Response of a Desert Lizard Community to Habitat Degradation: Do Ideas about Habitat Specialists/Generalists Hold?

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Response of a desert lizard community to habitat degradation: Do ideas about habitat specialists/generalists hold?

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ABSTRACT

We report the impact of human-induced desertification on the species richness, abundance, and composition of sand dune flora and herpetofauna of North Sinai, Egypt. Our hypothesis was that degraded habitats would have reduced vegetation complexity, richness, and abundance, and consequently lower reptile species richness and abundance. We also hypothesized that desert lizards would not follow the typical generalist/specialist responses to habitat degradation found in other biomes. Instead, we predicted that because vegetation loss intensifies the environmental extremity of deserts, those species specialized for open and sandy environments would be more likely to persist in desertified habitats than would desert generalists. Our results showed that areas protected from vegetation loss did not have significantly higher vegetation richness or abundance except for only a few species. However, protected sites did have significantly higher percent vegetation cover and height. Habitat protection clearly had strong effects on the reptile community as species richness and abundances were significantly higher in protected sites. The composition of the reptile community between protected and unprotected sites differed significantly. Contrary to past studies in other environments, desert generalist species were not able to persist in degraded sites and were only found in protected sites. Specialist species were ubiquitous in that they occurred in both areas protected and unprotected from vegetation loss. We propose that the effects of disturbance on species composition (specialists or generalists) depends on whether the disturbance exacerbates or reduces environmental harshness and the conditions that favor specialization. In extreme environments, specialist and generalist responses to habitat degradation are opposite to that of more productive environments.

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1. Introduction

Desertification, the process of vegetation loss in arid environments, is widespread and expanding, especially in the Middle East and Africa (Geist and Lambin, 2004). As desertification is likely to increase, ecologists want to predict the effects of these impacts on species abundance, richness, composition, and survival. Vegetation loss, through overgrazing, appears to be detrimental to most vegetation communities, as it reduces species diversity, richness, and density (Milchunas and Lauenroth, 1993; Fleischner, 1994). The structure of the vegetation community also changes as a result of anthropogenic disturbance, as vegetation height and percent vegetation cover often decrease (Van Vuren and Coblentz, 1987;

Milchunas and Lauenroth, 1993; Fleischner, 1994). Species composition is also changed by the selective food preferences of grazers, which eat the more palatable species such as grasses, allowing the unpalatable species (most often shrubs) to become dominant in the community (Milchunas and Lauenroth, 1993; Fleischner, 1994).

Given the strong effects of anthropogenic disturbances on plants, one would expect consequential impacts on associated animal communities that depend upon vegetation. Past studies have demonstrated that bird (Taylor, 1986; Van Vuren and Coblentz, 1987; Bowen and Kruse, 1993), mammal (Laurance, 1994), and lizard (Busack and Bury, 1974; Jones, 1981; Smith et al., 1996; Martin and Lopez, 2002) abundance and diversity decline as a result of vegetation loss. Species declines occur when vegetation complexity and abundance decrease, which causes a reduction in thermoregulatory patches, refuge sites, and food availability, while increasing environmental severity and predation risk (Saunders et al., 1991; Laurance, 1994; Bentley et al., 2000). Species not significantly affected by vegetation loss use non-palatable vegetation for shelter and foraging, whereas other species react negatively to structural changes of vegetation (Jones, 1981).

An important conservation concern is the shift in composition from specialist to generalist species in degraded habitats (Foufopoulos and Ives, 1999; Henle et al., 2004). Specialist species have a combination of morphological, behavioral, or physiological adaptations to various factors of the habitat, which are indicative of evolutionary history in a particular environment (Allee et al., 1949; Lavorel et al., 1997; Futuyma and Moreno, 1998; Tieleman et al., 2003). Habitat specialists have greater fidelity to a particular habitat type and are usually less tolerant of disturbance (Sarre et al., 1995; Pimm et al., 1988; Foufopoulos and Ives, 1999; Bentley et al., 2000; Henle et al., 2004). A generalist species has fewer adaptations than a specialist to a particular environment and has less stringent habitat requirements, with the trade-off being that the generalist could potentially be more successful in a greater variety of environments (Futuyma and Moreno, 1998; Southwood, 1988; Foufopoulos and Ives, 1999). Most of the empirical and theoretical evidence for responses to habitat degradation by habitat specialists and generalists is derived from forests and grasslands (Saunders et al., 1991; Bowers and Harris, 1994; Sarre et al., 1995; Smith et al., 1996; Pimm et al., 1988; Foufopoulos and Ives, 1999; Bentley et al., 2000; Kitahara and Sei, 2001; Davies et al., 2004; Henle et al., 2004). Deserts have not received the same attention as more biologically diverse and complex habitats, and the impacts of degradation on desert specialist and generalist species are not well understood (Schlesinger et al., 1990; Milchunas and Lauenroth, 1993; Lonsdale, 1999).

We examined the impact of anthropogenic disturbances, such as grazing and vegetation harvesting by pastoral peoples on the species richness, abundance, and composition of the sand dune flora and herpetofauna of North Sinai, Egypt. Our hypothesis was that degraded habitats would have reduced vegetation complexity, richness, and abundance, and consequently lower reptile species richness and abundance. We also hypothesized that desert lizards would not follow the typical generalist/specialist responses to habitat degradation found in other biomes. Instead, we predicted that because

vegetation loss intensifies the environmental extremity of deserts, those species specialized for open and sandy environments would be more likely to persist in degraded habitats than would desert generalists.

