Seasonal dynamics and breeding of amphibians in pristine forests (Białowieża National Park, E Poland) in dry years

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Received 19 November 2001; Accepted 8 July 2002

A b s t r a c t . In summer 1992 through spring 1994, amphibian abundance and breeding was studied in the pristine temperate forests, typical of central European lowlands. The years 1991, 1992, and 1993 were among the driest in the recent decades, with the spring-summer precipitation 35% lower than the long-term average. In the primeval forests of Białowieża National Park, common frogs *Rana temporaria* spawned in small (on average, 0.2 ha) ponds (postglacial melt-out hollows) devoid of wood cover and characterised by water pH 5.1-6.0 (as measured in April). Breeding success of frogs, monitored qualitatively in 1993, was rather poor due to pond desiccation. The capture of amphibians on forest grids revealed that densities and seasonal dynamics differed between wet and drier deciduous forests. No amphibians were captured in the mixed coniferous forests during the study. In the wet ash-alder forests, on average, 39 amphibians ha^{-1} were recorded in late April, 12 ind ha^{-1} in summer, and 195–222 ind ha^{-1} in autumn (September). In those forests, 90% of captured amphibians were common frogs, 6% common toads *Bufo bufo*, and 4% moor frogs *R. arvalis*. In the drier oak-lime-hornbeam forests, amphibians appeared in May, and increased in numbers towards summer (19–24 ind ha^{-1}) and autumn (45–71 ind ha^{-1}). Of all amphibians caught in those forests, 43% were common frogs, 38% common toads, and 19% were moor frogs. A majority of amphibians captured in autumn were young of the year. By mid-October, all amphibians had left the forest for their hibernation sites. Comparison of our data collected in very dry years with other available data from Białowieża Primeval Forest (various years between 1955 and 1998) revealed that summer indices of amphibian abundance were strongly positively correlated with rainfall in April-June of the census year and the previous year.

Key words: common frog, moor frog, common toad, density, spawning ponds, water pH, ash-alder forest, oak-lime-hornbeam forest, rainfall

Introduction

Amphibian populations are characterised by wide fluctuations in numbers and heterogeneous spatial distribution due to the life history demands of amphibians (seasonal migrations from and to hibernation sites, spawning sites, and summer quarters) and their low resistance to unfavourable ambient conditions, especially water deficit (e.g. K u t e n k o v 1995, M e y e r et al. 1998, G r o v e r 2000, P i k u l i k et al. 2001). Hence, the temporal and spatial variation in amphibian abundance in the forests is much greater than that recorded in other groups of small vertebrates: birds, rodents, and insectivorous mammals (J ę d r z e j e w s k a & J ę d r z e j e w s k i 1998). Furthermore, there is growing concern that amphibian populations are declining worldwide (P e c h m a n n et al. 1991, H o u l a h a n et al. 2000), thus more data are needed on factors affecting their densities at local and regional scales.

This study was conducted in Białowieża National Park (BNP), Eastern Poland, which represents one of Europe's last pristine forest, typical of the lowland temperate zone (F a l i ń s k i 1986). The aims were to describe (1) spawning sites of frogs in a pristine woodland, and (2) seasonal dynamics of abundance of terrestrial amphibians (frogs and toads) in three major forest associations. The time of the study (from summer 1992 till spring 1994) was characterised by a strong deficit of precipitation as compared with the long-term average, so the results are representative of rather unfavourable environmental conditions for amphibians. We then compared our results with those from other surveys conducted in Białowieża Primeval Forest between 1955 and 1998 in order to determine the factors affecting between-year variation in amphibian abundance.

Study Area

The strict reserve of Białowieża National Park (E Poland, 23°55'E, 52°45'N) covers 47.5 km^2. It is located in the centre of the Białowieża Primeval Forest (about 1500 km^2). The forest extends on both sides of the Polish-Belarussian border and preserves the remnants of the European temperate lowland forests of hemiboreal-nemoral type. In the BNP, the structure and character of the forest is typical of virgin forests unaltered by management, hunting, and tourism. The mosaic of fairly dry, swampy and river-flooded forest associations with many decaying uprooted trees makes the habitat extremely varied in micro- and macroscale. In the Park, hunting and timber exploitation are not allowed; tourism is restricted to a few pedestrian paths.

