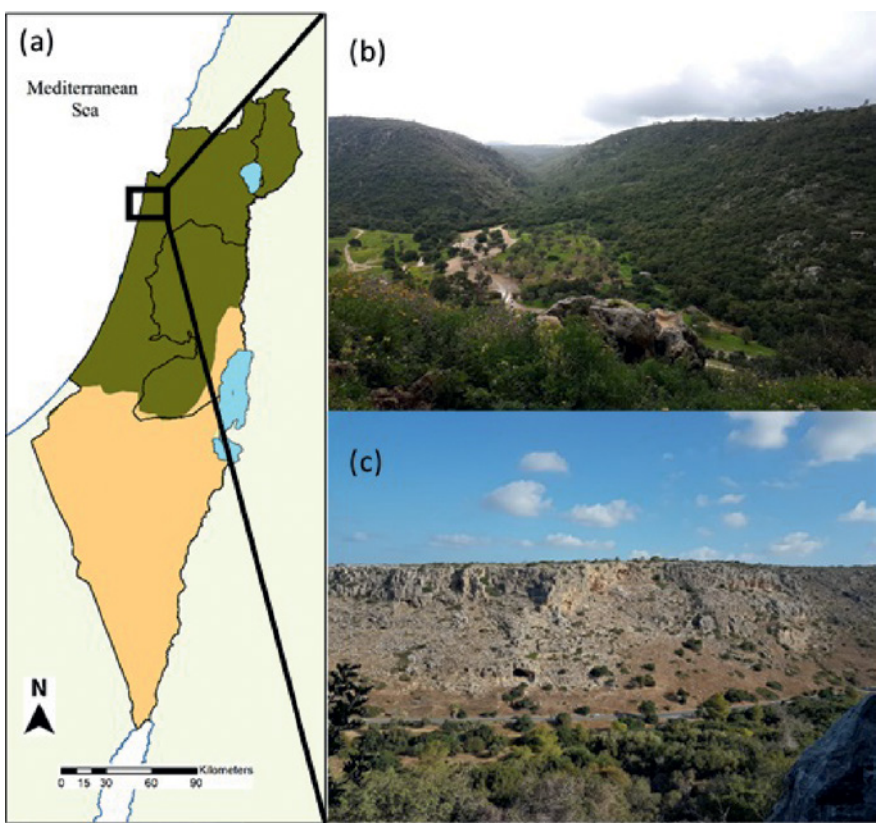

Figure 1 The study site. (a) The box indicates the location of lower Oren stream, Carmel Mountains, Israel. Green represents the Mediterranean biome and yellow the desert biome. (b) The north-facing slope (as seen from the south-facing slope). The vegetation of the north-facing slope is a typical Mediterranean maquis comprised of oaks and carob trees and tall Pistacia shrubs. (c) The south-facing slope (as seen from the north-facing slope; both photos taken by RS). The distance between the two slopes is ~400 meters. Map based on WWF biomes.

carob (*Ceratonia silique*) trees and tall *Pistacia* shrubs, while that of the south-facing slope is dominated by annuals dotted with scattered carob trees, low *Pistacia* shrubs and low perennial bushes such as *Pennisetum ciliare* and *Stachys palaestina* (Nevo, 1995; Nevo et al., 1998; Nevo et al., 1999; Fig. 1).

To make our study as closely comparable to the one conducted by Nevo et al. (1996) we followed their survey protocol closely in our 2017–2018 survey. To do so we consulted the authors of the 1993–1994 survey (Eviatar Nevo and Shmuel Raz), in person, to obtain a fuller, detailed description of their methods. Thus we conducted a monthly field survey in lower Oren stream, under permits from the Israeli Nature and Parks Authorities (permit #2017/41741 and #2016/41482). We searched visually for reptile species between 08:00–12:00, spending approximately two hours in each slope (always starting on the south-facing slope). The 1993–1994 survey (Nevo et al., 1996) comprised of 20 excursions, of which in five, no reptiles were recorded (in December 1993, January and February 1994 and twice on September 1994). Our survey comprised of 14 excursions, of which no reptiles were observed in January 2018 (Table A1 in the Appendix). Unlike Nevo et al. (1996) we did not invest much search effort in the valley bottom. For logistical reasons we sampled once (in October) during 2016, twice during June 2017, and surveyed in both the beginning and end of October 2017, but not in September 2017 (Table A1 in the Appendix). Nevo et al. (1996) on the other hand, sampled three times during November 1993, May 1994 and June 1994, and twice during March, July and September 1994 (Table A1 in the Appendix).

We obtained minimum and maximum temperatures for each day in both the 1993–1994 and 2017–2018 surveys from the Meteorological Service of Israel archives (https://ims.data.gov.il/ims/1), and calculated the mid-point range for each survey day (Table A1 in the Appendix). The closest meteorological station to Oren stream, which collected temperature data in both periods, is in Gal'ed (32.56N, 35.07E; altitude:180 m) about 20 km from Oren stream. To test whether the temperature collected from the meteorological station represents the actual temperature in the stream we performed paired *t*-test between mean air temperatures we measured in the field for 12 of our sampling dates, in which we measured air temperatures (on both slopes), against the mid-point range temperature recorded at the weather station in the same dates. To test whether the temperatures increased between studies we collected the daily minimum and maximum temperatures from the Gal'ed weather station for each day between 1 January and 31 December in 1994 and 2017, and calculated the midpoint range for each day. We then averaged the minimum, maximum and mid-point range temperature for each month, and performed paired *t*-tests between monthly temperatures between years.

