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Are snake populations in widespread decline?

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Long-term studies have revealed population declines in fishes, amphibians, reptiles, birds and mammals. In birds, and particularly amphibians, these declines are a global phenomenon whose causes are often unclear. Among reptiles, snakes are top predators and therefore a decline in their numbers may have serious consequences for the functioning of many ecosystems. Our results show that, of 17 snake populations (eight species) from the UK, France, Italy, Nigeria and Australia, 11 have declined sharply over the same relatively short period of time with five remaining stable and one showing signs of a marginal increase. Although the causes of these declines are currently unknown, we suspect that they are multi-faceted (such as habitat quality deterioration, prey availability), and with a common cause, e.g. global climate change, at their root.

Keywords: snakes; sharp population declines; carrying capacity; global climate change

1. INTRODUCTION

There is growing evidence from long-term studies of worldwide declines in vertebrate populations: fishes (Harshbarger *et al.* 2000; Light & Marchetti 2007), amphibians (Wake 1991; Alford *et al.* 2001), reptiles (Gibbons *et al.* 2000; Winne *et al.* 2007), birds (King *et al.* 2008) and mammals (McCloughlin *et al.* 2003). Some of these declines can be directly attributable to known causes, e.g. pollution (Harshbarger *et al.* 2000), habitat loss/change (Gibbons *et al.* 2000; Feyrer *et al.* 2007), disease (Pounds *et al.* 2006; LaDeau *et al.* 2007), over-exploitation (Whitehead *et al.* 1997) or climate change (Collins & Storer 2003; Reading 2007), while for others, the causes remain either unclear (Kiesecker *et al.* 2001; Collins & Storer 2003) or unknown (Gibbons *et al.* 2000; Winne *et al.* 2007). Although there is little evidence that snake populations are in decline, there are reports for other reptiles (Gibbons *et al.* 2000) and there is consensus,

among herpetologists, that snakes may, indeed, be disappearing worldwide (Mullin & Seigel 2009). One possible reason for this view is the relative lack of long-term individual-based studies of snake populations. Our data represent the first evidence that some species occurring in the tropics (Nigeria) have shown similar patterns of decline to others found in southern (Italy), central (France) and northern Europe (UK).

2. MATERIAL AND METHODS

We used data from studies of geographically widespread snake populations covering a broad diversity of snake lineages and environmental situations to determine changes in status over time (table 1). Survey methodologies were identical between years at each study site but not between sites. *Coronella austriaca* (Ca) and *Natrix natrix* (Nn¹) were surveyed one day per week for 21 weeks annually (April–October). *Vipera aspis* (Va¹) was surveyed five days per week for five months annually. *Hierophis viridiflavus* (Hv¹) and *Zamenis longissimus* (Zl¹) were sampled using daily collections of road-kills for five months annually. *Hierophis viridiflavus* (Hv²), *Z. longissimus* (Zl²) and *N. natrix* (Nn²) were surveyed three days per week for five months annually. *Notechis scutatus* (Ns) was surveyed for two weeks each spring. *Vipera aspis* (Va^{2,3}) was surveyed one day per week annually (March–November). *Vipera ursinii* (Vu^{1,2}) was surveyed one day per week annually (April–October). *Bitis gabonica* (Bg), *B. nasicornis* (Bn), *Python regius* (Pr) and *Dendroaspis jamesoni* (Dj) were all studied in sympatry for two days per week annually (May–October). Importantly, the methods used to monitor population trends were consistent through time at each site. Although we used simple techniques to count snake numbers, we nevertheless obtained only two distinct clear patterns (see §3), showing that uncontrolled factors (e.g. catchability, annual climatic fluctuations) did not obscure the detection of major trends. For all populations (excluding road-kills), we collected capture–mark–recapture data, as we intended to produce demographic parameters. However, since the resulting population estimates correlated with count data, we opted to use the latter because they were similar to road-kill counts. Although simple counting underestimates true population size (X. Bonnet, J. M. Ballouard & G. Naulleau 1993–2009, unpublished data), it does provide an index of abundance. We used the simplest methods for consistency among study cases and sites, and also for conciseness. Each captured individual in each independent study was given a permanent individual mark, using either ventral scale clipping or pit-tagging (passive integrated transponder), and thus the current study did not include pseudo-replicates (re-sampling the same individuals within a year was thus avoided). Importantly, several snake populations were monitored in well-protected areas (e.g. Chizé Natural Reserve, Gran Sasso National Park), where habitats were not directly perturbed by human intervention.

All statistical tests were two-tailed, with alpha set at 5 per cent. Data normality were tested prior to using parametric tests.