The main forest associations of BNP are the rich, multilayered deciduous stands dominated by oak *Quercus robur*, hornbeam *Carpinus betulus*, and lime *Tilia cordata*, with admixtures of maple *Acer platanoides* and spruce *Picea abies*. In such forests, the ground vegetation is dominated by spring geophytes and it becomes meagre in summer and autumn due to overshadowing by tree canopies. Oak-hornbeam-lime forests cover about half of the BNP's area (Fig. 1). Mixed coniferous forests, composed of spruce, pine *Pinus silvestris*, and oak, with admixtures of aspen *Populus tremula* and birch *Betula pendula* grow on drier sites and cover about 25% of the area. The herbs layer, in addition to soft-tissue plants, contains dwarf shrubs, some evergreen species (such as *Vaccinium* spp.) and mosses. Two other associations, bog alderwoods and streamside forests, are shaped by water and cover 18% of the BNP's area. The streamside forests (dominated by black alder *Alnus glutinosa*, ash *Fraxinus excelsior*, with admixtures of elm *Ulmus scabra*) are situated along flowing waters and are flooded in spring. Bog alderwoods (composed of black alder with admixtures of birch *B. pubescens* and spruce) occur at the peripheries of river and stream valleys and in depressions of the denudation plains. High groundwater level and its stagnation over a large part of the year are typical of bog alderwoods. The forest floor is distinctly structured with hollows and hummocks. Streamside forests and bog alderwoods usually occur near each other. The herbs layer in both associations is very prolific and the peak of its abundance occurs in summer. A small stream, the Orłówka (1–4 m wide, up to 1 m deep) flows through the Park (Fig. 1). The water level in the Orłówka varies seasonally, reaching its maximum in spring. The Orłówka often dries up in summer. In winter, it freezes but unfrozen air-holes can still be found, in its middle and lower course, at temperatures below -15 °C. The upper part of the stream freezes completely at about -5 °C. The BNP lies in the temperate subcontinental climatic zone. In 1993–1994, the mean daily temperature in January was 0.1 °C, and in July 19.6 °C. Snow cover persisted for an average of 193 days per year. More

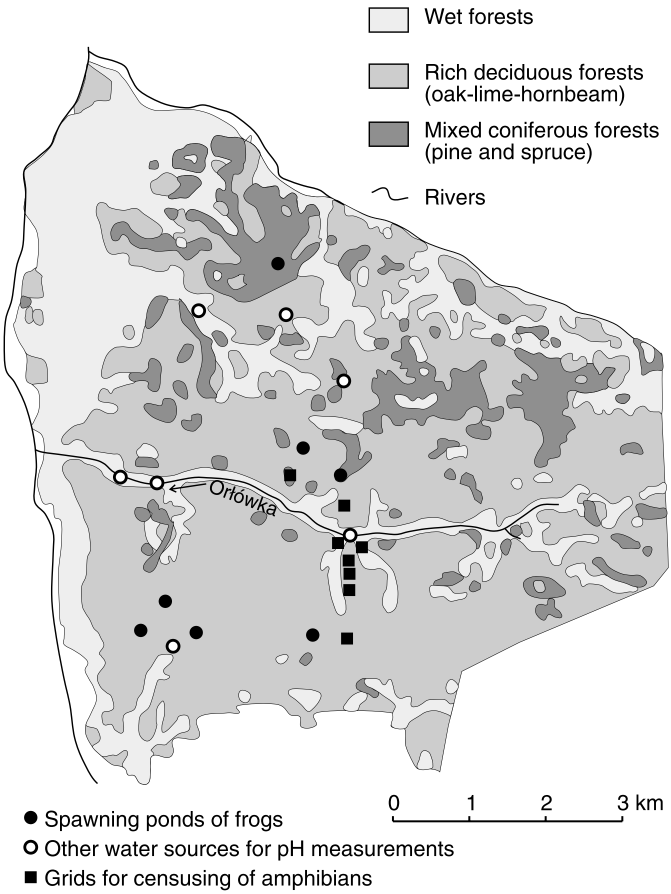

Fig. 1. Map of the strict reserve of the Białowieża National Park with localities of study sites. Spatial distribution of the main forest types after K w i a t k o w s k i (1994), simplified.

information on the vegetation of the BNP is given by F a l i ń s k i (1986) and J ę d r z e j e w s k a & J ę d r z e j e w s k i (1998).