We noted whether Oren stream is close to the northern, centre or southern edge of species global distributions based on distribution maps from Roll et al. (2017). We likewise determined whether its distribution is mostly restricted to the Mediterranean biome, or whether large parts occur both in Mediterranean and desert habitats ("wide"). We calculated the mean annual temperature across each species distribution (Roll et al., 2017) based on data from WorldClim 2 (Fick and Hijmans, 2017). Data on biome, distribution edge and mean annual temperatures are presented in Table A2 in the Appendix.

Statistical analysis

All statistical analyses were conducted with R (R Core Team, 2012). We tested whether the species abundance of the six most abundant species (each comprising at least 5% of the total number of observations) changed between studies, and slopes. We performed a Pearson's Chi-squared test of independence on the total number of observations of each species in each study to test whether abundance changed between studies. In order to test whether the proportion of observations of each species between slopes differ between studies, we performed two-tailed Fisher's exact tests on each of the six most abundant species separately.

To test the relationship between the temperature and abundance, we combined the data in Table 2 of Nevo et al. (1996) with our observation data for each slope (Table A1 in the Appendix). We used mixed effects generalized linear model with Poisson distribution (with log link function) implemented in the 'lme4' R package (Bates, Maechler and Bolker, 2012) with slope and mid-point range temperatures and their interaction (to test whether temperature has a different effect on the number of observations in each slope) as fixed effects and the survey as a random effect. The number of observations was the response. We also tested the possibility of a quadratic relationship between number of observations and temperature, because reptiles are known to have optimal performance temperatures, above and below which performance and activity decrease (Huey and Stevenson, 1979). Upon observing the scatterplot of number of observations and temperatures we identified an outlier (Fig. A1 in the Appendix) with many observations (27 individuals) at a low (13.4°C) temperature, in 23 March 1994. We excluded this datum but also ran a sensitivity analysis including it. In order to obtain an informative intercept (no reptiles are active at 0°C and Oren stream never gets this cold during daytime) we subtracted the lowest temperature in the dataset (12.5°C) from all temperatures, to rescale the intercept at the coldest value (Meiri, Simberloff and Dayan, 2011).

To test whether species which occupy warmer regions were observed more frequently on the south-facing slope we ran a multiple regression on the number of observations per species on the south-facing slope as a function of the mean annual temperature across their distributions, and the number of observations on the north-facing slope. We $\log_{10}$-transformed the number of observations (on both slopes) to reduce heteroscedasticity and improve normality of the residuals.

To examine on which slope species are more dominant, we calculated a Gibbons and Lovich two-step ratio (Smith, 1999) for the number of observations of each species across surveys (see supporting information Table A3 in the Appendix for details). To test whether species inhabiting

warmer regions became more common in 2017–2018 compared to 1993–1994, we regressed this ratio on the mean annual temperature across species' distributions.

To test whether the number of observations of species, which distribution is near its southern or northern edge, and whether the biome to which they are associated within their distribution differs between slopes or surveys, we performed two-way ANOVA tests. We used the sum of observations of each species across surveys or slopes as the response, and used four combinations of the predictors: slope (south-facing/north-facing), survey (1993–1994/2017–2018), biome (Mediterranean/wide) and distribution edge (close to northern edge/close to southern edge/center) with an interaction between them. We $\log_{10}$ transformed the number of observations to reduce heteroscedasticity and improve normality of the residuals.

Results

There was no significant difference between the minimum (1994 (mean ± SE) = 15.1 ± 1.5, 2017 (mean ± SE) = 16.2 ± 1.5, $t = 2.20$, $P = 0.07$), maximum (1994 (mean ± SE) = 25.1 ± 1.9, 2017 (mean ± SE) = 25.5 ± 1.7, $t = 2.20$, $P = 0.61$) and mid-point temperatures (1994 (mean ± SE) = 20.1 ± 1.7, 2017 (mean ± SE) = 20.8 ± 1.6, $t = 2.2$, $P = 0.25$) in Oren stream between the 1993–1994 and 2017–2018 surveys. Mean annual minimum temperatures, however, rose between 1993 and 2017 (slope = 0.10 ± 0.03 degrees per year; intercept = –188.59 ± 63.87, $t = 3.20$, $P < 0.005$, $r^2 = 0.35$, $n = 21$), but mean annual maximum temperatures did not (slope = 0.04 ± 0.03, intercept = -63.30 ± 64.98, $t = 1.36$, $P = 0.19$, $r^2 = 0.09$, $n = 21$; Fig. A2 in the Appendix). The 1993–1994 survey recorded 247 individuals belonging to 12 species (Table 1). Of these 102 individuals belonging to 9 species were on the north-facing slope and 145 individuals belonging to 12 species were on the south-facing slope. In the 2017–2018 survey we recorded 311 specimens belonging to 13 species, of which 132 individuals belonging to 10 species were on the north-facing slope and 179 individuals belonging to 9 species were on the south-facing slope (Table 1).