3. RESULTS

Our data revealed an alarming trend. The majority of snake populations had declined sharply, and synchronously (figure 1), while a few had remained stable (one species from the UK (Nn¹), two from mainland Europe (Nn², Zl²), one from Nigeria (Dj) and one from Australia (Ns)) and one showed evidence of a very weak increase (Hv²) (figure 2). All the stable populations were situated in protected areas while all the populations occurring in areas subject to increasing anthropogenic pressures declined (table 1). However, eight snake populations from protected areas (Ca, Va^{2,3}, Vu^{1,2}, Bg, Bn, Pr) also exhibited large and surprisingly similar patterns of decline. Most of the declining populations exhibited a ‘tipping point’ effect (Andersen *et al.* 2008), with a period of relative stability, up until about 1998, followed by a steep decline, over a period of approximately 4 years, and then a second period of relative stability, but at

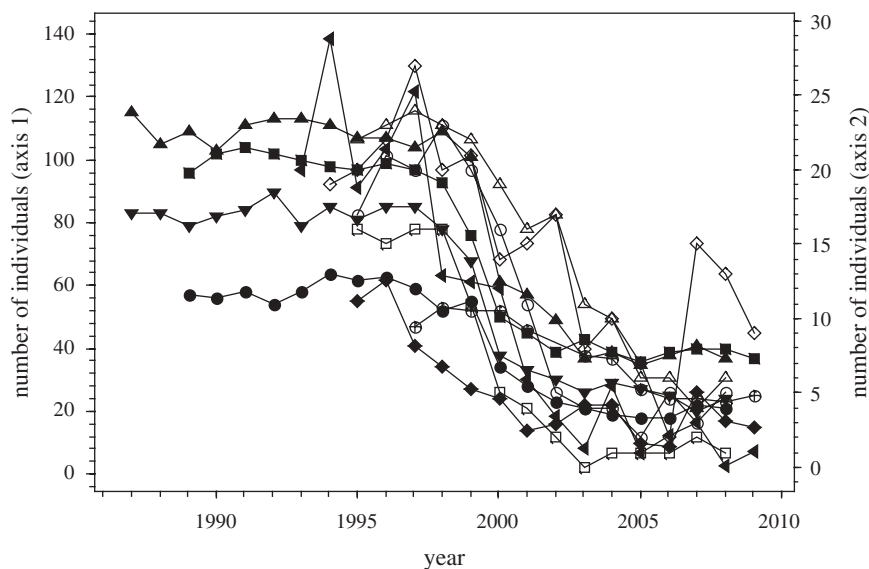


Figure 1. Annual total number of individuals found for each declining snake species population. Axis 1: filled left-pointed triangles, Va^1 ; filled circles, Va^2 ; filled squares, Va^3 ; filled triangles, Vu^1 ; filled inverted triangles, Vu^2 ; circles with crosses, Ca ; filled diamonds, Hv^1 . Axis 2: open circles, Bg ; open squares, Bn ; open triangles, Pr ; open diamonds, Zl^1 . Values shown for Va^1 are one-third of true values. See table 1 for key to snake species abbreviations and country of origin.

Table 1. Site locations, study duration and responsible authors for each species. Ca , *Coronella austriaca*; Nn , *Natrix natrix*; Va , *Vipera aspis*; Hv , *Hierophis viridiflavus*; Zl , *Zamenis longissimus*; Vu , *Vipera ursinii*; Bg , *Bitis gabonica*; Bn , *Bitis nasicornis*; Pr , *Python regius*; Dj , *Dendroaspis jamesoni*; Ns , *Notechis scutatus*.

species	country	site status	latitude	longitude	duration	researcher
Ca	UK	protected	50°44' N	2°08' W	1997–2009	CJR
Nn^1	UK	protected	50°44' N	2°08' W	1997–2009	CJR
Va^1	France	unprotected	47°04' N	2°00' W	1993–2008	GN/XB
Hv^1	France	unprotected	46°07' N	0°25' W	1995–2009	XB/JMB
Zl^1	France	unprotected	46°07' N	0°25' W	1994–2009	XB/JMB
Hv^2	France	protected	46°07' N	0°25' W	1997–2009	XB/JMB
Zl^2	France	protected	46°07' N	0°25' W	1997–2009	XB/JMB
Nn^2	France	protected	46°07' N	0°25' W	1995–2009	XB/JMB
Va^2	Italy	protected	43°16' N	11°09' E	1989–2008	LML/LR/GA
Va^3	Italy	protected	43°42' N	10°30' E	1989–2009	LML/LR/GA
Vu^1	Italy	protected	42°27' N	13°42' E	1987–2008	EF/LML/GA
Vu^2	Italy	protected	42°22' N	13°43' E	1987–2008	EF/LML/GA
Bg	Nigeria	protected	4°38' N	7°55' E	1995–2008	GCA/LML
Bn	Nigeria	protected	4°38' N	7°55' E	1995–2008	GCA/LML
Pr	Nigeria	protected	4°38' N	7°55' E	1995–2008	GCA/LML
Dj	Nigeria	protected	4°38' N	7°55' E	1995–2008	GCA/LML
Ns	Australia	protected	32°07' S	115°39' E	1997–2009	XB/DP

reduced population densities and with no subsequent signs of recovery to pre-crash levels.