Material and Methods

We applied the methods elaborated and tested by G ł o w a c i ń s k i & W i t k o w s k i (1970), and based on earlier methodological works by Z i p p i n (1956, 1958). We captured amphibians on 8 grids, 30 x 30 m (0.09 ha) each. Trapping (with a small net-bag and by hand) was usually done by 2 persons walking and carefully searching the forest floor on a grid. Two surveys were done daily: in early morning and before dusk. Capturing lasted 3 days in spring and summer, and 4 days in autumn. In 1992, two censuses were conducted: in July, on three grids in oak-hornbeam-lime forests (one of the grids was surrounded with cloth to prevent amphibian movements into and out of the grid during the census), and in September, on three grids in oak-lime-hornbeam forests and one grid located in the wet ash-alder forest. In 1993, all 8 grids (5 in the oak-hornbeam-lime forest, 2 in the ash-alder forest, and one in the mixed coniferous forest) were operated 5 times: in late April, early June, mid July, late September, and mid October.

Captured frogs and toads were identified to species, weighted, and put into a covered plastic bucket (bedded with moist litter and moss), where they stayed for 1–4 days, i.e. until the end of the census. Afterwards, they were released in the place of capture. Totally, 122 amphibians were caught in 1992–1993. Since the number of amphibians caught on the fenced grid did not differ from those captured in unfenced grids located in the same habitats, all data were treated in the same manner. For density calculations, we assumed that, during 3 to 4-day census, we caught 100% of amphibians inhabiting the grids. Owing to the low abundance of amphibians during the study, we could have checked this assumption for the pooled sample of data only. The numbers of amphibians captured on the grids declined on consecutive days of a census (r = -0.84), and the regression equation ($y = 65 - 12.9x$) indicated that on day 5, on average, only 0.5 amphibians would have been caught on all grids (see D e L u r y 1947, and H a y n e 1949, for the rationale of using linear regression to calculate densities from removal trapping).

In April 1993, spawning sites of frogs were searched for on the area of about 15 km^2 (Fig. 1). Seven ponds, where spawning frogs or the spawn had been found, were then monitored until April 1994. The presence of spawn and tadpoles were recorded, and water was sampled for pH measurements. Note that these seven ponds were not the only spawning places of amphibians in BNP. They represented breeding sites of frogs located deep in the forest interior. Other, unstudied spawning sites of frogs and toads were located in and along the two larger rivers (Narewka and Hwoźna), forming the borders of the strict reserve of BNP (see Fig. 1). Water pH was also measured in seven other sources (wooded bogs and ditches in the forest, and the Orłówka River), where no breeding of frogs was recorded.
Data on weather were obtained from the Białowieża meteorological station.

Results

Abiotic conditions of frog reproduction

Compared to the long-term mean conditions, spring and summer seasons of 1991–1993 were hot and dry. In 1948–1998 (51 years), the annual precipitation ranged from 426 to 939 mm (mean=637 mm, SD=123). In 1991, 1992, and 1993 (the study years and a preceding year), annual precipitation amounted 439, 525, and 531 mm, respectively (mean=498 mm, SD=51), i.e. 78% of the long-term mean value. Water deficit was especially severe in spring and early summer. In 1948–1998, April–June rainfall ranged from 94 to 338 mm (mean=189 mm, SD=58). By contrast, in 1991, 1992, and 1993, only 109, 129, and 127 mm of rainfall were recorded (mean=122 mm, SD=11), i.e. 65% of the long-term mean value. In 1994 and 1995, spring and summer seasons were again wet.