Both in the 1993–1994 survey and the 2017–2018 one, the most abundant reptile species were *Ptyodactylus guttatus*, *Phoenicolacerta laevis* and *Stellagama stellio*, comprising 10–46% of the total relative abundance (Table A3 in the Appendix). The 5th most abundant species was *Ablepharus rueppellii* in both studies. The 4th most abundant was *Heremites vittatus* in 1993–1994, but *Chalcides ocellatus* in 2017–2018 (Table 1). The abundance of the six most abundant species in Oren stream differed significantly between surveys (1993–1994 or 2017–2018; $\chi^2 = 92.53$, df = 5, $p < 0.0001$), with more observations in the 2017–2018 survey. The relative abundance of *P. guttatus* increased by 78%, while that of *P. laevis* and *S. stellio* decreased by 6% and 68%, respectively, between surveys (Table A3 in the Appendix). In 2017–2018 these three species remained more abundant on the slope on which they were most abundant in 1993–1994, i.e. *P. guttatus* and *S. stellio* were more abundant on the south-facing slope and *P. laevis* was more abundant on the north-facing slope in both studies (Table A3 in the Appendix). *H. vittatus* and *C. ocellatus* were also most abundant on the south-facing slope in both surveys, but *A. ruepelli* was more abundant on the north-facing slope in 1993–1994, and on the south-facing slope in 2017–2018 (Table A3 in the Appendix). The proportion of species across slopes differed significantly between surveys for four out of the six most abundant species in Oren stream (but not for *A. ruepelli* and *C. ocellatus*; Table 1). The number of observations of *P. laevis* and *P. guttatus* on the south-facing slope significantly increased in 2017–2018 compared to 1993–1994, while that of *H. vittatus* and *S. stellio* decreased (Table 1). On the north-facing slope, however, the number of observations of *H. vittatus*, *P. laevis* and *S. stellio* significantly decreased, while that of *P. guttatus* increased by 100% across surveys (Table 1). Although the number of observations of *A. ruepelli* and *C. ocellatus* on the south-facing slope increased in 2017–2018 compared to 1993–1994, their number of observations remained the same on the north-facing slope (Table 1).

The temperatures recorded from the weather station were not significantly different from the air temperatures

Table 1. Summary of reptile species observations from the south and north-facing slopes of Oren stream, Carmel Mountains, Israel, in the 1993–1994 survey by Nevo et al. (1996), and our 2017–2018 survey. Two tailed Fisher's exact test results of number of observations for the five most abundant species from the south and north-facing slopes in the 1993–1994 study by Nevo et al. (1996) and our current survey. Significant results ($P < 0.05$) indicate that proportions of observations across slopes are not the same between studies.

Year	1993–1994			2017–2018			Fisher's exact test
Species / Slope	South-facing	North-facing	Total	South-facing	North-facing	Total	*P*
Ablepharus ruepelli	2	6	8	10	6	16	0.19
Chalcides guentheri	1	0	1	1	0	1	NA
Chalcides ocellatus	3	1	4	17	1	18	0.34
Chamaeleo chamaeleon	1	1	2	0	1	1	NA
Hemidactylus turcicus	1	1	2	0	2	2	NA
Heremites vittatus	19	10	29	15	0	15	<0.01
Mediodactylus orientalis	0	0	0	0	4	4	NA
Phoenicolacerta laevis	6	64	70	25	43	68	<0.0001
Platyceps collaris	3	1	4	0	2	2	NA
Pseodopus apodus	3	0	3	1	0	1	NA
Ptyodactylus guttatus	29	0	29	81	56	137	<0.0001
Stellagama stellio	70	17	87	28	16	44	0.05
Testudo graeca	7	1	8	1	1	2	NA
SUM	145	102	247	179	132	311	NA

we recorded in the field during 12 excursions (paired *t*-test: field temperature (mean ± SE) = 24.8 ± 0.8, weather station (mean ± SE) = 22.9 ± 1.2, t = 2.20, P = 0.08). Thus the temperatures collected from the weather station represent the actual temperatures in Oren stream well. Abundance increased linearly with temperature on the south-facing slope (Abundance = 1.89 + 3.30 × [temperature in °C − 12.5]; Fig. 2). Abundance showed a hump-shaped relationship with temperature on the north-facing slope. (Abundance = 1.48 + 2.05 × [temperature in °C − 12.5] − 2.50 × [temperature in °C − 12.5]^2; Fig. 2) but only when we omitted the high-abundance/low temperature outlier from 23.03.1994 (13.4 °C and 27 specimens observed; Fig. A1 in the Appendix). Abundance on the north facing slope increases to about 22°C and then starts to decrease as temperatures increase further. With this outlier, there was a significant relationship between the number of observations and mid-point range temperatures on the south-facing slope only (Fig. A1 in the Appendix). There was a significant interaction between temperatures and slope, meaning that the effect of temperature on number of observations was stronger by 1.9 ± 0.9 Individuals per degree (χ^2_3 = 15.62, p < 0.005) on the south-facing slope.

There was no relationship between the number of observations of species on the south-facing slope and the mean annual temperature in their distribution (intercept = –0.28 ± 0.83, slope = 0.04 ± 0.05, t = 0.80, P = 0.44), meaning that warm adapted species are not more abundant on the south-facing slope than relatively cold-adapted species. There was a statistically significant positive relationship between the ratio of observation numbers per species across surveys and the mean annual temperature of each species distribution (intercept = –9.66 ± 2.51, slope = 0.55 ± 0.14, t = 3.86, P = 0.003, r^2 = 0.60; Fig. 3). This means that species which occur in warmer regions were observed more frequently in the 2017–2018 survey, while species which occur in cooler regions (mean temperature less than ~18°C) were observed less frequently (Fig. 3).

Species from Mediterranean or both Mediterranean and arid biomes did not have a preference for a certain slope (interaction term not significant), nor did their frequency change between surveys. Thus species from different biomes were observed on both slopes and in both surveys at similar rates. There was also a similar number of observations of species close to their south, centre or north edge of their distribution across slopes and studies. In general, however, we observed significantly more individuals belonging to species which are close to the northern edge of their distribution (e.g. *Ptyodacytylus guttatus*; mean ± SE = 4.2 ± 1.0) compared to species which are at the centre (mean ± SE = 1.84 ± 0.46, t = –2.27, P = 0.03) or south edge of their distribution (mean ± SE = 1.56 ± 0.51, t = –2.47, P = 0.02, n = 26, e.g. *Stellagama stellio* and *Phoenicolacerta laevis,* respectively).