2.   Study site

This study was conducted at Zaranik Protected Area (ZPA) in North Sinai, Egypt. ZPA occupies 250 km^2, has an altitude of 0–30 m, and is located 30 km west of the town El Arish (N 31° 05′, E 33° 25′). ZPA is characterized by stable and unstable sand dunes which receive an annual rainfall of 50–100 mm. We performed this study on six sites, 50 m × 50 m and which were located roughly 248 m + 43.8 (mean + SE) from one another in rotating order of treatment. The six sites were located in semi stable sand dunes and similar in vegetation cover and composition at the start of the study (Fig. 1). We fenced in three sites (protected sites) with barbed wire to exclude livestock and people. The remaining three sites were unprotected and classified as disturbed, as the vegetation was subjected to grazing, seasonal and small scale watermelon Citrullus lanatus agriculture, and harvesting of vegetation by pastoral people who live in the reserve.

Grazing in ZPA varies seasonally, with light grazing from April through the end of August/beginning of September in areas where watermelons are planted, but heavy grazing whenever and wherever there are no watermelons. The most abundant livestock were goats and sheep that often grazed together in small herds ranging from 10 to 50 individuals. Multiple herds visited the vicinity of the study sites almost daily. Camels and to a lesser extent, donkeys, also grazed in the area but less frequently than goats and sheep. There are no native ungulates in ZPA, as the Dorcas Gazelle Gazella dorcas became extinct in the 1950s, according to local sources. The largest native grazer in the park is the Cape hare, Lepus capensis, which never occurred in our study site.

The watermelon is planted by the local Bedouins in small plots, usually less than 100 × 100 meters in area. The watermelons are planted in late April and early May, after the winter rains, and harvested in late summer, typically in August/ September. Watermelon patches are not monocultures as most large vegetation is removed while smaller perennials and annuals are left intact prior to cultivation. Watermelons are not treated with pesticides, watered, or maintained in any way.

3.   Methods

3.1.   Flora

Vegetation surveys occurred in December 1998 just prior to the establishment of the exclusion fence later that month, and in September, 1999, and April, June, and September 2000. We determined percent vegetation cover and height by the line transect method, sampling five equally spaced 50 m transects, in each site. We used the grass Stipagrostis scoparia as an indicator of vegetation height because it was the most common palatable perennial in all six sites. Vegetation species richness and abundance for each site was determined by direct counts of all the plants within each site. However,
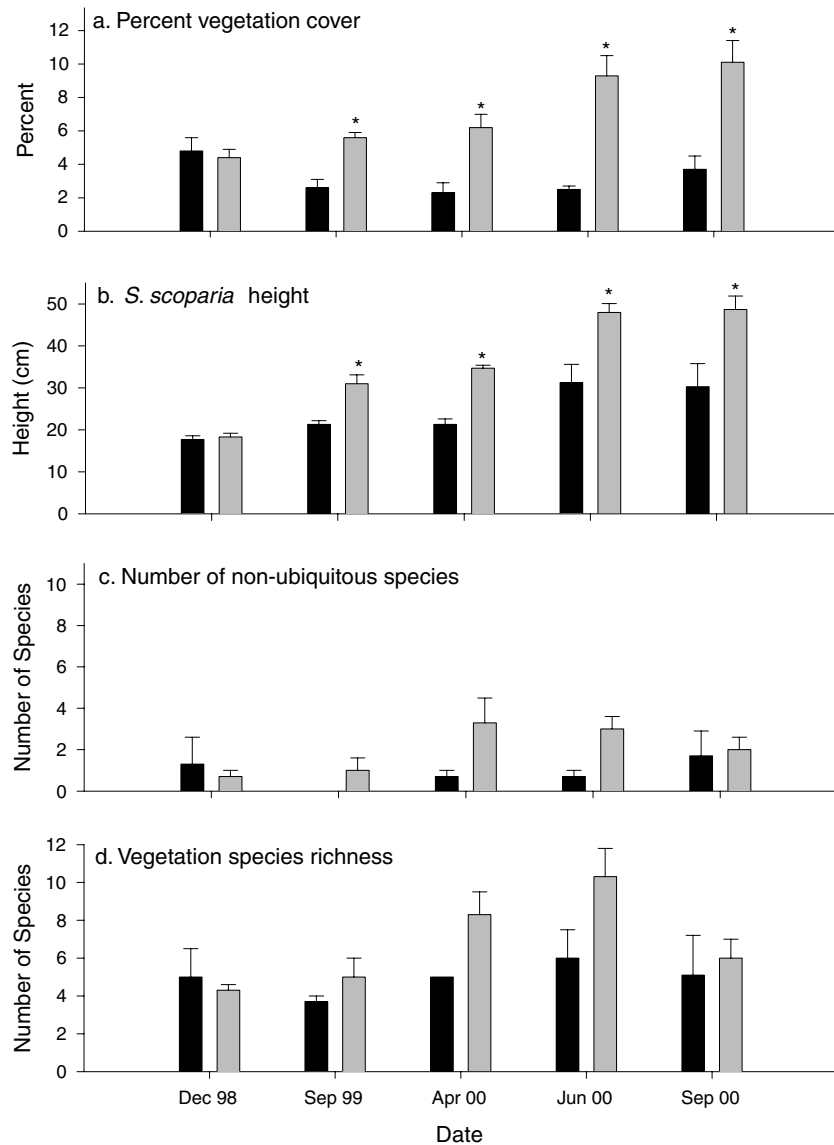
Fig. 1 – The effect of habitat degradation on: (a) vegetation cover, (b) height of *Stipagrostis scoparia*, (c) number of non-ubiquitous species and (d) vegetation species richness. ˙ Effect of protection significant.

for two species of bunch grasses, *S. scoparia* and *Panicun turgidum*, we considered each bunch to be one plant, as it was difficult to differentiate between individuals. We considered a species to be ubiquitous if it occurred in both protected and unprotected sites.