In spring 1993, we located breeding individuals and the spawn of the common frogs *Rana temporaria* in six ponds and those of the moor frogs *R. arvalis* in one pond (Table 1). All ponds were postglacial melt-out hollows, devoid of tree and shrub cover, surrounded by oldgrowth forest, and as summer advanced, they became overgrown with herbaceous vegetation. The spawning ponds were small (mean size 0.2 ha in spring) and in general were located about 1 km from the nearest river or stream (Fig. 1, Table 1). Mean water pH in the ponds used by the common frogs was 5.5 (SD=0.3) in April, and increased to 6.0 (SD=0.6) in

May. The site used by moor frogs had lower pH, 4.1 and 4.4, respectively (Table 1). In 1994, common frogs were found lekking in five ponds (including one previously occupied by moor frogs) and their mean pH was 5.6 (SD=0.25). Generally, very little variability was recorded in the acidity of water used by spawning common frogs in spring (pH from 5.1 to 6.0; Table 1).

Table 1. Characteristics of frog spawning ponds in Białowieża National Park, 1993-1994. a – lekking moor frogs; in all other cases the common frogs were recorded. + yes, - no, (s) – breeding success possible, ? no data. Mean values of water pH calculated for the common frog's spawning sites, only. See Fig. 1 for the spatial distribution of frogs' spawning ponds.

No. of pond	Pond size (ha)	Straight-line distance to the nearest river or stream (km)	Water pH in 1993		Presence of spawn in spring 1993	Presence of tadpoles in May-June 1993	Water pH in April 1994	Presence of spawn in spring 1994
			April	May				
1	0.20	1.57	4.1a	4.4a	+a	-	5.4	+
2	0.22	1.37	5.6	?	+	+(s)	6.0	+
3	0.20	0.83	5.7	5.7	+	+	?	-
4	0.18	1.33	6.0	7.0	+	-	5.6	-
5	0.11	0.57	5.1	5.8	+	+(s)	5.3	+
6	0.27	0.67	5.6	5.6	+	+(s)	5.7	+
7	0.20	1.02	5.1	5.3	+	+	5.7	+
Mean (SD)	0.20 (0.05)	1.05 (0.38)	5.5 (0.35)	5.9 (0.65)			5.6 (0.25)	

In spring 1993, we measured water pH in four sites with standing water (bog alderwoods and other places with tree cover) where no spawning frogs were recorded. It ranged from 5.5 to 7.1 in April (mean=6.4, SD=0.8) and from 6.3 to 7.1 in May (mean=6.6, SD=0.4). Flowing water of the Orłówka stream had almost invariable pH of 7.6 in April and 7.7 in May in the lower and middle course of the stream. In the upper part (which dried out in May), pH of water in April was 5.6. Water pH in six spawning sites of the common frog differed significantly from the values recorded in the seven sites of standing and flowing waters not used by amphibians (Mann-Whitney *U*-test, $U_s = 35$, $P = 0.04$).

Breeding success and densities of amphibians

In April 1993, spawn was laid in each of the seven ponds (Table 1). Reduced rainfall and hot weather caused rapid drying of the ponds, which were subsequently overgrown with tall herbaceous vegetation. Actually, two ponds dried nearly completely before the eggs hatched, and by July, all other ponds were very small and shallow (5–30% of their size and water capacity as estimated visually in April). In June–July, large-sized tadpoles were not observed in any of the ponds, but given the amount of persisting water, some tadpoles could have metamorphosed in three ponds.

In spring 1994, after 2 years with very dry springs and summers, fewer ponds were used for spawning (Table 1), despite the fact that abiotic conditions were favourable. It was only in 1995 (another wet year), that the spawning of common frogs was again abundant. A large spawning aggregation of frogs, many times exceeding those in each of the forest ponds, was found in the widely flooded springs of the Orłówka stream. That place, characterised by suitable acidity for common frogs (water pH 5.6), was very poor in water in 1993, when no lekking frogs were found.

Censuses on grids in the oldgrowth stands of BNP revealed highest densities of amphibians in wet ash-alder forests and substantially lower densities in the drier deciduous forests. Except for a single specimen of the tree frog *Hyla arborea* caught in 1993, no amphibians were ever captured or seen in the mixed coniferous forests. The seasonal pattern of amphibian abundance markedly differed among the wet ash-alder forests and drier oak-hornbeam-lime forests (Fig. 2). In wet forests, common frogs were fairly numerous in late April (on average, 39 ind ha^{-1} and 190 g ha^{-1} of crude biomass), declined in summer (11–12 ind ha^{-1} and 50–130 g ha^{-1}), and rose again in autumn, when a cohort of young individuals appeared (195–222 ind ha^{-1} and 82–122 g ha^{-1}). In the drier forests, amphibians appeared later (in May) and their abundance was highest in summer and/or early autumn (mean 19–24 ind ha^{-1} and 193–276 g ha^{-1} in July and 45–71 ind ha^{-1} or 146–304 g ha^{-1} in September; Fig. 2). By mid October, all amphibians had left the forest floor for their hibernation sites.