Discussion

We hypothesized that reptile diversity and abundance in Oren stream changed between slopes during the last 25 years, as a consequence of rising temperatures. Most of our predictions were refuted. We found no evidence for species extinction or for major composition shifts in the stream during the last 25 years, as all species were observed in both surveys except *Mediodactylus orientalis*, that was observed only in the 2017–2018 survey. Furthermore, we observed more reptiles in 2017–2018 than were observed in the 1993–1994 survey, strengthening this claim. We also found little evidence that the overall abundance of species changed between studies. The three most abundant species in the stream in both studies were the same ones, and they remained most abundant on the same slopes between studies. The proportions of some of the species across slopes,

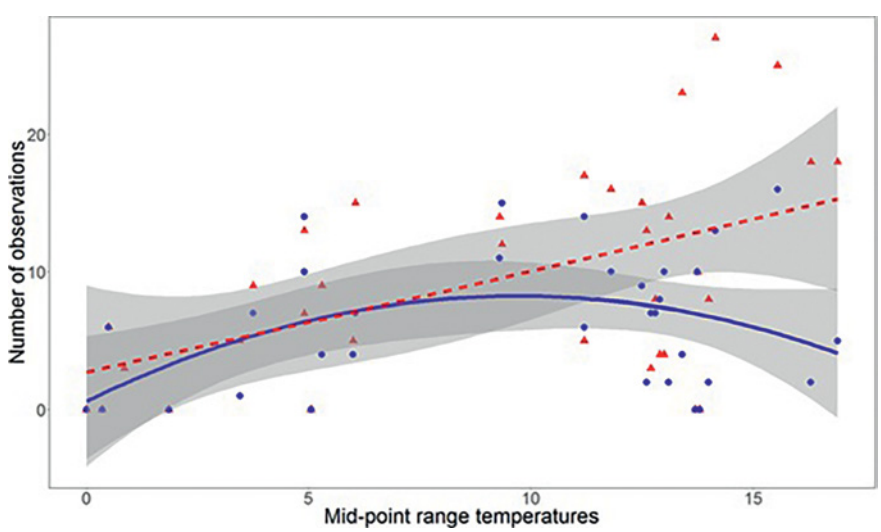

Figure 2. Relationship between the number of observations per survey date (1993–1994 and 2017–2018, pooled), against midpoint range temperature, calculated from min and max temperatures collected from the Meteorological Service of Israel archive. The outlier from 23.03.1994 was omitted from the dataset (see Fig. A1, top-left, in the Appendix). Red triangles and dashed line represents observations from the south–facing slope (Abundance = 1.89 + 3.30 × [temperature in °C − 12.5]) and the blue circles and continuous line represent observations from the north-facing slope (Abundance = 1.48 + 2.05 × [temperature in °C − 12.5] − 2.50 × [temperature in °C − 12.5]^2;). We centered the temperature data on the origin by reducing the lowest temperature in the dataset (12.5°C) from all temperatures in order to get a biologically informative intercept. For results including the 1993–1994 outlier, see Fig. A1 in the Appendix.

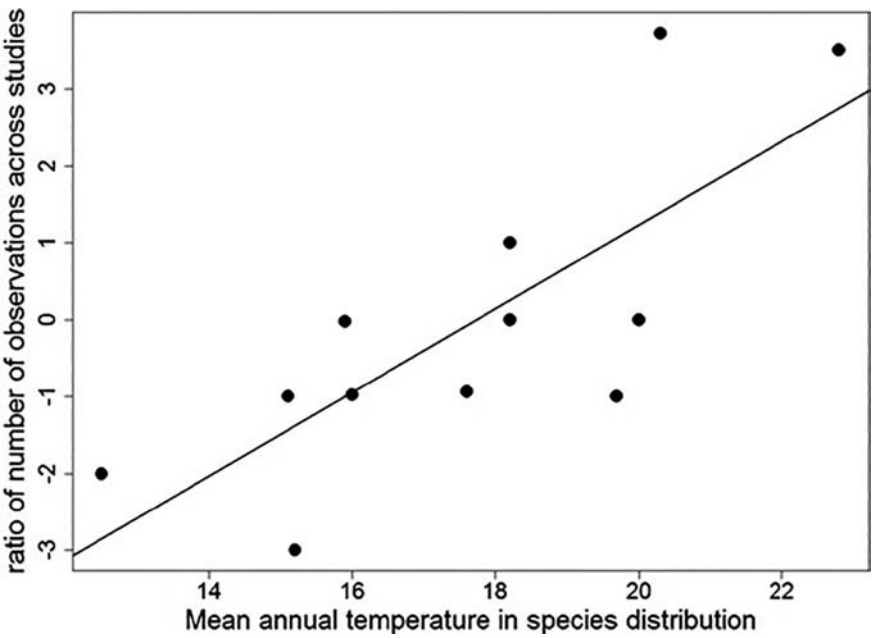

Figure 3. Relationship between the Gibbons and Lovich two-step ratio between the number of observations of each species across surveys and the mean annual temperature in each species distribution (intercept = –9.66 ± 2.51, slope = 0.55 ± 0.14, t = 3.86, P = 0.003, R^2 = 0.60). Thus, species which occur in warmer regions were observed more frequently in the 2017–2018 survey, while species which occur in cooler regions were observed less frequently.

however, did change between studies, but not always in the anticipated direction. In the 2017–2018 survey, we observed more individuals on the slope on which they were less common in the 1993–1994 survey (although this did not shift their dominance on the same slope across studies, see above). This means that the differences between the proportions of species across slopes decreased, suggesting either an inter-slope abundance shift or more equal detection ability of species across slopes by our group compared to the previous group. Not only did species from the south-facing slope not shift to the cooler north-facing slope, there were more observations on the south-facing slope in both surveys in general, similarly to what Kutiel and Lavee (1999) found for Oren stream plants. There was also an increase in the number of observations of some species (*P. laevis* and *P. guttatus*) on the south-facing slope across surveys. Furthermore, while on the north-facing slope the number of species detected decreased across surveys, on the south-facing slope it increased.

