Lessons from Europe

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Amphibians and reptiles are coming to be regarded in Europe as indicator groups for a general decline in species diversity (Thielcke et al., 1983; Blab, 1985, 1986). The decline of these groups has been well documented in Europe and on other continents as a result of numerous surveys (e.g., Lemmel, 1977; Feldmann, 1981; Hayes and Jennings, 1986; Hölzinger, 1987; Osborne, 1990; Carey, 1993; Mahony, 1993). Even in areas little affected by human activity, declines seem to have occurred. However, to date, adequate investigations of the declines and their actual causes are lacking (Pechmann et al., 1991; but see Osborne, 1989).

The global decline of amphibians over large land masses is presumed to be attributable to as yet essentially unknown factors (Blaustein and Wake, 1990; Yoffe, 1992), while previously established causes of decline have been neglected. However, the reverse tendency exists for local and regional investigations—in those cases, as a rule, factors are readily identified as causes, but are seldom investigated because the causal relation to observed declines is often difficult to clearly establish (Henle and Streit, 1990). Thus, there is frequently not a clear distinction between potential threats and proven causes, and many opportunities to prove causal connections, or at least to carefully construct foundations for hypotheses, are missed. A scientifically based analysis of causal relations is essential to effective conservation efforts since it leads to the prediction of appropriate countermeasures.

The most important type of database for the documentation of the declines of amphibians and reptiles and their potential causes results from regular surveys of a specific geographic area. Surveys will maintain this important role in the future. Therefore, attempts should be made to fully utilize the potential of these surveys for causal analysis of declines within the bounds of permissible conclusions. That is, the limits of herpetofaunal surveys as a tool for determining the causes of decline must be explicitly defined. The available methods for causal analysis are insufficiently known to many people engaged in surveying projects because of inadequate education in

* Translation by William T. Leja of Möglichkeiten und Grenzen der Analyse von Ursachen des Artenrückgangs aus herpetofaunistischen Kartierungsdaten am Beispiel einer langjährigen Erfassung. 1996. Zeitschrift für Feldherpetologie 3:73–101. statistics and research planning. The goal of this work is to demonstrate the available methods of causal analysis, as well as their limitations, by applying the methods in the analysis of a long-term surveying project (Henle and Rimpp, 1994). Further, remarks on the optimization of surveying projects that will facilitate subsequent causal analyses are presented. By suggesting improvements in the planning and assessment of future surveying projects, I hope to contribute to the technical support of herpetological conservation work, and with that, to the protection of our amphibians and reptiles.

Methods for Analysis of the Causes of Species Decline

The principles of planning and analysis of experiments furnish three experimental approaches for evaluating causal relations in ecology: (1) laboratory experiments, (2) field experiments, and (3) unplanned or natural experiments (Diamond, 1986; Henle and Streit, 1990). In all three types of experiments the presence of adequate control populations that remain unaffected by the factor in question (e.g., road traffic) is essential. Likewise, it is important to formulate a precise question in the form of a so-called null hypothesis, for example, "Addition of pollutant chemicals to a water body does not lead to increased mortality in comparison to unpolluted water bodies." The probability that the null hypothesis is correct is then determined statistically. The advantages and disadvantages of the three different experimental approaches are briefly summarized below.

Laboratory Experiments

Laboratory experiments have the advantage that disturbances are largely eliminated; independent variables (in our case, potential threats) are controlled, allowing the effect of a specific threat to be clearly determined. They have a disadvantage in that their relevance to natural systems is highly questionable because of the stark simplicity of the laboratory system. This problem can be minimized, but not fully eliminated, by the use of experimental conditions that simulate natural conditions as much as possible. There has been considerable investigation in the laboratory of the threat posed to amphibians by predators (e.g., Glandt, 1984; Kats et al., 1988; Semlitsch, 1993). However, in this case the results are frequently of severely limited applicability or are actually inapplicable to field situations because of the generally simplified and artificial laboratory conditions.

Field Experiments

Field experiments are of far greater relevance. The chief problem is the difficulty of finding a suitable research area for the desired manipulation within a landscape utilized by humans. Further problems are the difficulty in obtaining permission from the responsible government authorities, and the difficulty of holding the effect of disturbance factors (such as the conditions on the shore of amphibian breeding ponds or the vegetation structure of reptile habitats) constant. Because of these difficulties, relatively few field experiments on the influence of threats to amphibians or reptiles exist (for one example, predation by fish, see Breuer and Viertel, 1990; Breuer, 1992).

Unplanned or Natural Experiments

Unplanned or natural experiments offer a better alternative. Two different categories must be distinguished: natural *snapshot* experiments, in which a final steady state (or an intermediate state) resulting from a perturbation is observed by comparison of affected and unaffected systems; and natural *trajectory* experiments, in which the progression of changes in a system caused by a perturbation are observed as they unfold over time. The principal advantage of these experiments lies in their relevance to large areas over long periods of time. For this reason they are more realistic and of greater general validity. Natural experiments "interpreted by experience" generally form the basis of our empirical knowledge. That knowledge is clearly derived from complex nonlinear associations, as very commonly occur in nature conservation, and it can easily be misleading.

A particular disadvantage of natural experiments is the difficulty of eliminating confounding factors. In this regard, it is generally necessary to develop an extensive database from which an adequate partial database can be chosen, or to identify confounding factors and when possible to "remove" their influence with various statistical methods. With snapshot experiments, moreover, two factors can be merely correlated with each other coincidentally or because both depend on a third factor. An example of such a situation is the well-known correlation of the decline of the stork population in East Prussia and the human birth rate (both factors are independent of each other and caused by a third factor, industrial growth; Sachs, 1982). In snapshot experiments, therefore, this possibility must be eliminated as much as possible, or hypotheses need to be supported indirectly (see below). The value of hypotheses resulting from natural trajectory experiments is severely reduced if, as is often the case in nature conservation, a system is first studied during the beginning of a disturbance or even after it is in progress, and if it is not monitored with adequate controls. Natural trajectory experiments can result from fish stocking, entry of pesticides, or enlargement of agricultural fields, among others.

The three types of experiments are mutually complementary. Additional support of an interpretation, particularly for natural snapshot experiments but also for natural trajectory experiments, can be provided through knowledge of the biology of the affected species or the ecology of the affected habitat

Amphibian and Reptile Populations in the Rutesheim/Renningen Region



FIGURE 12-1 Location and dynamics of amphibian and reptile populations in the study site. Hatched = forested areas; Dark = villages; White = agricultural areas.

(for example, Schlüpmann, 1982; King, 1984; Dickman et al., 1993). These opportunities are seldom utilized during the analysis of survey data (see below).