3.2.   Herpetofauna

Based on the published literature, we classified *Acanthodactylus longipes, Scincus scincus, Sphenops sepsoides*, and *Stenodactylus petri* as sand specialists or psammophilic lizards (Baha El Din, 2001; Attum and Eason, 2006; Attum et al., in press). The relative judgment of the degree of specialization is more accurate when the distribution of specialists is included within that of the generalists, as in this study (Futuyma and Moreno, 1998). The morphological adaptations of these sand specialists include toe fringes, which aid on sand locomotion (Carothers, 1986); a convex snout and countersunk jaws for

diving into sand (Arnold, 1995); long hind legs relative to snout-vent length, a trait indicative of high sprint speed and associated with lizards that occupy open spaces (Pianka, 1969); and the other extreme of leg length, very reduced limbs that are associated with fossorial movement (Gans, 1975). Behavioral adaptations include diving into sand as an escape method and the thermoregulatory behavior of stilting, which are both independent of vegetation (Attum and Eason, 2006; Attum et al., in press). The specialists occupy soft sand dunes, occur far away from vegetation, and can be active at extreme substrate temperatures (Baha El Din, 2001; Attum et al., in press; Attum and Eason, 2006). The generalist lizard species, *Acanthodactylus scuttelatus, Chalcides ocellatus, Chamaeleo chamaeleon, Mesalina olivieri*, and *Trapelus savignyi*, are not as morphologically specialized for sand dune environments, typically run to vegetation to escape predators, are active within the vicinity of vegetation, climb on or in vegetation to avoid high substrate temperatures, and are found on

harder substrates (Baha El Din, 2001; Attum et al., in press). These generalists are also eurytopic because they occupy more diverse habitat types, while sand specialists typically only occur in sand dunes (Arnold, 1984; Schleich et al., 1996; Baha El Din, 2001; Disi et al., 2001). We did not classify snakes as specialists or generalists given the lack of species and publications on their natural history.

We determined reptile presence by pitfall trap capture, direct observation, and tracks. Sixteen pitfall traps were placed in each plot for two to four days a month. Sampling for reptile species richness and ubiquity occurred in December, 1998 (before we set up the fences), in September and October of 1999, and in February, March, April, May, June, August, and September of 2000. Those species that occurred in both protected and unprotected sites where termed ubiquitous. Species that occurred in only one treatment were termed non-ubiquitous and unique. We sampled relative abundance for diurnal species by walking through each plot once every hour from 8:00 until two hours prior to sunset, two to four days a month in September and October of 1999 and in April, May, August, and September of 2000. We sampled relative abundance for nocturnal species in March, April, May, June, and September of 2000, with walks starting at sunset and ending at 01:00. We used the sand sweep method to determine the relative abundance of species that were difficult to observe; S. scincus, S. sepsoides, C. ocellatus, and snakes (Baha El Din, 2001; Attum et al., in press). A sand sweep consisted of dragging a burlap sack partially filled with sand in order to erase all previous lizard tracks. At the beginning of every hour, we walked the transect to record any lizard activity that had taken place. When a track of one of the species crossed the transect during the fifty-five minute time frame, it was recorded as an observation.

3.3. Statistical analysis

The effects for all analysis were: protection (protected and unprotected), month, protection*month interaction, and site. Site was considered to have a random effect and nested within protection. Month and protection were considered fixed factors. The interaction between protection and month was examined whenever possible to determine if the effect of protection differed among months. We then used follow-up contrasts where appropriate to identify the months for which the effect of protection were significant.

Species abundance was modeled with two types of analysis conducted with SAS: (1) ANOVA performed with the GLM procedure and (2) generalized linear model using the Poisson sampling distribution of the GENMOD procedure. When ANOVA was used, the assumptions of homogeneity of the residuals variance was examined by the Brown–Forsythe test for equal variances. The assumption of ANOVA, normality of residual distribution, was examined using the Shapiro–Wilk test of goodness-of-fit. If either assumption was violated (P-value < 0.05), a transform of the original variable was used. Most species analyzed had acceptable fit to the assumptions of ANOVA. Species with low or frequent counts of zero did not fit the ANOVA assumptions and were modeled using the ln(abundance + 1) transform. This resulted in acceptable fit for most species. Plant species abundance fit the assumptions

of ANOVA, while reptile species abundance did not because of excessive counts of zero. Reptile species abundance was then analyzed using a generalized linear model with a Poisson sampling distribution. All analyses presented were found to have acceptable fits using the deviance criteria of goodness of fit. We were only able to test the effect of protection on reptile abundance because more complicated models testing the effects of month, protection*month, and site failed to fit the data. We excluded the desert monitor, Varanus griseus, lesser sand viper, Cerastes vipera, and diadem snake Lytorhynchus diadema from the abundance analysis because of their rarity. In order to minimize type I errors as a result of multiple tests on species abundance, we corrected P-values by the sequential Dunn–Sidak method (Quinn and Keough, 2002). We considered tests to be significant if the P-value was less than the new adjusted P-value (α_{adj}). Vegetation richness, species ubiquity, percent cover, and S. scoparia height were analyzed by MANOVA. Reptile richness and ubiquity were analyzed by a second MANOVA. We then performed follow-up ANOVAs when a MANOVA was significant.