Temperature affected the number of observations on both slopes, as predicted, and its effect differed across slopes, but not in the way we anticipated. We predicted that the number of observations will increase with temperature faster on the cooler, north-facing slope. Our results, surprisingly, showed the opposite. Up until a temperature of 22°C the number of observations rises in a similar rate with temperature on both slopes. Above this threshold, however, the number of observations continues to rise linearly with temperature in the south-facing slope, but declines in the north-facing slope. This result may explain why our prediction, that species will migrate or disappear from the hotter and drier south-facing slope and will become more abundant on the north-facing slope, was refuted. It seems that the reptiles on the south-facing slope can tolerate, and even prefer, higher temperatures compared to reptiles on the north-facing slope, by either local genetic adaptation or phenotypic plasticity. Further research into the thermal ecology of the populations across species and slopes is needed to better understand this result.

Our results also refute our prediction that species from regions in which the mean annual temperatures are higher will prefer the south-facing slope. They do, however, support the prediction that species from hotter regions were more abundant in the 2017–2018 survey, perhaps because of global warming. Detailed climate assessments in Israel found that temperatures over the last decades rose (by 1.1°C, on average), mainly as a result of an increase in minimum temperatures (IMS, 2015a). We found similar results testing the minimum and maximum mean annual temperatures in the Gal'ed weather station between 1993–2017 (Fig. A2 in the Appendix). Thus the shift in abundance and species composition which we detected in this study may be the result of rising temperatures. Should temperatures continue to rise, it is likely that the only species which will remain in Oren stream (and elsewhere) will be the more hot-adapted ones.

Whether the distribution of species was close to the southern or northern edge, or whether the species mainly occur in a mainly Mediterranean or in both a Mediterranean and desert biomes, did not affect the number of observations. This refutes our prediction and suggests that, at least for a local-scale study such as ours, this broad categorization of species cannot predict which species are more likely to disappear due to global warming. It may also suggest that microhabitat differences on a relatively small scale, such as between two slopes of a canyon, are not strong enough to resemble and project on differences on a global scale, such as between different biomes.

We tried to perform our survey as similar to the 1993–1994 survey as possible. There may, however, still have

been differences in the detection ability of certain species between study teams. In the 2017–2018 survey, for example, we detected the gecko *Mediodactylus orientalis*, which was not observed in the 1993–1994 survey. It is unlikely that this species was absent from Oren stream in 1993–1994, as it was known from the region at the time (records from the Steinhardt Museum of Natural History). Thus we assume that this cryptic gecko was observed in our survey because we have previous experience locating it (e.g. Slavenko et al., 2015; Schwarz et al., 2016; Itescu et al., 2017). As long as surveys such as this are not performed by the same team members, differences in the detectability of the reptiles are likely to have an effect on the results (Mazerolle et al., 2007; Lardner et al., 2015). Thus we cannot rule out that at least some of the results of this study are affected by the ability of certain team members to better locate certain reptile species.

To conclude, according to the results of this study, the reptile fauna in lower Oren stream did not go through major species composition shifts during the last 25 years, but there was a shift of abundance of some of the species across slopes. The number of observations was correlated with the temperatures, and more reptiles inhabiting generally hotter areas were observed in the present survey. The results of this study may suggest that over the next decades, as the temperatures are predicted to rise due to global warming, some reptile species may be able to cope with a hotter climate better.

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References

Araújo, M.B., Thuiller, W., Pearson, R.G. (2006). Climate warming and the decline of amphibians and reptiles in Europe. *J. Biogeogr.* 33, pp. 1712–1728.

Bates, D.M., Maechler, M., Bolker, B. (2012). lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15, pp. 365–377.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J. (2008). Synergies among extinction drivers under global change. *Trends Ecol. Evol.* 23, pp. 453–460.

Calosi, P., Bilton, D.T., Spicer, J.I. (2007). Thermal tolerance, acclimatory capacity and vulnerability to global climate change. *Biol. Lett.* 4, pp. 99–102.

Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science* 333, pp. 1024–1026.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad..Sci.-Biol.* 105, pp. 6668–6672.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O. (2000). Climate extremes: observations, modeling, and impacts. *Science* 289, pp. 2068–2074.

Fick, S.E., Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, pp. 4302–4315.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., Winne, C.T. (2000). The global decline of reptiles, Déjà Vu Amphibians: reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. *AIBS Bulletin* 50, pp. 653–666.

Gunderson, A.R., Dillon, M.E., Stillman, J.H. (2017). Estimating the benefits of plasticity in ectotherm heat tolerance under natural thermal variability. *Funct. Ecol.* 31, pp. 1529–1539.

Huey, R.B., Stevenson, R.D. (1979). Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* 19, pp. 357–366.

IMS (2015a). [שינויים אקלימיים בישראל, ממצאי השירות המטאורולוגי *Climate Changes in Israel, the Meteorological Service Report]*. Israel: The Meteorological service of Israel.

IMS (2015b). מסקנות הדו"ח החמישי של האי.פי.סי.סי לגבי שינויי האקלים הצפויים בעולם ובישראל [*Conclusions of the IPCC Fifth Report about the Anticipated Climate Changes in the World and in Israel]*. Israel: The Meteorological service of Israel.