Materials and Methods

Research Area and Study Methods

The research area, about 50 square kilometers in size, lies on the western edge of the Stuttgart region (southern Germany). Agricultural fields predominate, occupying 57% of the land surface, followed by forest, occupying 33% of the land. The remaining 10% consists of settlements and small gardens. Aside from expansion of settlements on agricultural land, which is of little value to amphibians and reptiles, land use changed only slightly during the research period. The number of water bodies clearly decreased (see below). The research area is poor in natural water bodies and in thermally favorable sites. Henle and Rimpp (1994) published a more complete description.

Since 1966, herpetofaunal populations, their habitats, and the factors that posed potential threats have been surveyed with varied intensity within the research area (Rimpp and Hermann, 1987; Rimpp, 1992; Henle and Rimpp, 1993, 1994; Fig. 12-1). Breeding waters were characterized by employment of the following parameters, among others: type; surface area and depth (>2 m or <2 m); shading (four categories); shallow water zones—narrow (<1 m wide) or extensive (>1 m wide); shore structure (flat/steep, obstructed/unobstructed); degree of cover of submerged vegetation, floating-leaf vegetation, reeds or shore shrubbery; location (distance to roads; type of surroundings—deciduous forest, wet meadows, settlements, etc.). For reptile habitats the following characteristics were noted: type of habitat; general penetration of sunlight; presence of sunning places and open areas; degree of cover by low vegetation, bush and tree layers (four classes for each parameter); and the location. Further, all potential threats to mapped populations were recorded.

During the annual observations, coarse estimates of relative abundance were made. However, quantitative determinations of population sizes were not attempted. Amphibian populations were considered large if the estimated population at a breeding site exceeded 100 adults or small if the estimate was fewer than 50 adults. Irregular observations of individual reptiles were considered to represent a small population, whereas populations were considered large if there were regular observations of snakes or slow worms (*Anguis fragilis*) or more than 10 observations of other lizard species.

Observations were made throughout the research area in the course of the 26-year mapping project, with the intention of surveying all potential habitats for amphibians and reptiles at least once. Apart from the smallest habitats and habitats that came into existence after the first traverse, the monitoring of amphibian and reptile habitats is believed to be complete. Numerous habitats were selected for observation after the survey began, as is usually the case for most surveying projects. Annually, the largest and most biologically rich habitats were traversed thoroughly; the remaining habitats were surveyed irregularly (for an overview of the monitored habitats, see Henle and Rimpp, 1994).

Extinction and Colonization Dynamics

A total of 13 amphibian and 7 reptile species were found in the research area (Henle and Rimpp, 1994; Table 12-1), of which palmate newts (*Triturus helveticus*), European pond turtles (*Emys orbicularis*), and pond sliders (*Trachemys scripta*) were definitely released and were not native to the research area. Palmate newts occur in neighboring regions (Rimpp and Hermann, 1987). During the study period, natterjack toads (*Bufo calamita*) and European treefrogs (*Hyla arborea*) disappeared, whereas agile frogs (*Rana dalmatina*) were actively colonizing new areas.

Amphibian populations occurred at 91% of the 54 observed wetland complexes. Twenty (24%) of the 82 water bodies that were investigated within these wetland complexes disappeared: seven disappeared or were rendered unsuitable through human construction activity; five were intentionally filled; four were excavation pits that disappeared through change in use or through abandonment; two disappeared through natural succession to land; one dried out due to a failure of the seal on the bottom; and one disappeared primarily because of a lowering of the water table. Countering these losses were the creation or installation of five ponds (one of them was created in the 1930s) by the forest administration; the installation of six amphibian conservation ponds; the installation of a cattle watering pond as a substitute for a filled sinkhole pond; and the construction of three rainwater interception ponds alongside a highway. However, the rainwater interception ponds were unsuitable amphibian habitats because of their location

and structure. Additionally, one pond was renaturalized to serve as a nature conservation pond.

During the research period a total of 107 colonizations (94 by amphibians and 13 by reptiles) were recorded (Henle and Rimpp, 1993). Of these, however, only 51 amphibian and two reptile populations persisted. The successful colonizations by amphibians occurred in the newly created or renaturalized ponds. Further colonizations occurred at the preexisting ponds, but were as a rule unstable and at most based on few individuals (status as of 1991). On the other hand, 102 amphibian populations and 22 reptile populations (Table 12-1) disappeared.

Data Evaluation

Research aimed at analyzing the degree of isolation of neighboring populations was not conducted. Therefore, the observed colonizations and extirpations cannot be differentiated into populations and subpopulations. Of course there were indirect and accidental observations of dispersions (Henle and Rimpp, 1993, 1994) that suggest that most of the amphibian and some of the reptile species in the research area exist as metapopulations, with limited exchange among subpopulations. However, generally, as expected in larger research areas, a continuum of fully isolated populations to barely separated subpopulations occurred. Arbitrary division of this continuum was not attempted. The term *population* is therefore used independent of the degree of isolation of the individuals in a biotope used for breeding (e.g., a pond) that is spatially isolated by biotopes that are not suitable for breeding. Connected, heterogeneously structured breeding habitats are considered to be one habitat. Because summer habitats of amphibians were not specifically mapped, they cannot be included in the analysis. The database is altogether typical for long-term surveying projects of defined research areas.

Given the time constraints inherent in surveying many sites over large areas, it is difficult to devise a method that distinguishes between areas where a species is simply overlooked, where there are actual disappearances (Den Boer, 1990), or where there are complete shifts to a neighboring breeding site in species that do not exhibit philopatry (Tester, 1990). In keeping with the need for a conservative approach, absences of species that are difficult to find were only judged as losses if no individuals were found in spite of intensive searches for at least 5 years. Five years was chosen because most native amphibian species in climatically comparable regions exhibit a turnover of the breeding population of at most 5 years (Heusser, 1970; Bell, 1977; Ryser, 1986; Tester, 1990; Kuhn, 1994; Wolf, 1994). The following are regarded as difficult to find: newts in large, richly structured ponds; snakes; slow worms; and lizards in small populations within large, potentially suitable habitats. Likewise, losses at ponds that occasionally dry up and are later resettled are only recorded as losses if the interval is at least 5 years-amphibians can also seek breeding ponds in the years following their destruction (Heusser, 1970; Blab, 1986; Kuhn, 1994), and an observed collapse may be the collapse of an age class rather than the loss or emigration of a population.

Detailed reports of the investigated habitats and changes in their species composition were published by Henle and Rimpp (1993, 1994). A few unimportant departures from those publications are based on additional data first available for consideration in the present work. Three previous classifications and one printing error in Henle and Rimpp (1993) were corrected.