The observed population declines were not uniform across the sexes (table 2) such that, with the exception of *Z. longissimus* (Zl^1), there was a significant difference (Student's $t = 2.64$, d.f. = 12, $p = 0.022$) between the mean decline of females (mean = 81.2%, s.d. = 8.071, $n = 10$, range: 69.5–96.0%) and males (mean = 63.8%, s.d. = 19.22, $n = 10$, range: 25.2–89.2%). However, although there was no significant difference ($t = -1.45$, d.f. = 3, $p = 0.243$) between the magnitude of the decline of females from Europe (mean = 78.9%, s.d. = 7.39, $n = 7$) and Nigeria (mean = 86.7%, s.d. = 8.03, $n = 3$) there was one ($t = -2.43$, d.f. = 7, $p = 0.045$) between that of males from Europe (mean = 57.2%, s.d. = 18.80,

$n = 7$) and Nigeria (mean = 79.2%, s.d. = 9.71, $n = 3$). The sex ratio within the stable populations did not change over time.

4. DISCUSSION

The snake population declines shown by these data, though alarming, remain observational as we have no firm evidence to suggest possible causes. Two-thirds of the monitored populations collapsed, and none have shown any sign of recovery over nearly a decade since the crash. Unfortunately, there is no reason to expect a reversal of this trend in the future. Interestingly, six of the eight declining species are characterized by having small home ranges, sedentary habits and ambush foraging strategies while, with the

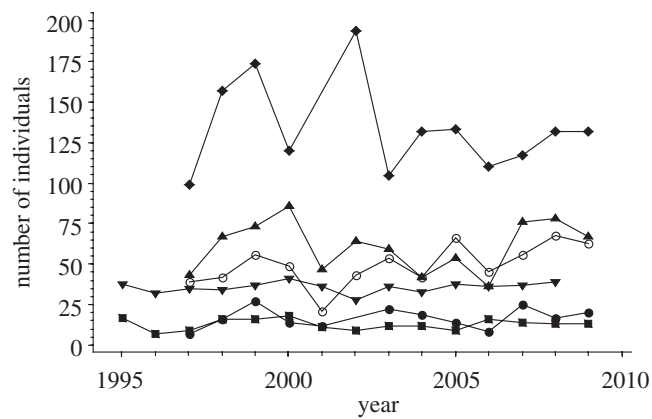


Figure 2. Annual total number of individuals found for five stable and one increasing snake species population. Filled circles, Nn^1 ; filled squares, Nn^2 ; filled triangles, Zl^2 ; filled inverted triangles, Dj ; open circles, Hv^2 ; filled diamonds, Ns . Linear regression analyses of the change in the number of individuals of each species present over time. Stable populations: Nn^1 -nos = $-684 + 0.350$ year, $p = 0.476$, $r^2 = 0.052$, $n = 12$; Nn^2 -nos = $6 + 0.04$ year, $p = 0.987$, $r^2 = 0.0$, $n = 15$; Zl^2 -nos = $-522 + 0.290$ year, $p = 0.814$, $r^2 = 0.005$, $n = 13$; Dj -nos = $-237 + 0.136$ year, $p = 0.548$, $r^2 = 0.031$, $n = 14$; Ns -nos = $2936 - 1.40$ year, $p = 0.537$, $r^2 = 0.039$, $n = 12$. Increasing population: Hv^2 -nos = $-3813 + 1.93$ year, $p = 0.037$, $r^2 = 0.339$, $n = 13$. See table 1 for a key to species abbreviations.