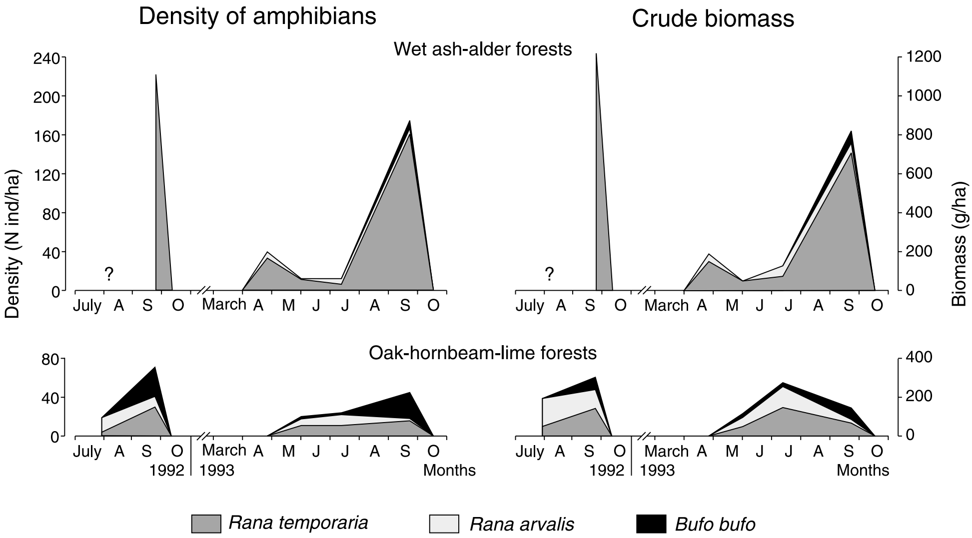

Fig. 2. Seasonal dynamics of amphibian abundance (in numbers of individuals and biomass per unit area) in the oldgrowth forests of BNP, in 1992–1993. Ash-alder forests – data averaged for 2 trapping grids; oak-lime-hornbeam forests – data averaged for 5 grids.

Not only the seasonal dynamics pattern but also the species composition of amphibians differed between the two habitats. Data averaged for all censuses in 1993 showed that among amphibians caught in ash-alder forests, the common frog strongly dominated (90% by numbers and 92% of biomass). The moor frog (4% by numbers and 6% of biomass) and the common toad *Bufo bufo* (6 and 2%, respectively) were rare. In oak-hornbeam-lime forests, the common frog was also the most numerous, but it formed less than half of amphibian numbers (43%) and biomass (49%). The common toad constituted 38% of amphibian numbers and 19% of biomass, and the moor frog 19 and 32%, respectively.

The age structure (as approximated by body mass distributions) of common frogs inhabiting forests changed seasonally. In spring, only young and subadult non-breeding frogs were captured (body mass 1.5–9.5 g, mean=5.2 g), as the breeding adults gathered at spawning sites. Reproductively mature adults (body mass 18–38 g, mean=26 g) were found in forests in summer and autumn. In September, 59% of all individuals were in body weight class 1–3 g, 32% were in class 3.5–6 g, 3% in class 6.5–9 g, and 6% in class 24–38 g. Thus, a majority of captured common frogs were young of the year. Moor frogs were captured in small numbers in spring through autumn with no clear differences in body mass (mean=10.4 g, min–max 1–20.5). Toads captured in summer were subadults (7.5–10.5 g) and all those captured in the autumn seasons were young of the year (body mass from 1 to 4.5 g, mean=2.2, SD=1.0).