4. Results

4.1. Vegetation species richness, ubiquity, cover, and height

The MANOVA showed that there was a significant protection*month interaction ($F_{4,16} = 17.65$, $P < 0.0001$). The main effects of month and site also significantly affected one or more of the dependent variables (month: $F_{4,16} = 46.66$, $P < 0.0001$; site: $F_{4,16} = 6.63$, $P = 0.0024$). The main effect of protection was not significant ($F_{4,16} = 4.50$, $P = 0.34$). Accordingly, we next performed ANOVAs on each of the dependent variables.

Protected sites tended to have higher species richness although this difference was not significant ($F_{1,4} = 2.73$, $P = 0.17$; Fig. 1). Site ($F_{4,16} = 4.48$, $P = 0.013$) and month ($F_{1,16} = 6.22$, $P = 0.003$) did have significant effects on species richness, with the highest richness occurring in the spring and early summer. There was no significant protection*month interaction on species richness ($F_{4,16} = 2.27$, $P = 0.11$). The number of ubiquitous species was not significantly affected by protection ($F_{1,4} = 3.41$, $P = 0.14$), month ($F_{4,16} = 1.90$, $P = 0.16$), site ($F_{4,16} = 2.94$, $P = 0.053$), or the protection*month interaction ($F_{4,16} = 2.18$, $P = 0.12$; Fig. 1). Protection significantly increased vegetation cover ($F_{4,16} = 10.06$, $P < 0.0001$) and height ($F_{4,16} = 4.09$, $P = 0.018$). Linear contrasts showed that percent cover and height were significantly higher ($P < 0.05$) in protected sites for all months, except prior to protection in December, 1998 (Fig. 1). Percent vegetation cover steadily increased in the protected sites and at the end of the study was 2.8 times greater than in the unprotected sites. S. scoparia height increased throughout the duration of this study for both treatments; however, S. scoparia's height at the end of the study was 1.6 times greater in protected sites (Fig. 1). Site did not significantly affect either percent vegetation cover ($F_{4,16} = 2.99$, $P = 0.051$) or height ($F_{4,16} = 1.99$, $P = 0.15$).

4.2. Vegetation species abundance

Almost every species was more abundant in the protected sites, although this difference was significant only for three

Table 1 – ANOVAs for vegetation abundance

	A. carduus		A. monosperma		A. tomentosu		C. conglomerates		C. lanatus		C. memphitica	
	df	f	df	f	df	f	df	f	df	f	df	f
Protection	1,4	5.88	1,4	1.16	1,4	2.29	1,4	1.91	1,4	0.09	1,4	60.66[*]
Month	4,16	2.79	4,16	1.29	4,16	0.61	4,16	2.49	4,16	0.34	4,16	60.66[*]
Protection*month	4,16	3.95	4,16	1.11	4,16	0.61	4,16	2.35	4,16	1.07	4,16	60.66[*]
Site (protection)	4,16	1.79	4,16	2.98	4,16	1.22	4,16	8.09[*]	4,16	17.08[*]	4,16	1.00
	C. monacantha		E. aegyptiacum		E. fruticosum		H. digynum		I. spicata		N. procumbens	
	df	f	df	f	df	f	df	f	df	f	df	f
Protection	1,4	1.09	1,4	7.13	1,4	1.08	1,4	0.34	1,4	1.00	1,4	0.09
Month	4,16	0.84	4,16	11.35[*]	4,16	1.90	4,16	0.65	4,16	1.00	4,16	1.61
Protection*month	4,16	2.14	4,16	6.20[*]	4,16	0.82	4,16	1.35	4,16	1.00	4,16	0.39
Site (protection)	4,16	2.88	4,16	1.71	4,16	10.46[*]	4,16	2.11	4,16	1.00	4,16	1.79
	P. turgidum		S. scoparia		S. plumose		S. villosa		Z. album			
	df	f	df	f	df	f	df	f	df	f		
Protection	1,4	1.33	1,4	10.34	1,4	1.54	1,4	0.62	1,4	0.70		
Month	4,16	3.14	4,16	5.52	4,16	2.78	4,16	11.36[*]	4,16	5.10		
Protection*month	4,16	2.13	4,16	8.18[*]	4,16	3.60	4,16	1.13	4,16	0.78		
Site (protection)	4,16	19.74[*]	4,16	12.70[*]	4,16	1.00	4,16	1.74	4,16	1.24		

[*] $P < 0.05 < \alpha_{adj}$.

species (ANOVA results for all species in Table 1; Fig. 2). The most common grass, S. scoparia was significantly more abundant in protected sites only during certain months (ANOVA: protection*month, $F_{4,16} = 8.18$, $P < \alpha_{adj}0.0027$). However, linear contrasts failed to show for which months this difference in abundance was significant, probably because of the high heterogeneity of abundance among sites ($F_{4,16} = 12.70$, $P < \alpha_{adj}0.0027$). Two species that were annuals at this site, the sedge *Cutandia memphitica*, and the forb *Eremobium aegyptiacum*, also had significant protection*month interactions (*C. memphitica*: $F_{4,16} = 60.66$, $P < \alpha_{adj}0.0026$; *E. aegyptiacum*: $F_{4,16} = 6.20$, $P < \alpha_{adj}0.0029$). *C. memphitica* was significantly more abundant in the protected sites in April ($P < 0.0001$; X ± SE: protected $112.7 ± 49.7$; unprotected $0.0 ± 0.0$) and *E. aegyptiacum* was significantly more abundant in the protected sites in June ($P = 0.011$; protected: $16.0 ± 7.8$; unprotected $0.7 ± 0.7$).