TABLE	12-1
Known and Inferred	Causes of Decline

Causes of Loss of Populations							
Species	Number of Populations	Habitat Loss (L–D)	Chemical Pollutants	Fish	Natural Losses (S–T–E)	Unknown	
Salamandra salamandra	11	1-0	_	_	_	-	
Triturus alpestris	44	6-1	(1)	-	2-3-3	6	
T. cristatus	6	2-0	_	(1)	-	2	
T. helveticus	3	-	-	_	0-0-2	-	
T. vulgaris	17	2-0	(1)	-	2-2-1	4	
Bombina variegata	15	3–0		-	2-3-2	1	
Bufo bufo	37	4-0	5	-	0-4-1	1	
B. calamita	2	2-0	-	-	_	-	
B. viridis	5	2-0	_	-	-	-	
Hyla arborea	7	1-0(1)	-	-	0-0-3	2	
Rana dalmatina	9		-	-	0-0-1	-	
R. esculenta/lessonae	12	4-0	2	-	0-0-1	2	
R. temporaria	34	3-0	(1)	2	2-1-3	1	
(Emys orbicularis)	1	-	-	-	0-0-1	-	
(Trachemys scripta)	2	-	_	-	0-0-2		
Lacerta agilis	19	1-0		-	(2)	2	
L. vivipara	21	1-8	_	-	_	-	
Anguis fragilis	16	1-0(1)	-	-	-	-	
Coronella austriaca	6	-		-	-	-	
Natrix natrix	10	1-0	-	-	0-0-1	1	
Totals	277	43 + (2)	7 + (3)	2 + (1)	42 + (2)	22	

NOTE: L = lethal habitat losses; D = habitat losses demonstrated or considered very likely on the basis of dynamic experiments; S = losses due to natural succession; T = losses due to the drying out of spawning sites; E = unsuccessful colonization attempts. The number of observed losses coinciding with assumed causes but with insufficient controls for an analysis of natural experiments are included in parentheses.

The statistical methods of Sachs (1982) were employed. Applications of probability theory were based on Bosch's (1976) textbook.

Results: Analysis of the Causes of Population Extirpations

A limited number of factors causing the extirpation of populations have repeatedly appeared in the literature. These factors have been divided into seven groups (Henle and Streit, 1990). Using these seven groups of factors, the possibilities and limitations of such an analysis of extirpation causes is presented below for the present survey project. The results of the analysis are summarized in Table 12-1.

Destruction and Alteration of Habitats

Sixteen out of 82 breeding ponds studied during the research period were completely destroyed. Along with these ponds, 32 amphibian populations (31% of the losses) and a population of

ringed snakes (*Natrix natrix*; 5% of the reptile losses) were extirpated. The time at which a population of European treefrogs disappeared is not precisely known. Although the population may have disappeared before the complete destruction of its breeding pond, that destruction is considered as the presumed cause of the extirpation. However, because the entire surroundings had been developed previously, resulting in decreasing terrestrial habitat, this loss can probably be listed as due to habitat alteration. This extirpation should not be attributed to unknown causes (Table 12-1). Ten large and 10 small populations disappeared; the sizes of the remaining 12 populations are not sufficiently known.

The habitats of four reptile populations were eliminated when they were covered with concrete and sod. Biological knowledge that reptile populations cannot live on concrete and sod substitutes in this case for otherwise indispensable control habitats. Similarly, no control is necessary with the complete destruction of a breeding pond because it is essential to the life of an amphibian.

For two species, common lizards (*Lacerta vivipara*) and alpine newts (*Triturus alpestris*), comprehensive natural trajectory

experiments involving habitat changes have been evaluated. During the research period, 21 populations of common lizards were found, with 14 of these inhabiting wooded regions. The habitats of eight of these populations were forested with conifers or dense beech stands; none of these populations has survived. The habitats of the remaining six populations continue to be maintained as open deciduous or mixed deciduous forest with clearings or wide, sunny path edges; all these populations have survived. Under the extremely conservative assumption that exactly eight populations would have to survive, the probability of an accidental extirpation of eight populations exclusively in the changed habitats amounts to:

$$\alpha = \begin{bmatrix} 8 \\ 14 \end{bmatrix} = 0.0003$$

With a probability of error of 0.03%, the null hypothesis that the habitat changes in the forests had no influence on the disappearance of common lizards can be rejected.

Closed forest canopies, which prevent direct sunlight from reaching the ground, offer only infrequent opportunities for common lizards to achieve their preferred temperature range of 29–34 °C (Van Damme et al., 1986). Most essential physiological processes, such as various aspects of feeding, reach 80% of their optimal value at body temperatures of 25–30 °C (Van Damme et al., 1991); common lizards cease all activity in the summer at temperatures below 16 °C (Van Damme et al., 1990). Thormophysiological information, along with appropriate temperature measurements, could also have explained the observed losses without reference to a natural trajectory experiment with control populations. However, this would be uncertain, since the microclimatic conditions severely limit activity but are not directly lethal.

Ten bomb craters or sinkholes of 1–175 m² size (depending on annual rainfall) north and west of Rutesheim were surveyed almost every year. Eight of them are situated in beech stands (Fagus sylvatica), or in mixed stands primarily of beech with some Norway spruce (Picea abies) and a few pines (Pinus species); one was located at the transition zone between deciduous forest and old spruce forest. Alpine newts bred annually in nine of these sinkholes. The tenth sinkhole was located in a spruce nursery. As the nursery matured, alpine newts steadily decreased during the 1980s and disappeared in 1986. If one of 10 populations disappears, the chance that this would accidentally occur at the impaired pond is 1 out of 10, or 0.1. Excluding populations that disappeared because of habitat destruction, a total of 15 out of 37 alpine newt populations included in the study disappeared. This indicates an average probability of extirpation of 0.41 (in 26 years). In view of this extinction probability, the chance of an accidental extirpation of the population in the spruce forest is only 0.04. The hypothesis that "the growth of the spruce forest led to the extirpation of the population" is additionally supported by the fact that another population about 1.5 kilometers away disappeared after increased shading from a spruce monoculture. However, the water level of its breeding pond also sharply decreased (Henle and Rimpp, 1994) so that population is not directly applicable as a control.

A parallel snapshot experiment permits confirmation of the conclusion that dense spruce forests (in the research area) led to the disappearance of alpine newt populations. An additional bomb crater, located in a dense spruce forest about 15 m from one of the 10 other bomb craters, was avoided between 1966

and 1989. After intense storm damage in the winter of 1989–90 and subsequent complete deforestation of the surrounding area, alpine newts oviposited in this bomb crater in the following 2 years. Of course, alpine newts breed in other research areas (although infrequently) in shaded ponds within spruce stands (Loske and Rinsche, 1985). For this reason the snapshot experiment by itself must be carefully interpreted. It is conceivable that a lighter stand of spruces or a difference in the buffering capacity of the pond water could have permitted settlement of the ponds observed by Loske and Rinsche (1985).

The snapshot experiment, as well as the result of the above trajectory experiment, is valid in the same way for common toads (*B. bufo*). They were definitely absent in the sinkhole in the matured spruce nursery in which alpine newts disappeared. Therefore, for common toads, a colonization rather than an extirpation was proven to result from habitat change.