IPCC (2013). Climate Change 2013: The Physical Science Basis. In: T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung… , P.M. Midgley, eds., *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge/New York: Cambridge University Press.

Itescu, Y., Schwarz, R., Meiri, S., Pafilis, P. (2017). Intraspecific competition, not predation, drives lizard tail loss on islands. *J. Anim. Ecol.* 86, pp. 66–74.

Kutiel, H., Sher, G. (1991). Mapping of solar radiation percentage calculated in relation to a horizontal plane at Nahal Oren. Dissertation, Geography Department, University of Haifa (in Hebrew).

Kutiel, P., Lavee, H. (1999). Effect of slope aspect on soil and vegetation properties along an aridity transect. *Isr. J. Plant Sci.* 47, pp. 169–178.

Lardner, B., Rodda, G.H., Adams, A.A.Y., Savidge, J.A., Reed, R.N. (2015). Detection rates of geckos in visual surveys: turning confounding variables into useful knowledge. *J. Herpetol.* 49, pp. 522–532.

Levy, O., Buckley, L.B., Keitt, T.H., Smith, C.D., Boateng, K.O., Kumar, D.S., Angilletta, M.J. (2015). Resolving the life cycle alters expected impacts of climate change. *P. R. Soc. B.* 282, pp. 20150837.

Malkinson, D., Wittenberg, L. (2007). Scaling the effects of riparian vegetation on cross-sectional characteristics of ephemeral mountain streams-a case study of Nahal Oren, Mt. Carmel, Israel. *Catena* 69, pp. 103–110.

Mazerolle, M.J., Bailey, L.L., Kendall, W.L., Andrew Royle, J., Converse, S.J., Nichols, J.D. (2007). Making great leaps forward: accounting for detectability in herpetological field studies. *J. Herpetol.* 41, pp. 672–689.

Meiri, S., Simberloff, D., Dayan, T. (2011). Community-wide character displacement in the presence of clines: a test of Holarctic weasel guilds. *J. Anim. Ecol.* 80, pp. 824–834.

Nevo, E. (1995). Asian, African and European biota meet at 'Evolution Canyon', Israel: local tests of global biodiversity and genetic diversity patterns. *P. Roy. Soc. London B* 262, pp. 149–155.

Nevo, E. (2012). "Evolution Canyon," a potential microscale monitor of global warming across life. *Proc. Natl. Acad. Sci.-Biol.* 109, pp. 2960–2965.

Nevo, E., Raz, S., Beiles, A. (1996). Biodiversity of reptiles at "Evolution Canyon", Lower Nahal Oren, Mout Carmel, Israel. *Isr. J. Zool.* 42, pp. 395–402.

Nevo, E., Fragman, O., Dafni, A., Beiles, A. (1999). Biodiversity and interslope divergence of vascular plants caused by microclimatic differences at "Evolution Canyon", Lower Nahal Oren, Mount Carmel, Israel. *Isr. J. Plant Sci.* 47, pp. 49–59.

Nevo, E., Travleev, A.P., Belova, N.A., Tsatskin, A., Pavlíček, T., Kulik, A.F., Tsvetkova, N.N., Yemshanov, D.C. (1998). Edaphic interslope and valley bottom differences at "Evolution Canyon", Lower Nahal Oren, Mount Carmel, Israel. *Catena* 33, pp. 241–254.

Pan, Y. (2013). Mediterranean hydrological change projections for the 21st century assessed from CMIP5 simulations. MSc. Thesis, University of Maryland.

Parmesan, C., Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, p. 37.

Pavlíček, T., Frenkel, Z., Korol, A.B., Beiles, A., Nevo, E. (2008). Drosophila at the" Evolution Canyon" microsite, Mt. Carmel, Israel: selection overrules migration. *Isr. J. Ecol. Evol.* 54, pp. 165–180.

Pavlícek, T., Sharon, D., Kravchenko, V., Saaroni, H., Nevo, E. (2003). Microclimatic interslope differences underlying biodiversity contrasts in "Evolution Canyon", Mt. Carmel, Israel. *Isr. J. Earth Sci*. 52, pp. 1–9.

R Core Team (2012). *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.* Vienna, Austria.

Rodriguez-Trellis, F., Rodriguez, M.A. (1998). Rapid microevolution and loss of chromosomal diversity in Drosophila in response to climate warming. *Evol. Ecol.* 12, pp. 829–838.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G.R., Dabool, L., Das, I., Doan, T.M., Grismer, L.L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., Lewin, A., Martins, M., Maza, E., Meirte, D., Nagy, Z.T., de C. Nogueira, C., Pauwels, O.S.G., Pincheira-Donoso, D., Powney, G.D., Sindaco, R., Tallowin, O.J.S., Torres-Carvajal, O., Trape, J.-F., Vidan, E., Uetz, P., Wagner, P., Wang, Y., Orme, C.D.L., Grenyer, R., Meiri, S. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nat. Ecol. Evol.* 1, p. 1677–1682.

Schwarz, R., Gavriilidi, I.A., Itescu, Y., Jamison, S., Sagonas, K., Meiri, S., Pafilis, P. (2016). *Mediodactylus kotschyi* in the Peloponnese peninsula, Greece: distribution and habitat. *Acta Herpetol.* 11, pp. 179–187.

Sinervo, B., Mendez-De-La-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Rafael Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda, P.V., Duarte Rocha, C.F., Ibargüengoytía, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., Sites Jr. J.W. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328, pp. 894–899.