4.3. Herpetofauna species abundance, richness, and ubiquity

All diurnal species had significantly higher abundances in the protected sites when using the Dunn–Sidak adjusted significance level $P <_{adj}$ (Table 2; Fig. 3). However, there was no significant effect of protection on the abundance of nocturnal species, despite the trend of nocturnal species being more abundant in protected sites (Table 2; Fig. 3). The MANOVA on species richness and ubiquity showed that there was a significant protection*month interaction, ($F_{9,36} = 5.89$, $P < 0.0001$). The follow-up ANOVAs showed that the interaction between protection and month was significant for both reptile richness and ubiquity (richness: $F_{9,36} = 2.82$, $P = 0.013$; ubiquity: $F_{9,36} = 5.89$, $P < 0.0001$). Contrasts showed that there was no significant difference between protected and unprotected sites during winter months (December, 1998 and Feb-

ruary, 2000) when many of the reptiles hibernate or have reduced activity ($P > 0.05$). However, species richness and ubiquity were significantly higher ($P < 0.05$) in protected sites for all other times of the year, except for April, 2000 (Fig. 4).

4.4. Specialists and generalists lizards

The four sand specialist lizards, A. *longipes, S. scincus, S. sepsoides*, and S. *petri* were ubiquitous, as they were always found in both protected and unprotected sites. The five generalist lizards, A. *scuttelatus, C. ocellatus, C. chamaeleon, M. olivieri*, and T. *savignyi*, were almost always found only in the protected sites and thus were not ubiquitous (Fig. 5). The sand specialists were significantly different from the generalist lizards in their ubiquity (Fisher's exact test, $P = 0.008$). Snakes were not included in the analysis because of their rarity.

5. Discussion

Habitat protection clearly had strong effects on the vegetation and reptile community, despite the harshness of the environment and a relatively short recovery period of less than two years. Vegetation structure in protected sites dramatically improved as percent vegetation cover and S. *scoparia* height increased, which consequentially affected the reptile community. Higher reptile richness and abundances might have resulted from increased availability of food, refuges, microhabitats, and/or thermoregulatory patches in the more complex vegetation of the protected sites. Food was clearly higher in the protected area for at least some species, as the two lizards A. *longipes* and C. *chameleo* are prey for the other reptiles in this study (Amr and Disi, 1998; Baha and Attum, 1998; Attum et al., 2004). Also, previous work in deserts has shown that areas with more vegetation have increased
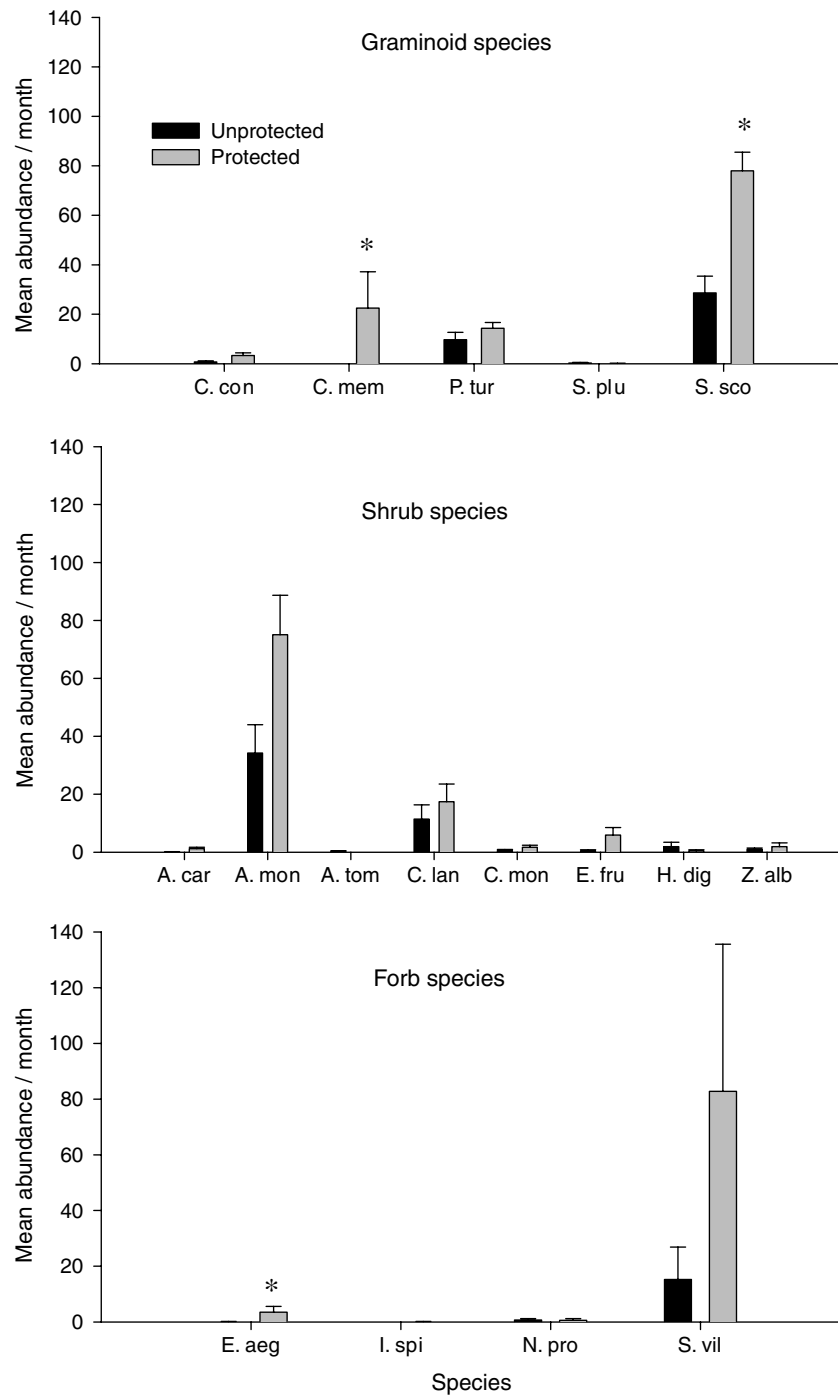
Fig. 2 – Mean abundance of plant species. Graminoids: C. con = *Cyperus conglomeratus*, **P. tur =** *Panicum turgidum*,
S. plu = *Stipagrostis plumose*, **S. sco =** *Stipagrostis scoparia*. **Shrubs: A. car =** *Atractylis carduus*, **A. mon =** *Artemisia monosperma*,
A. tom = *Astragalus tomentosu*, **C. lan =** *Convolvulus lanatus*, **C. mon =** *Cornulaca monocantha*, **E. fru =** *Echiochilon fruticosum*,
H. dig = *Heliotropium digynum*, **Z. alb =** *Zygophyllum album*. **Forbs: C. mem =** *Cutandia memphitica*, **E. aeg =** *Eremobium*
aegyptiacum, **I. spi =** *Ifloga spicata*, **N. pro =** *Neurada procumbens*, **S. vil =** *Silene villosa*. * **Effect of protection significant.**