The reasons for the unsuitability of the pond and the disappearance of alpine newts cannot be determined with complete certainty. Possibilities other than the cool, shady location are the acidification of the ground or the water. No measurements related to either factor were made at the site. Investigations of the minimal temperature at which alpine newt larvae can still successfully develop or of preferred breeding water temperatures are lacking to my knowledge. In some cases, shady breeding waters in the research area are settled by alpine newts (Henle and Rimpp, 1994). In other places the species lives under substantially more extreme climatic conditions, but breeds, as would be expected, only in thermally favorable ponds (Nöllert and Nöllert, 1992).

In conifer forest monocultures low pH values in the soil (<pH 5) frequently occur (Mückenhausen, 1985). However, this may not cause a problem for terrestrial alpine newts because adults can be encountered in breeding waters of pH less than 5 (Stevens, 1987). In contrast, embryos exhibit increased mortality under pH 4.5, and complete mortality at pH 4 (Böhmer et al., 1990). Acid pulses in spring after snowmelt could therefore be responsible for the avoidance of ponds. Unfortunately no measurements were made, but Loske and Rinsche (1985) measured pH values of less than 4 in pools within spruce stands and observed strings of dead spawn of common toads infected with fungi. Although a slight drop in the water table that occurred at the same time as the increased shading may have contributed to a reduction in the population, it can be excluded as the main cause since three of the remaining sinkholes exhibited considerably lower water levels (of 20 cm maximum) for a period of 1-3 years without abandonment by alpine newts.

In the course of widening a highway along the edge of the habitat of a slow worm population, the reconstructed road shoulder became smaller and much steeper and was fortified with stone blocks. This population disappeared after this qualitative change in its habitat. No other population in the research area was affected by similar habitat changes. In the other 15 slow worm habitats surveyed, severe changes occurred in some cases. In the most extreme case, widely spaced homes were built on the habitat; none of these other populations disappeared. Because a sufficient number of similarly altered habitats (as well as unaltered control habitats) are lacking to allow an experimental evaluation, in this case, habitat alteration is merely presumed as the cause of disappearance of the slow worm population.

At five ponds on fallow land or within meadows under light agricultural use, 3-7 (average = 5.4) amphibian species were found. Common toads and common frogs were always present

at the ponds; either smooth newts or alpine newts were also invariably present; water frogs (*R. esculenta/lessonae*), agile frogs, European treefrogs, or crested newts (*Triturus cristatus*) were sometimes present. Ringed snakes were also present at four of these ponds. In contrast, there were no amphibians at a pond in a meadow in the middle of an intensively farmed area. There were no woods, hedges, field borders, or old fields within 300 m of the pond. This pond is completely encircled by shrubs and lacks a surrounding reed belt, further differentiating it from the others.

Pools with diameters of up to 5 m exhibited similar relationships. Common frogs always oviposited in such water bodies on lightly farmed meadows or fallow land (n = 4), whereas they were lacking at two similar ponds on intensively farmed fields. Essential summer and winter quarters are provided for most amphibians by hedgerows and woodlots (e.g., newts, Beebee, 1985; European treefrogs, Stumpel, 1993), whereas intensively farmed fields and pastures are microclimatically unsuitable (Wolf, 1994) and presumably offer scant protection from predators. Moreover, thermally favorable locations for oviposition by ringed snakes (Zuiderwijk et al., 1993) are lacking in the absence of vegetative cover.

In summary, alteration or destruction of habitats within the research area was definitely responsible for the disappearance of 43 populations or subpopulations and probably responsible for the disappearance of two others. This represents 35–36% of the losses.

Chemical Pollutants

Five water bodies were significantly overloaded with environmental pollutants or fertilizers. From 1972 to the early 1980s near the Rutesheim dog training club, used oil, styrofoam, and other refuse was dumped repeatedly (in violation of the law) into a shallow residual water body of about 200 square meters. This pond is a remnant of a large wetland that was drained in 1928. Animal excrement also entered from a neighboring small-animal rearing facility belonging to a small farm animal fanciers club. Alpine newts and smooth newts disappeared during this period of pollutant loading. The last individuals of both species were found in 1975. A population of common frogs in this water body steadily decreased in the second half of the 1970s, but held out as a small breeding population until 1988 in a bordering depression that was only affected by the pollutant loadings at extraordinarily high water levels.

A quite similar water body about 150 m away, part of the same former wetland complex, serves as a control water body. The two water bodies are separated by an expressway. All three species still occur here. Common frogs also survived at another water body with similar depth, shore structure, size, shading, growth of vegetation, and surroundings (meadows; distance to woods of 100-250 m). Newts were first regularly observed at this water body after 1980, for which reason it cannot serve as a control water body in the present case. Additional control water bodies (with two populations of alpine newts as well as three populations each of smooth newts and common frogs) are of limited applicability here because they are clearly different in size, depth, or shore structure. Another nine potential control populations of alpine newts inhabited water bodies that are quite comparable in size and shore structure, but all of them are situated in deciduous forest and in some cases are significantly deeper. Upon consideration of these populations, the probability of an accidental extirpation in the polluted water body approaches significance only for alpine newts ($\alpha = 0.09$).

The continued oviposition by common frogs in the unpolluted depression definitely proves that, at least for this species, the reasons for its extirpation must have lain in the breeding habitat rather than the terrestrial habitat. Also, the common disappearance of all three species with the entry of pollutants points to the pollutants as the cause. However, it must be remarked that common toads disappeared before 1970 at the polluted water body, before the occurrence of substantial pollution. The hypothesis that the disappearance of the three species accidentally occurred at the polluted water body cannot be rejected, even though much evidence suggests that it is incorrect. Therefore, these three losses should be designated as "presumably caused by chemical pollutants" (Table 12-1).

The two Längenbühl Ponds, one lying directly behind the other, were polluted with liquid manure from a swine fattening operation. Both ponds were designated as Nature Monuments at the beginning of the 1970s on the basis of formerly large water frog populations (Henle and Rimpp, 1994). During my first year of observations (1973), the water bodies were already severely polluted. At that time, only common toads and common frogs were still breeding at both ponds. The pollution has clearly decreased since the end of the 1980s. Common frogs have continued to breed regularly since the late 1980s, but, as previously, their spawn have always failed to develop. Additionally, every few years there have been attempts at breeding by common toads from a quite large breeding population 250 m away. There were at least five failed attempts. Likewise, the lack of success is probably a result of the severe pollution. Common frogs are not considered to be extirpated at these water bodies, although there definitely has been a lack of successful larval development during the research period. On the basis of the life expectancy of common frogs (Heusser, 1970), the isolated oviposition that has been observed, at least in the 1980s, probably resulted from individuals that annually migrated from a very large breeding population 250 m away. Apart from two populations in dried out water bodies, the only other case of oviposition by common toads without successful embryo development occurred at a water body that was potentially polluted by runoff from a highway drain. With the remaining 15 populations of common toads, which serve adequately as controls, embryo development was successful and there was no indication of pollution. This difference is highly significant ($\chi^2 = 17$; $\alpha = < 0.001$).