Slavenko, A., Itescu, Y., Foufopoulos, J., Pafilis, P., Meiri, S. (2015). Clutch size variability in an ostensibly fix-clutched lizard: effects of insularity on a Mediterranean gecko. *Evol. Biol*. 42, pp. 129–136.

Smith, R.J. (1999). Statistics of sexual size dimorphism. *J. Hum. Evol*. 36, pp. 423–458.

Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., Huey, R.B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl. Acad. Sci.-Biol.* 201316145.

Tchernov, E., Yom-Tov, Y. (1988). *Zoogeography of Israel. The Zoogeography of Israel, the Distribution and Abundance at a Zoogeographical Crossroad*. Dordrecht: Dr W. Junk Publishers.

Telemeco, R.S., Fletcher, B., Levy, O., Riley, A., Rodriguez-Sanchez, Y., Smith, C., Teague, C., Waters, A., Angilletta, M.J., Buckley, L.B. (2017). Lizards fail to plastically adjust nesting behavior or thermal tolerance as needed to buffer populations from climate warming. *Glob. Change Biol.* 23, pp. 1075–1084.

Thomas, C.D., Lennon, J.J. (1999). Birds extend their ranges northwards. *Nature* 399, p. 213.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N.. de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L., Williams, S.E. (2004). Extinction risk from climate change. *Nature* 427, pp. 145–148.

Van Berkum, F.H. (1988). Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *The Amer. Natur.* 132, pp. 327–343.

Webb, J.K., Shine, R. (1998). Using thermal ecology to predict retreat-site selection by an endangered snake species. *Biol. Conserv.* 86, pp. 233–242.

Appendix

Table A1. Dates and minimum and maximum temperatures for both surveys (1993–1994 and 2017–2018), extracted from the meteorological service of Israel archives (https://ims.data.gov.il/ims/1), and calculated daily mid-point range temperatures. The data were collected by the Gal'ed meteorological station, which is the closest station to Oren stream (about 20 Km), which collected temperature data during both surveys.

Date	Minimum temperature	Maximum temperature	Mid-point range temperature	Total number of reptile observations
1993–1994 survey				
27.10.1993	20	30.8	25.4	12
02.11.1993	14	23.1	18.6	22
24.11.1993	12.3	23.3	17.8	13
30.11.1993	10.8	21.1	16.0	6
22.12.1993	14.4	20.7	17.6	0
23.1.1994	8.9	16.1	12.5	0
15.2.1994	10.1	18.6	14.4	0
03.03.1994	8.3	17.7	13	12
23.03.1994	9.1	17.6	13.4	30
21.04.1994	22.5	36.3	29.4	23
04.05.1994	14.5	22.5	18.5	9
11.05.1994	15	36	25.5	14
26.05.1994	19.6	38	28.8	20
26.06.1994	20	30.6	25.3	15
27.06.1994	20	30.2	25.1	15
28.06.1994	17.1	30.3	23.7	31
21.07.1994	20.6	30.6	25.6	16
25.07.1994	20.2	32.8	26.5	10
07.09.1994	21.1	31.3	26.2	0
08.09.1994	21	31.6	26.3	0
2017–2018 survey				
19.10.2016	19.9	27.5	23.7	11
06.03.2017	11.9	22.9	17.4	21
13.04.2017	16.7	26.9	21.8	25
29.05.2017	18.2	34.3	26.3	20
19.06.2017	20.8	31	25.9	27
20.06.2017	21.3	28.7	25	24
24.07.2017	23	33.1	28.1	41
28.08.2017	22.6	30.7	26.7	40
03.10.2017	21.4	29	25.2	10
26.10.2017	16.9	31.7	24.3	26
16.11.2017	14.5	29.2	21.9	27
28.12.2017	13.5	19	16.3	16
29.01.2018	9.8	15.9	12.9	0
05.02.2018	13.5	21.3	17.4	23

Table A2. Data describing whether species location in Oren stream is in the center of their global distribution (Roll et al., 2017), or close to its northern or southern edges, and whether their distribution includes mainly a Mediterranean biome, or both Mediterranean and desert biomes ("Wide"). The mean annual temperature of each species distribution is calculated based on data from WorldClim 2 (Fick and Hijmans, 2017, using range data from Roll et al., 2017). The Gibbons and Lovich two-step ratio (Smith, 1999) for the number of observations of each species across surveys was calculated by dividing the larger by the smaller number, and reducing 1 from each ratio. The ratio is then multiplied by (–1) when the number of observations is larger in the 1993–1994. Thus negative and positive numbers mean that the number of observations in the 1993–1994 and 2017–2018 surveys, respectively, was larger.

Species	Close to edge of species distribution	Biome	Mean annual temperature	Gibbons and Lovich ratio
Ablepharus rueppellii	Centre	Mediterranean	18.2	1
Chalcides guentheri	Centre	Mediterranean	18.2	0
Chalcides ocellatus	Centre	Wide	22.8	3.5
Chamaeleo chamaeleon	Centre	Wide	19.7	–1
Hemidactylus turcicus	Centre	Wide	20	0
Heremites vittatus	Centre	Mediterranean	17.6	–0.93
Mediodactylus orientalis	Southern	Mediterranean	13.3	N/A
Phoenicolacerta laevis	Southern	Mediterranean	15.9	–0.03
Platyceps collaris	Southern	Mediterranean	15.1	–1
Pseudopus apodus	Southern	Mediterranean	12.5	–2
Ptyodactylus guttatus	Northern	Wide	20.3	3.72
Stellagama stellio	Centre	Wide	16	–0.98
Testudo graeca	Southern	Mediterranean	15.2	–3

Table A3. Relative abundance of reptile species across slopes (south and north-facing) between studies (1993–1994 and 2017–2018).