numbers of invertebrates, suggesting there would also be increased food availability for insectivorous lizards on the protected sites (Robinson, 1981; Sanchez and Parmenter, 2002). Lizards in protected sites were found closer to vegetation, suggesting they have greater access to refuges if threatened by a predator (Attum and Eason, 2006). In addition, increased availability of niches through vegetation complexity generally promotes species coexistence and greater richness (MacArthur and MacArthur, 1961; Pianka, 1967; Baker et al., 2002).

Our results suggest that specialists were more likely than desert generalists to persist in areas experiencing vegetation loss. The desert specialists, which were the more common species, almost always occurred in both unprotected and protected sites. However, desert specialists were observed less

Table 2 – Generalized Linear Model using Poisson distribution for the effects of protection on reptile abundance

Species	df	χ^2
A. longipes	1	230.58[*]
A. scuttelatus	1	20.72[*]
M. oliveri	1	12.40[*]
S. scincus	1	7.10[*]
C. chameleo	1	15.96[*]
T. savigni	1	5.82[*]
P. shokari	1	23.57[*]
C. ocellatus	1	0.20
S. petri	1	0.25
S. sepsoides	1	0.68

[*] $P < 0.05 < \alpha_{adj}$.

frequently in unprotected sites, suggesting that although these species are better adapted than generalists for less vegetated areas, the unprotected sites may be suboptimal habitat even for them. Despite this reduced abundance, the desert specialists were still able to persist in the unprotected sites, unlike many of the desert generalists, which were often observed only in protected sites. Vegetation in arid environments stabilizes sand dunes, provides refuge from predators, and creates islands of environmental conditions that are less harsh than open desert (Heatwole and Muir, 1979; Larmuth, 1979; Adolph, 1990; Carrascal et al., 1992; Hughes and Ward, 1993; Vasquez et al., 2002). When this vegetation disappears, the bare desert may be too severe for generalists and thus these species accounted for the differences in species richness between protected and unprotected sites.

Our finding that specialist species are more likely to survive than generalists in highly disturbed areas contradicts previous studies conducted in other habitats (Sarre et al., 1995; Pimm et al., 1988; Foufopoulos and Ives, 1999; Bentley et al., 2000; Henle et al., 2004). Past studies in forests have shown that degraded habitats have reduced complexity and experience more extreme environmental conditions than in-

tact habitats, and these conditions are generally too harsh or otherwise unsuitable for species that are forest specialists (Saunders et al., 1991; Zhu et al., 2004). Specialists tend to decline and are replaced by generalist species that thrive in the less complex disturbed forest or edge habitat (Niemalae, 1997; Bentley et al., 2000; Petit and Petit, 2003).

The same traits that allow desert specialists to persist in more open and degraded habitats – their morphological specializations for movement on and/or in sandy soils, their ability to escape predators without relying on vegetation, and their behavioral adaptations for thermoregulation. (Carothers, 1986; Arnold, 1995; Baha El Din, 2001; Attum and Eason, 2006; Attum et al., in press; see Saunders et al., 1991 for review) – may also allow sand specialists to be better dispersers across open deserts to find islands of vegetation. Dispersal ability is believed to be an important factor in determining a species' vulnerability to habitat degradation (Ford et al., 2001). In contrast, open deserts may be too extreme and act as barriers to desert generalists, as they are less adapted for locomotion, escape, and thermoregulation in these conditions.