Severe pollution due to over-fertilization was observed at two further water bodies: the pond on the southwest edge of the Village of Silberberg and the settling pond at the Hardtsee. A buildup of putrid sludge has been observed at both water bodies since the second half of the 1980s. The Silberberg Pond lies in a water protection zone, but that has not prevented a farmer from dumping liquid manure on adjacent pastures and fields. Discoloration of large portions of the bottom and occasional intense releases of sewer gas have occurred at this pond. The Silberberg Pond originally possessed eight amphibian and one reptile species; today only common frogs and common toads remain. The losses (alpine newts, crested newts, smooth newts, yellow-bellied toads [Bombina variegata], European treefrogs, and water frogs) cannot, however, clearly and exclusively be attributed to hypereutrophication. The pond was drained in 1978 and 1979 and was previously reduced in size by partial filling; additionally, a few species had declined or disappeared (crested newts and European treefrogs) before hypereutrophication.

Control water bodies, in which either sludge buildup occurred without habitat changes or corresponding habitat changes occurred without sludge buildup, would be necessary for evaluation of a natural experiment. Intense sludge buildup occurred, however, only at one additional pond-the previously mentioned settling pond at the Hardtsee. It was installed as a settling basin for the removal of sediments in water entering a larger pond, the Hardtsee. Alpine newts, crested newts, smooth newts, common toads, agile frogs, water frogs, and common frogs bred in the settling pond. All the species produced large populations at the beginning. With the exception of common toads, common frogs, and agile frogs, all the populations decreased as the pond filled with sludge, and crested newts completely disappeared. This is consistent with the Silberberg Pond, which was also polluted with putrid sludge. The settling pond at the Hardtsee, however, cannot be employed as a control for this pond since, additionally, fish were released in it. In the Hardtsee, which receives effluent from the settling pond, the same species decreased as in the settling pond, and crested newts likewise disappeared. However, the Hardtsee is unacceptable as a control because it was also stocked with fish (to a considerably higher degree than the settling pond), and nutrient pollution only occurred in some years, in particular as a result of large-scale feeding of mallards (Anas platyrhynchos). Because the population shifts slowly occurred at all three ponds, and other factors (habitat alteration and fish stocking) were probably involved, and further because there were no further potential control water bodies, these losses must be considered to be of unknown (presumably complex) origin rather than due to pollution.

In connection with pollution, it should further be mentioned that common frogs spawned in two of three ponds constructed in the course of the widening of a highway. Runoff from the highway drained into each of the ponds. Common toads also spawned in one of the ponds. All the spawn clumps of common frogs were destroyed by fungi, and larger larvae or juveniles of common toads were never observed. In 1991 and 1992, common toads no longer spawned in these ponds. The lack of successful development suggests that chemical pollution was the cause of the extirpation (see above). Moreover, it was the only case (n = 10) of the colonization of a newly constructed pond by common toads that failed. Chemicals leached from materials used in highway construction can lead to acidification of adjacent water bodies and the loss of amphibian populations (Harte and Hoffman, 1989), and attack of spawn by fungi occurs frequently in acidic waters (Clausnitzer, 1987). Nevertheless, this loss cannot be attributed to pollution, but is classified as "unknown." Chemical pollution can only be the presumed cause because analytical demonstration of the presence of chemicals in toxic concentrations is lacking and other causes cannot be excluded. The three ponds alongside the highway are clearly different from the remaining newly constructed ponds in their location and shore structure. Accidental factors must also be considered in regard to high extirpation rates of small, newly founded populations (Wissel and Stephan, 1994).

Seven populations (6% of the losses of amphibian populations) were extirpated at the three water bodies at which chemical pollution could be proved as the cause.

Predators

Two attempts by common frogs to breed in a trout-rearing pond were unsuccessful because the spawn was consumed. No

amphibian spawned on any of the remaining basins used for intensive rearing of trout. However, common frogs regularly spawned on an adjacent basin that was not used for trout rearing.

In one pond, crested newts disappeared after the stocking of fish. However, there were no controls for this observation, so it is not proven that fish were the cause; also, the fish did not reach such an extreme density (as would exist in a trout-rearing installation) that total predation would be certain. However, there are indirect observations that corroborate the hypothesis that fish exert a negative influence. After the disappearance of crested newts, the pond was maintained free of fish for two years. During these years, the survival of common toads and common frogs to metamorphosis increased several-fold (K. Rimpp, personal communication). But since semiquantitative control studies at comparable ponds are lacking in this case, this hypothesis remains speculative-especially since Schlüpmann (1982) observed that tadpoles of common toads remain undisturbed in concrete basins of rainbow trout (Oncorhynchus mvkiss).

In order to settle the often hotly debated controversy between amphibian conservationists and anglers, predation experiments were carried out in the laboratory (Bauer, 1983) with various fish species: roach (Scardinius erythrophthalmus), European carp (Cyprinus carpio), eel (Anguilla anguilla), chub (Leuciscus cephalus), tench (Tinca tinca), and rainbow trout. In a 200-L container, 6–8 large larvae of alpine newts or smooth newts (crested newts were not tested) were added in each experiment to each fish species. The investigations indicated that all the fish species tested consumed all the larvae within eight hours to seven days. A detrimental effect of fish on the above-mentioned crested newt population is therefore possible. However, the laboratory investigation is not considered valid for crested newts, nor is it at all likely to have any relevance to field conditions, because amphibians exhibit a variety of defense mechanisms (for example, skin toxins, behavior, and choice of microhabitat) against fish (Duellman and Trueb, 1986). Also, in the above-mentioned laboratory experiments, no cover was offered. Adequate cover substantially alters the survival rate (Kats et al., 1988; Semlitsch, 1993). Laboratory experiments of various authors, for example, illustrate that common toad tadpoles possess better defensive mechanisms against predation from most fish species than other native amphibian species (see literature overview in Breuer, 1992). Moreover, fish species vary in their predation on a given amphibian species under laboratory conditions (Glandt, 1984, 1985; Breuer, 1992).

Seminatural experiments (Semlitsch and Gibbons, 1988) or carefully evaluated natural trajectory experiments are largely lacking so far for European amphibians (Henle and Streit, 1990). However, Breuer and Viertel (1990) and Breuer (1992) have shown in field experiments that European carp and rainbow trout clearly increase the mortality of tadpoles of common toads and common frogs (rainbow trout more considerably affect mortality than do carp). Common frogs have poorer defense mechanisms at their disposal than do common toads, and in contrast to the latter they do not survive to metamorphosis in every experiment.