Species / Slope	1993–1994			2017–2018		
	South-facing	North-facing	Total	South-facing	North-facing	Total
Ablepharus ruepelli	0.007	0.020	0.026	0.031	0.019	0.050
Chalcides guentheri	0.003	0.000	0.003	0.003	0.000	0.003
Chalcides ocellatus	0.010	0.003	0.013	0.053	0.003	0.056
Chamaeleo chamaeleon	0.003	0.003	0.007	0.000	0.003	0.003
Hemidactylus turcicus	0.003	0.003	0.007	0.000	0.006	0.006
Heremites vittatus	0.062	0.033	0.098	0.047	0.000	0.047
Mediodactylus orientalis	0.000	0.000	0.000	0.000	0.013	0.013
Phoenicolacerta laevis	0.020	0.208	0.235	0.078	0.135	0.219
Platyceps collaris	0.010	0.003	0.016	0.000	0.006	0.009
Pseodopus apodus	0.010	0.000	0.013	0.003	0.000	0.003
Ptyodactylus guttatus	0.094	0.000	0.094	0.254	0.176	0.436
Stellagama stellio	0.228	0.055	0.456	0.088	0.050	0.144
Testudo graeca	0.023	0.003	0.029	0.003	0.003	0.006
Total	0.472	0.332	1	0.561	0.414	1

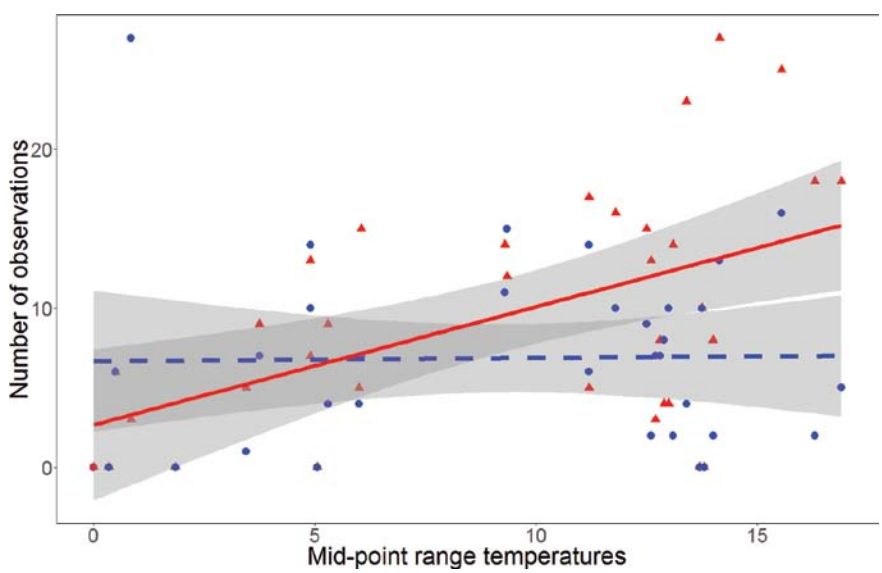

Figure A1. Result of dataset with the 23.03.1994 outlier. Relationship between number of observations and mid-point range temperatures of reptile species in the south-facing slope (orange triangles and solid line; $R^2 = 0.26$) and the north-facing slope (blue circles and dashed line; $R^2 = 0.17$) in Oren stream. Notice that the dashed blue line represents a non-significant relationship between the number observations and mid-point range temperature on the north-facing slope. The outlier is at the top left (blue circle). We centred the temperature data on the origin by reducing the lowest temperature in the dataset (12.5°C) from all temperatures, and rescaled them accordingly in order to get a biologically informative intercept.

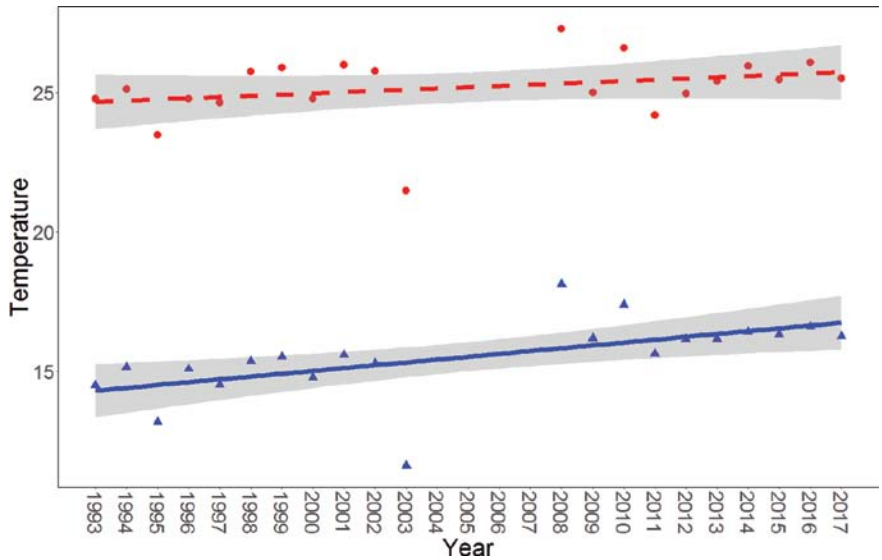

Figure A2. Regression analysis between the minimum (blue triangles and solid line) and maximum (orange circles and dashed line) annual temperatures in the Gal'ed weather station from 1 January 1993 until 31 December 2017. Note that the dashed line represents a statistically insignificant relationship. Note the gap between 2004–2008, resulting from a malfunction in the Gal'ed weather station.