Table 2. Comparing the mean numbers of individuals (male and female) found each year before and after the observed decline of each species shown in figure 1. See table 1 for a key to species abbreviations. Comparisons between means were made using Student's *t*-test.

species	sex	period (before)	mean (<i>n</i>)	period (after)	mean (<i>n</i>)	comparing means			decline (%)
						<i>t</i>	<i>p</i>	d.f.	
<i>Ca</i>	♂	1997–2001	27.8 (5)	2004–2009	20.8 (6)	3.07	0.015	8	25.2
	♀	1997–2001	22.2 (5)	2004–2009	5.8 (6)	11.29	<0.0001	5	73.9
<i>Va</i> ¹	♂	1993–1997	163.2 (5)	2002–2009	26.6 (8)	9.11	<0.0001	5	83.7
	♀	1993–1997	168.0 (5)	2002–2009	10.9 (8)	9.46	0.001	4	93.5
<i>Hv</i> ¹	♂	1995–1996	40.0 (2)	2001–2009	12.8 (9)	8.04	0.079	1	68.0
	♀	1995–1996	18.5 (2)	2001–2009	4.0 (9)	15.14	<0.0001	7	78.4
<i>Zl</i> ¹	♂	1994–1999	16.0 (6)	2003–2009	5.4 (7)	6.27	<0.0001	9	66.2
	♀	1994–1999	5.5 (6)	2003–2009	3.7 (7)	1.63	0.134	10	32.7
<i>Va</i> ²	♂	1989–1999	32.4 (11)	2002–2008	14.9 (7)	16.61	<0.0001	15	54.0
	♀	1989–1999	25.6 (11)	2002–2008	5.5 (7)	35.57	<0.0001	15	78.5
<i>Va</i> ³	♂	1989–1998	57.5 (10)	2002–2009	30.9 (8)	26.05	<0.0001	15	46.3
	♀	1989–1998	41.3 (10)	2002–2009	8.3 (8)	39.37	<0.0001	15	79.9
<i>Vu</i> ¹	♂	1987–1999	60.3 (13)	2003–2008	27.5 (6)	24.64	<0.0001	16	54.4
	♀	1987–1999	48.0 (13)	2003–2008	10.3 (6)	41.96	<0.0001	16	78.5
<i>Vu</i> ²	♂	1987–1999	46.3 (13)	2003–2008	14.3 (6)	24.34	<0.0001	16	69.1
	♀	1987–1999	35.4 (13)	2003–2008	10.8 (6)	25.05	<0.0001	15	69.5
<i>Bg</i>	♂	1995–1999	10.8 (5)	2002–2008	2.3 (7)	18.09	<0.0001	8	78.7
	♀	1995–1999	9.4 (5)	2002–2008	1.7 (7)	10.93	<0.0001	4	81.9
<i>Bn</i>	♂	1995–1998	8.3 (4)	2002–2008	0.9 (7)	20.46	<0.0001	8	89.2
	♀	1995–1998	7.5 (4)	2002–2008	0.3 (7)	21.06	<0.0001	5	96.0
<i>Pr</i>	♂	1995–1999	12.6 (5)	2005–2008	3.8 (4)	15.58	<0.0001	5	69.8
	♀	1995–1999	10.2 (5)	2005–2008	1.8 (4)	11.92	<0.0001	5	82.3

exception of *N. scutatus* (*Ns*), whose movements are restricted by the small size of the island on which it occurs, all of the stable/increasing species are wide ranging, active foragers (Luiselli *et al.* 2000). These patterns fit the prediction that 'sit-and-wait foragers may be vulnerable because (i) they rely on sites with specific types of ground cover, and anthropogenic activities disrupt these habitat features, and (ii) ambush foraging is associated with a suite of life-history traits that involve low rates of feeding, growth and reproduction' (Reed & Shine 2002).

In Europe, although habitat loss/change may be the main cause of these declines, other factors, such as prey availability, habitat edge destruction and pollution, may also be involved because several declines occurred in well-protected areas. A similar scenario may have also occurred in Nigeria, where the study sites that included both declining and stable populations were adjacent to the Stubbs Creek Forest Reserve, which is a well-protected area. Nevertheless, the shape of the observed population declines, leading to significantly reduced snake densities after the 'crash'

is indicative of a change in habitat quality, rather than habitat loss, with a subsequent reduction in its carrying capacity, e.g. reduced prey availability (McLoughlin *et al.* 2003). It is possible that the declines are co-incident and that the causes vary between sites. However, this seems unlikely as all the declines occurred during the same relatively short period of time and over a wide geographical area that included temperate, Mediterranean and tropical climates. We suggest that, for these reasons alone, there is likely to be a common cause at the root of the declines and that this indicates a more widespread phenomenon (Pounds *et al.* 2006; Feyrer *et al.* 2007; LaDeau *et al.* 2007). For instance, synchrony could be attributable to common stochastic environmental factors (Weatherhead *et al.* 2002); worldwide and synchronized declines have been already observed in amphibians (Pounds *et al.* 2006). Although, in this study, the small sample size (17 populations of eight species) with taxonomic, geographical and ecological biases makes extrapolation difficult, the declines are sufficiently striking to warrant attention.

Overall, the worrying trends we report suggests that snake researchers should work more closely with one another to better identify the factors responsible for the widespread population declines of snakes in order to understand, stop and ultimately reverse them.

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