Clear but unsupported indications of fish as a cause of the loss of breeding populations are available from personal investigations of a pond just outside the research area. After heavy stocking of European carp, grass carp (*Ctenopharyngodon idella*), rainbow trout, catfish (*Silurus silurus*), northern pike (*Esox lucius*), and pike perch (*Lucioperca lucioperca*), the following

amphibian species disappeared from a pond in an abandoned quarry: alpine newts, smooth newts, yellow-bellied toads, green toads (B. viridis), and common frogs. At the same time, green toads and common frogs continued to inhabit four control ponds (likewise outside the research area). There were only two control populations for smooth newts and only one for alpine newts and yellow-bellied toads. For the species with four control populations, the probability of accidental extirpation in the pond where fish had been stocked was 20%. The parallel extirpation of five species would therefore be significant ($\alpha <$ 0.01). Because a portion of the terrestrial habitat had been altered at the same time the fish had been stocked, the possibility that the habitat alteration was responsible for the extirpations cannot be excluded. However, a substitute pond in the immediate vicinity that was constructed 2 years after fish stocking as an amphibian breeding pond was utilized successfully for at least 5 years by green toads and smooth newts. Therefore, the changes in the surrounding terrestrial habitat cannot be responsible for the disappearance of these two species in the original breeding pond. Fish stocking remains the sole cause of disappearance of at least these two species.

Isolated observations of predation on spawn by mallards occurred in three ponds, but common frogs did not disappear from any of them. Common frogs are indeed absent from park and farm ponds in Westphalia that are heavily stocked with mallards (Schlüpmann, 1981), but mallards are only seldom likely to present a serious threat to this species (Kwet, 1996).

Predators (fish stocking) were responsible for the loss of 2% of the amphibian populations. Fish predation was the presumptive cause of extirpation for one large population of the crested newt. All other populations involved were small.

Collecting

The influence of the collecting of amphibians and reptiles on the survival of the affected populations is a hotly debated issue for which little supportive information exists (Ehmann and Cogger, 1985; Henle and Streit, 1990). The danger from the collecting of amphibians and reptiles depends, among other factors, on the size of the range and the survival strategy of the affected species (Henle and Streit, 1990), and can only be determined objectively by field experimentation or estimated reliably by extrapolation from thorough investigations of population dynamics (Henle and Streit, 1990).

Animals were taken more or less regularly out of several populations in our research area. These removals were more frequent in the 1960s and 1970s than in the 1980s, when removals were only seldom observed—presumably because of decreasing interest as a consequence of tighter legal restrictions on collecting and rearing. Convincing evidence of endangerment by collecting is unavailable for any of the populations in this study.

The evaluation of a trajectory experiment at nine small ponds in a deciduous forest stand eliminated the possibility of a threat from observed collecting of adult alpine newts as well as from the collecting of spawn and larvae of common toads. In two of the pools, regular collecting was carried out in the 1960s and 1970s by youths. During the breeding period, the removal of perhaps at most 10 newts and fewer than 50 tadpoles per week was observed. In contrast, in the remaining seven pools removals were the exception (fewer than five per year recorded) because of their substantially greater distance from a woodland path and more difficult accessibility of the shore area. A qualitative decline of the populations in the investigated pools in comparison to the control pools could not be established, and all populations survived the collecting. These results confirm the argument advanced by Henle and Streit (1990) for common toads that endangerment of this species from collection of the larvae can generally be excluded because of its survival strategy—high numbers of offspring, high natural mortality, and, presumably, strong density-dependent regulation of larval mortality (Grossenbacher, 1981; Kuhn, 1994).

Traffic

During the entire research period, with the exception of recently metamorphosed common toads and common frogs and of at least 25 slow worms, only 15 amphibians and reptiles were found dead on the road. These were primarily fire salamanders (*Salamandra salamandra*) on asphalted woodland paths. Although no systematic studies of isolated roadkills were attempted, mass mortality was largely excluded because crossings of considerable numbers occurred only on the highway between Malmsheim and Weil der Stadt, and this highway is closed during the spring migration. No populations have disappeared in the affected breeding waters. Road traffic did not therefore contribute to loss of populations. However, it must be kept in mind that no new highways were constructed or substantially widened within the research area during the period of observation.

Expressways probably indirectly affect populations by isolating them. After its partial cleanup and regeneration, the pond at the Hundesportplatz (mentioned above under "Chemical Pollutants") was not colonized (or recolonized) by common frogs, common toads, alpine newts, smooth newts, or ringed snakes over a period of 3 to more than 12 years, even though populations existed on the other side of the expressway at a distance of about 150 m. In contrast, newly constructed ponds that were separated by a railway track rather than an expressway were settled by these species, and also by crested newts, European treefrogs, and water frogs, within 1–3 years from a distance of at least 750 m.

Underground storm sewers and cellar shafts can lead to substantial losses of amphibians (Bitz and Thiele, 1992; Strotthatte-Moormann and Forman, 1992; Wolf, 1994). The residents of Leonberg-Silberberg gave me an alpine newt and a smooth newt that had fallen into cellar shafts. Systematic controls were of course lacking. Nevertheless, storm sewers and cellar shafts cannot be excluded as causes for the loss of populations within the research area. Amphibian and reptile habitats in the vicinity of villages are lacking, with the exception of the edge of Leonberg-Silberberg and populations of slow worms. The only populations in the vicinity of villages to disappear died out after the destruction of their breeding ponds or after temporary drainage and extreme nutrient pollution.

In summary, highway traffic was not proven to cause the loss of populations, although an expressway has so far prevented colonization of a pond.

Competition with Introduced Species

A few exotic amphibian and reptile species have been released in the research area, but their populations have failed to survive (Table 12-1). They have therefore apparently not exerted a negative influence on the other populations of the research area.

Natural Causes

It is difficult to relate observed species losses in the landscape created by European civilization to natural causes since indirect effects of human activity can seldom be excluded. Drying of ponds or a lowered water level led to the disappearance of four populations of common toads, three populations each of alpine newts and yellow-bellied toads, two populations of smooth newts, and a population of common frogs. Although the proximate cause is natural, human activity may have contributed to the lowered water table and more rapid drying out of the ponds. In one case, the cause was clearly anthropogenic the plastic sheet that was sealing a pond failed. Only two large populations, one of alpine newts and one of common toads, were affected. Further, an annually decreasing water level in a former stone quarry severely threatened formerly very large populations of alpine newts, crested newts, and fire salamanders; at the time of the last observation in 1991 there was only a little water present under stone rubble. As a result, the likelihood of continued survival is starkly limited or actually nonexistent.

Four road ruts disappeared through natural succession, and with them two small populations each of alpine newts, smooth newts, and yellow-bellied toads. Common frogs spawned at two fens until they became completely overgrown. An attempt by common toads to breed in a complex of road ruts failed to establish a population. Additionally, there were 14 other populations and six releases or human-mediated recolonization attempts that failed to become established—that is, they lasted fewer than 5 years. There was no indication of other possible causes. The number of individuals in all these cases amounted to less than 10.