We propose that the effects of disturbance depend on the habitat's harshness and on whether the disturbance exacerbates or reduces that harshness. In already harsh desert habitats, the increasing harshness caused by disturbance creates extreme conditions that are intolerable for desert generalists, and it is only the specialized species that are able to persist. The disturbance essentially acts as a trait filter that allows specialized species adapted to extreme deserts to pass through and persist (Statzner et al., 2004). As a result, the trait composition of the community becomes similar in that all surviving species are adapted to the specialized environment of sand dune deserts (Lancaster and Scudder, 1987; Statzner et al., 2004). Other harsh habitats, such as saline waters, have similar responses when disturbance moves the habitat farther along the axis on which it is already tending to be harsh. For example, when a brackish water habitat experiences increased salinity, only species tolerant of extreme salinity and that normally occur in such areas, persist with the resulting community comprising of specialized species with similar
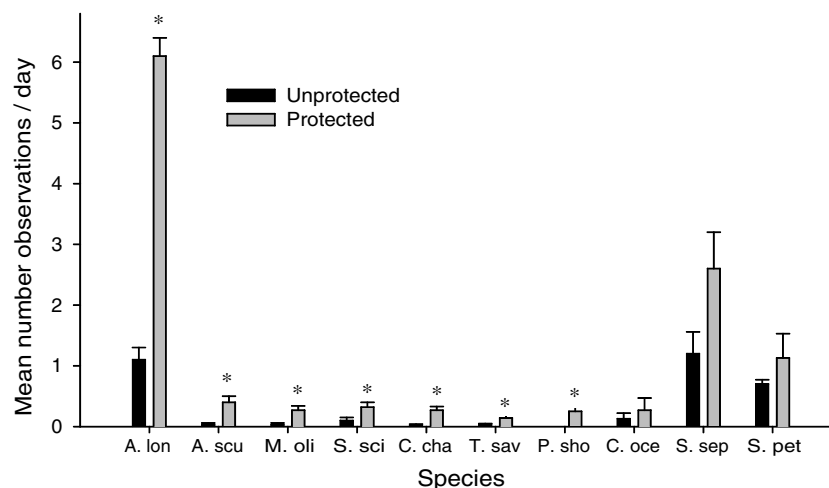

Fig. 3 – Mean number of observations for reptiles. A. lon = *Acanthodactylus longipes*, A. scu = *Acanthodactylus scuttelatus*, M. oli = *Mesalina olivieri*, S. sci = *S. scincus*, C. cha = *Chamaeleo chamaeleon*, C. oce = *Chalcides ocellatus*, S. sep = *Sphenops sepsoides*, S. pet = *Stenodactylus petri*. T. sav = *Trapelus savignyi*, P. sho = *Psammophis schokari*. [*] Effect of protection significant.
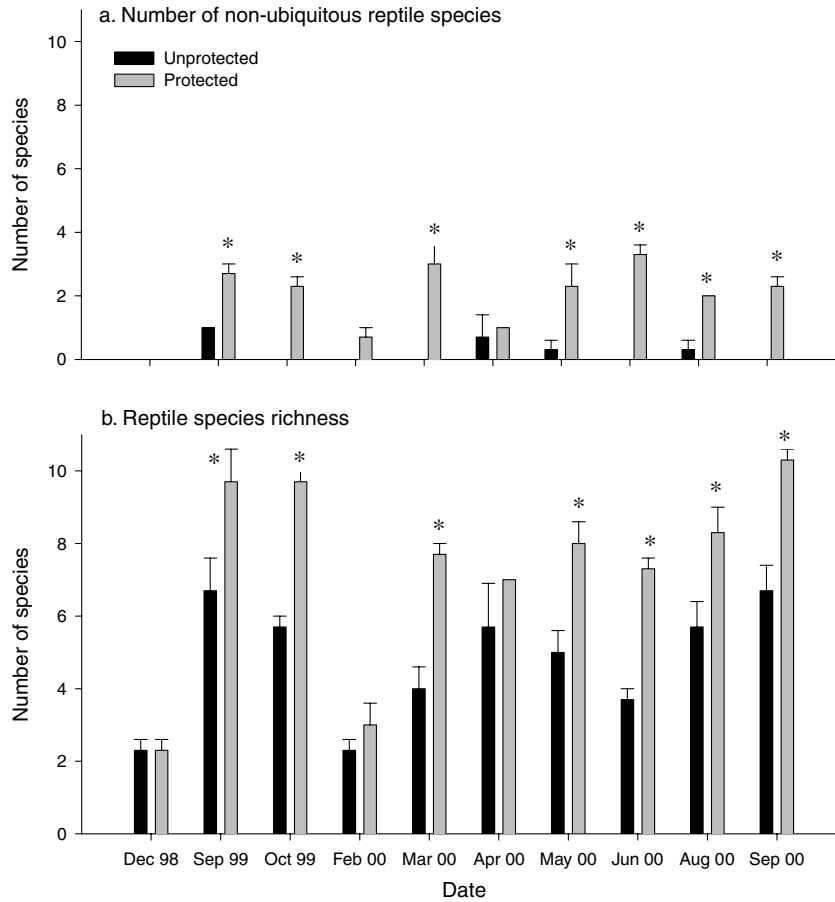
Fig. 4 – Effects of habitat degradation on mean number of non-ubiquitous reptile species and richness. * Effect of protection significant.
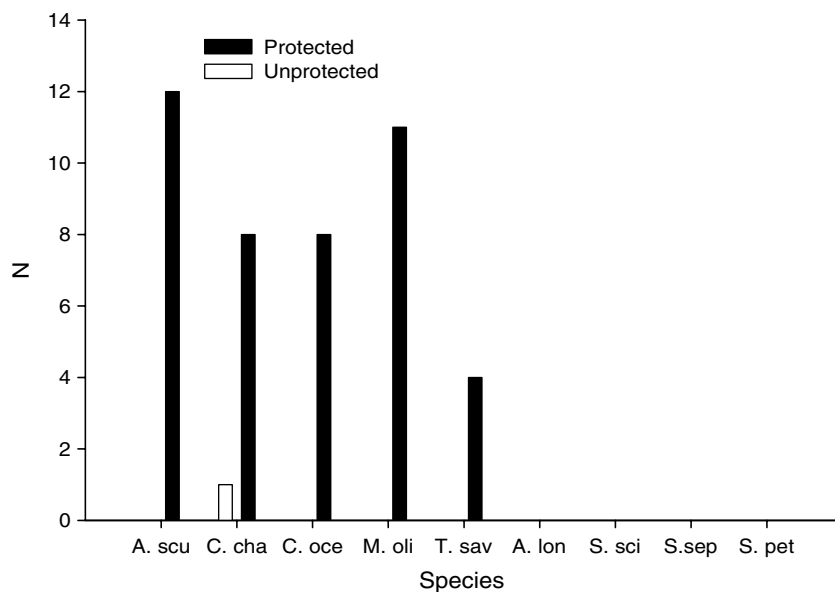