Two very small populations (<10 individuals) of sand lizards lived for only a few years, each on an area of road shoulder of less than 100 square meters. Populations of this magnitude have only a small chance of survival (see Hildenbrandt et al., 1995, for wall lizards *[Podarcis muralis]*); both sand lizard populations are likely to have disappeared due to stochastic fluctuations.

Natural factors, with the above-mentioned limitations, explain 37% of the losses of amphibian populations and 27% of the losses of reptile populations. These values are respectively reduced to 21% and 9% if unsuccessful colonizations are excluded. Only two large populations were affected.

Unknown Causes

Causes are classified as unknown if there is no indication of a definite cause or if various factors exert an influence, but no factor or complex of factors can be proved to be responsible.

Of a total of 22 populations that disappeared for unknown reasons, 68% were classified as small. Disappearances of large populations for unknown reasons occurred once each for crested newts, smooth newts, and common toads, as well as twice each for European treefrogs and water frogs. Crested newts disappeared at the settling pond at the Hardtsee. Clearly, the addition of fish and increasing buildup of sludge are potential causes, but cannot be proven (see above). Smooth newts, European treefrogs, and water frogs died out at the Silberberg Pond presumably because of a combination of several factors: the pond became smaller, it was drained for 2 years, and there was a severe buildup of sludge (for details see the section entitled "Chemical Pollutants"). A large European treefrog population and the largest population of water frogs with several hundred adults disappeared at the Renninger See (a pond) without any indication of the cause. Common toads died out at a remnant pond of a large former wetland long after the wetland was drained and after the construction of an expressway about 50 m away. The expressway cut the population off from suitable summer habitat, with the exception of the immediate surroundings and a very small patch of woodland (<1 ha). Possibly, the extirpation was a delayed consequence of these massive landscape alterations, but no evidence of that exists.

Discussion

Causes of Species Decline

Numerous publications indicate that a general decline of amphibians and reptiles has occurred in Central Europe (Grossenbacher, 1974; Brunken and Meineke, 1984; Thurn et al., 1984; Berger, 1987; Löderbusch, 1987; Riffel and Braun, 1987; Rimpp and Hermann, 1987; Stangier, 1988; Rimpp, 1992). For example, in the 26-year period of investigation of Henle and Rimpp (1994), two species were extirpated; on the other hand, one species actively immigrated. Only a few species appear to be unaffected regionally by the general decline. Indeed, green toads (Rimpp, 1992) and agile frogs (Henle and Rimpp, 1994), contrary to the general trend, expanded within the area covered by this study. Water frogs very sharply decreased in the 1980s. With one exception they now exist only in small populations, for which the reasons are only partially known (Table 12-1), while they are increasing in areas of North Rhine-Westphalia because of recolonization attempts and newly created habitats (Klewen, 1988; Kordges, 1988).

Similar relationships (sharp decline, but only of some of the species, and not always the same ones) occur on other continents (Osborne, 1990; Dodd, 1993a; Ingram and McDonald, 1993; Mahony, 1993), for which largely unknown global causes of decline are discussed (Blaustein and Wake, 1990; see also Reaser and Blaustein, this volume). In contrast, unknown factors are only seldom mentioned in Central Europe. The same causes of decline are cited repeatedly here (see Henle and Streit, 1990). Of these, habitat destruction also clearly represents a global, frequently proven cause of the loss of biodiversity (Henle and Streit, 1990; Saunders et al., 1993; McDade et al., 1994).

In order to devise conservation measures that promise success, it is not as important to postulate presumptive global phenomena as it is to provide detailed knowledge of the relative significance of various factors (Henle and Streit, 1990). This knowledge, which can be further developed only by critical analyses, will facilitate the targeting of the actual causes, rather than the symptoms (Henle, 1995).

Because detailed causal analyses of observed changes of amphibian and reptile populations are generally lacking, at this time a sufficiently accurate assessment of the relative significance of the various potential threats is only possible within limits. The causal analysis of the long-term surveying project (Henle and Rimpp, 1994) discussed here demonstrates that it is generally possible to carry out such analyses in spite of the methodological problems posed by having to repeat surveys over an extended period of time. In this example, the causes remained unknown for only 24% of the extirpations.

Habitat destruction and alteration were proven to represent the leading cause of extirpation within the research area of Henle and Rimpp (1994). Numerically, this is the leading cause for reptiles and the second cause—behind natural losses—for amphibians (Table 12-1). When considering natural losses, however, one must bear in mind that these losses almost exclusively affected the smallest populations. On the other hand, about half of the amphibian populations that disappeared because of habitat destruction were large, in spite of only minor changes in land use. This underscores the greater importance of habitat destruction/alteration as a cause of loss of populations. This conclusion is supported additionally by the fact that habitat alterations are involved in perhaps half of the losses classified as natural. Also, indirect effects of human intervention in some cases cannot be fully excluded.

The sharp decline of ponds and wetlands, essential habitats of amphibians (Honegger, 1981; Stangier, 1988), and of seminatural ecosystems (Saunders et al., 1993) confirms the essential role that habitat changes play in the global decline of amphibians and reptiles and of biodiversity in general (Settele et al., 1996). Works that analyze population changes of particular Central European species (Comes, 1987; Fritz, 1987; Fritz et al., 1987; Glandt and Podloucky, 1987; Corbett, 1988; Podloucky, 1988) reach similar conclusions; therefore, the first priority of conservation measures must be to deal effectively with habitat destruction and change. It is not enough, however, to place a large number of small areas under protection (see the example above). Rather, strategies must be developed that change land use practices so that habitat destruction and negative habitat alterations are generally counteracted (Saunders, 1996); otherwise symptoms, instead of causes, will be addressed (Henle, 1995).

In other regions, additional factors besides the biotope changes in the present example presumably contribute to local declines, but their relative significance is considerably more difficult to assess at this time. Chemical pollution may be the most important cause after direct habitat alterations, as it was in the research area analyzed here. The situation on islands, where pursuit by man and introduced predators plays a more important role (Henle and Streit, 1990), is apparently an exception. However, losses due to invasive species may frequently be promoted by habitat alterations, and may not occur in the absence of the alterations (King, 1984).

Although a relatively large number of populations in the research area of Henle and Rimpp (1994) died out as a result of stochastic events, this factor cannot be regarded as a fundamental cause of a general decline, since small populations were almost always involved. Generally, clear evidence of a natural factor (such as climate) posing a serious threat to the regional survival of an amphibian or reptile population is rarely encountered (Böhme, 1989; Osborne, 1990), but it must be remembered that it is quite difficult to establish a natural factor as a cause, and in most investigations natural factors are disregarded (Henle and Streit, 1990).