Fig. 5 – Number of times a lizard species was non-ubiquitous (unique to one treatment). Missing bars indicate that the species was never unique to one treatment and ubiquitous because it occurred in both treatments. Specialist lizards were never unique to any treatment. For an explanation of species abbreviations, see Fig. 3.

traits (Herbst, 2001; Williams, 2002). In contrast, species that are tolerant of a broader range of salinities, but not extremely high levels, disappear from the community (Herbst, 2001; Williams, 2002). In relatively moderate habitats such as forests, although disturbance may similarly increase harshness, the change is not too severe for generalist species. Generalists can exist in these degraded forests that have harsher environmental conditions, but not when habitat degradation increases the harshness of already extreme environments, such as deserts.

Some evidence in support of our hypothesis comes from situations in which disturbance has made extreme environments less harsh and thus enlarged the trait filter size. Here, we predict that disturbance should result in occupation by generalist species and concomitant reduction in specialists, and generally this appears to be the case. For example, generalist species occur in deserts experiencing afforestation, but desert specialists disappear (Bock et al., 1984; Perry and Dmi'el, 1995). In Arctic systems, climate change is believed to make a more benign environment, which will allows generalist species to expand their distribution (Callaghan et al., 2004). Arctic specialists will be more vulnerable to extinction in this more benign environment (Callaghan et al., 2004). For example, the arctic fox specialist, *Alopex lagopus* is becoming rarer and outcompeted by the generalist red fox *Vulpes vulpes* in warmer areas, with Arctic foxes persisting in less productive and harsher arctic environments that are too extreme for generalist species (Macpherson, 1964; Hersteinsson and Macdonald, 1992; Tannerfeldt et al., 2002). A specialist species decline in milder habitats is believed to be the cost of specialization to adverse environments where interspecific competition and predation are less. In these milder habitats, competitive ability and predation are more important in determining a species survival (Wilson and Keddy, 1986; Hersteinsson and Macdonald, 1992; Southwood, 1988; Herbst, 2001; Tannerfeldt et al., 2002).

Our generalist/specialist application may have other important implications for conservation as it predicts alien and generalist vertebrates would be able to colonize extreme environments undergoing change that make the environment less harsh (Callaghan et al., 2004). For example, we predict generalists would be likely to colonize arid lands that are highly vegetated or experience afforestation, although deserts are considered among the least invasible biomes (Lonsdale, 1999). Our theory appears to be supported in birds, as immigrant species of afforested habitat in the Negev desert consisted of generalist species (Shochat et al., 2001). Anectodal evidence also indicates that our predictions can be applied to mammals, as rats (*Rattus* sp.), red foxes and feral dogs and cats have been able to colonize deserts that do not experience grazing, clearing of vegetation, or have been converted to agricultural lands (Mendelssohn and Yom-Tov, 1999; Kutiel et al., 2000). We would predict that generalist species would not be able to colonize or invade more extreme deserts, and to our knowledge there is no record of the *Rattus* sp., feral dogs or cats, or *V. vulpes* invading more extreme deserts such as the sand seas of the Sahara or the Empty Quarter of Arabia, even though these species occur in human settlements and agricultural areas on the fringes of such habitats (Harrison and Bates, 1991; Osborn and Helmy, 1980; Wacher and Attum, 2005).

A promising finding of our study is that the sand dune ecosystem can recover quickly from habitat degradation if given the opportunity. The protected sites in this study were relatively small and yet were successful in supporting higher lizard abundance and richness. This is encouraging because managers with few funds or limited capability to protect large expanses may still be able to protect small areas scattered through a zone experiencing habitat degradation; those small islands of protected land may be sufficient to maintain source populations of at least some species of desert lizards, unlike in forests where habitat specialists need larger tracts of land (Bentley et al., 2000). In addition, in regions where it is not possible to protect large areas because local residents' livelihoods depend on those areas, protecting small islands may provide a compromise between management needs and the needs of the local people.

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