Other factors played no role or only a comparatively unimportant role in our research area. Likewise, Henle and Streit (1990) stress that additional factors contribute importantly to regional or global extinction of amphibians and reptiles only under limited conditions. Among these are, for example, threats to endemic island species from introduced predators and pursuit by humans, as well as commercial trade in species groups with a survival strategy characterized by low reproduction rate, late sexual maturity, and long life expectancy—a combination that is not generally characteristic of native amphibians and reptiles, and generally characteristic of only a few amphibian and reptile groups (Duellman and Treub, 1986; Dunham et al., 1988; Wilbur and Morin, 1988; see also Green, this volume).

Road traffic in heavily populated Central Europe can also contribute substantially to losses of amphibians or other faunal groups (Stubbe et al., 1993) and can lead to a decrease in genetic variability through isolation (Reh and Seitz, 1989). With regard to the influence of traffic on the survival probability of amphibian and reptile populations, the criticism must be clearly stated that, to date, causal analyses are lacking, in spite of a practically overwhelming number of expensive, labor intensive conservation measures and intervention experiments (Henle and Streit, 1990; Wolf, 1994). Field experiments, which are generally best suited for analysis of declines (Mahony, 1993), are required for clarification. Normally, such experiments are rarely justified or performed in order to investigate a threat to a given species, but since new highways are regularly constructed and pose a threat to many species, it would be easy to integrate appropriate field experiments into highway planning.

Detailed Population Vulnerability Analyses (PVAs; Clark and Seebeck, 1990; Hildenbrandt et al., 1995) provide an alternative. These are often quite expensive and restricted to specific, spatially limited problems (but see Henle and Streit, 1990). For these reasons they have been largely reserved for the "flagship species" of nature conservation, for example Leadbeater's possum (*Gymnobelideus leadbeateri*; Lindenmayer and Possingham, 1995). They recently have been developed for routine employment in the practice of nature conservation (Settele et al., 1996). To date, this type of analysis has been applied to only one of our native herpetofauna—wall lizards—after a predictive model was developed and the required knowledge of its population biology was worked out (Hildenbrandt et al., 1995).

Optimization of Surveying Projects

Improvements in contemporary population surveying practices may also furnish better evidence of the relative significance of risk factors. To date, surveying projects primarily have been carried out to obtain an overview of the actual distribution and the specific habitats occupied by the mapped species. Over time there has been increasing focus on the use of extensive survey data to probe the reasons for changes in populations, although most compilations and evaluations have been restricted to the listing of potential risk factors.

Discriminant analysis can be used as a first step in the analysis of snapshot experiments, even to some extent with data that has already been compiled. That is, the parameters investigated in the previously encountered situation are analyzed in order to determine which parameters are particularly useful for distinguishing the occupied habitats from the unoccupied ones (Foeckler, 1990; Ildos and Ancona, 1994). This initial step presupposes, however, that the parameter (for example, measurement of the distance to the nearest road, the concentration of chemical pollutants, or the stocking of fish in a pond) is adequately standardized and quantified. From the results, well-founded hypotheses about the relative significance of various potential risk factors can be derived. However, the disadvantages of snapshot experiments (see above) remain.

Along with discriminant analysis, habitat models can be constructed by means of additional multivariate methods. They can provide a basis for a spatial representation of detailed PVAs (Kuhn and Kleyer, 1996). Systematic recording of critical habitat parameters and potential threats in investigated habitats is essential for discriminant analysis and for construction of habitat models. In particular, biotopes in which amphibians and reptiles are absent must also be included. In this manner, a foundation is created for a better understanding of colonization processes and metapopulation dynamics of the surveyed species (Settele et al., 1996). Repeat surveys are essential for this purpose and additionally serve as an indispensable foundation for the evaluation of trajectory experiments.

The long-term surveying project discussed here indicates that the causes of extirpations as well as the relative significance of the various risk factors can be fairly objectively assessed for a large number of herpetofaunal populations even when the repeat surveys are not systematically executed. However, this requires an extensive data record. It is often difficult to find a sufficient number of affected and unaffected control populations within a restricted area. One must attempt to keep interfering factors to a minimum when choosing control populations. This means that factors other than the risk factor under examination should be as similar as possible among the assessed populations. The fewer comparable populations available, the more important this becomes for reliable interpretation of the results. A unique opportunity for planning of future survey activities in the interval between survey periods (perhaps annual) is available with survey programs in which a number of qualified individuals are providing assistance. Ponds can be selected systematically as investigation or control ponds on the basis of unplanned experiments (for example, habitat changes, fish stocking, etc.) reported in the previous year or years and assigned to particular co-workers for resurvey. Finally, when repeat surveys are planned systematically and standardized survey methods for risk factors based on previous literature are applied, the likelihood of being able to pursue a trajectory experiment at the right point in time is considerably increased, and the number of potential control populations is also increased. Ideally, repeat surveys must be executed at firmly established intervals. By careful planning, the responsibility for conducting repeat surveys can be allocated among the collaborators in keeping with their individual schedules.

With improved methods, as proposed here, efforts can be concentrated on specific causes of decline according to their relative importance. In this manner, the conservation of our native herpetofauna can be more effectively guided.

Summary

Survey data have been major sources for the documentation of amphibian and reptile declines and of potential threats. Often, all potential threats are taken as proven actual causes of decline, although the presented data analysis is seldom sufficient for such claims. The potential for causal inferences is limited because of a general lack of rigorous field designs. Nevertheless, the potential of survey data for such inferences is seldom fully realized. Therefore, comparisons of the relative importance of various potential threats among regions and, thus, the development of effective conservation strategies are hampered.

In this paper, potential methods for causal inferences are outlined briefly. The potential and limits of causal inferences from survey data are illustrated with an example from an approximately 50 square kilometer area west of Stuttgart, Baden-Württemberg, Germany. During a 26-year period of data collecting that lacked a rigorous design, 13 and 7 species of amphibians and reptiles, respectively, were observed. Two amphibian species, European treefrogs (Hyla arborea) and natterjack toads (Bufo calamita) were extirpated, and two species, crested newts (Triturus cristatus) and water frogs (Rana esculenta/lessonae) showed a considerable decline. A total of 124 populations were extirpated, including 54 unsuccessful recolonization attempts out of a total of 107 observed recolonizations. Analyzing the data as natural field experiments, only 24% of the extirpations (22 unknown and 8 uncertain causes) remained unexplained in spite of the lack of a rigorous design. Habitat change was the prime factor responsible for declines (e.g., 24% of the water bodies used for spawning disappeared). Pollution was the second major cause. Many extirpations were due to natural causes; with the exception of two populations, extirpations were limited to small and very small populations. Predation by fish caused two losses. No extirpation could be attributed to other predators, collecting, competition with exotic species, or road traffic. However, a highway built before the start of the survey project acts as a barrier to the reinvasion of a partially restored spawning site at which amphibians became extirpated due to pollution.

Recommendations for planning the collection of survey data are made to improve their potential for causal inferences on declines.

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