Worth mentioning is the fact that young, metamorphosed common frogs and common toads captured in September 1993 were significantly smaller than those captured in September 1992. In common frogs, mean body mass of a froglet was 3.7 g (SD=1.0, min–max 2–5.5 g) in 1992, and 2.5 g (SD=0.8, min–max 1–4.5 g) in 1993 (Mann-Whitney *U*-test, $U_s = 630.5$, $n_1 = 23$, $n_2 = 33$, $P < 0.0005$). The respective values for the young toads were 3.3 g (SD=0.8, min–max 2–4.5 g) in 1992, and 1.6 g (SD=0.5, range 1–2.5 g) in 1993 ($U_s = 130.5$, $n_1 = 8$, $n_2 = 17$, $P < 0.0005$).

Discussion

Our study represented the situation of amphibians typical of severely dry years. Undoubtedly water supply is decisive for the embryonic development and survival of tadpoles and metamorphosed amphibians. Z a m a c h o w s k i (1977) documented experimentally that, in frogs and toads, the resistance to water shortage increased from spring till autumn. They would survive out of water for 1.5–3 days in spring, and 3–5 days in autumn. Two factors seem essential for the survival of frog embryos: chemical properties and the amount of water where the spawn had been deposited. A s t o n et al. (1987) recorded in northern England that water pH in 61 ponds with common frogs' spawn ranged from 4.2 to 8.9. In laboratory studies, the survival of common frog embryos was much lower in pH 4.5 than in pH 6.0 (B e a t t i e et al. 1992). In the BNP, common frogs were found spawning in waters of very narrow range of pH (5.1–6.0), but this might have been caused partly by the fact that, generally, very few suitable water sources were available in the dry years. In Belarus, P i k u l i k (1980) reported that spawn clumps of common frogs in wet years were found in a variety of both prospective and obviously short-lasting waters, such as ditches by forest roads, deep puddles on dirt roads, flooded river valleys, old river beds, and slowly flowing waters of forest streams and canals. Most likely, the acidity of such a wide array of places was also rather variable.

Although we did not measure directly the breeding success of frogs in the monitored ponds, it seemed very poor as nearly all spawning sites dried by early summer. Breeding success of both *R. temporaria* and *R. arvalis* depends on the persistence of spawning waters until the tadpoles metamorphose. K u t e n k o v (1995) reported that the survival of common frog tadpoles in Karelia, Russia, was strongly correlated with the water balance (precipitation minus evapotranspiration) in May–June. In the Oka River Reserve, Russia, from 0.1 to 8.9% of moor frog eggs deposited in 1971–1978 (mean=3%) gave rise to metamorphosed froglets (P a n c h e n k o 1980). As much as 95% of the variation in frogs' breeding success was explained by year-to-year variation in water capacity in the studied reservoirs, which in turn was shaped by precipitation and flooding. P a n c h e n k o (1980) found that, in spring, the amount of spawn deposited per 1 m^3 of water varied from 15 to

520 eggs (mean=127, CV=135%). In summer, however, the number of metamorphosed froglets per 1 m^3 of water was rather stable, from 1 to 1.4 individuals (mean=1.2, CV=13%). Thus, the amount of water persisting throughout the full cycle of frog reproduction and metamorphosis is a crucial factor limiting the breeding success and autumn numbers of young frogs in the forests.

The strong effect of prolonged drought has also been recorded in other species of amphibians. In north-central Florida, D o d d (1993, 1994, 1995) monitored the populations of the eastern narrow-mouthed toad *Gastrophryne carolinensis*, the striped newt *Notophthalmus perstriatus*, the oak toad *Bufo quercinus*, and the southern toad *B. terrestris* during 5 very dry years. In all four species, the deficit of rainfall and subsequent drying of a spawning pond severely limited or eliminated reproduction for up to 5 consecutive years, reduced the size of the local populations in some of the studied species, and affected the activity patterns of amphibians. On the contrary, M e y e r et al. (1998), who analysed the 23–28-year long time-series of the common frog *R. temporaria* in the region of Bern, Switzerland, found only a weak effect of rainfall on the population fluctuations. In one of the three studied sites, for which data on precipitation were analysed, the number of breeding frogs correlated with rainfall of previous year (from the spawning date to end of October).

Densities of amphibians recorded in the BNP in 1992–1993 were very low as compared to other data from Polish temperate forests collected by the same method (capturing on grids). In the Niepołomice Forest, S Poland, G ł o w a c i ń s k i & W i t k o w s k i (1970) estimated the densities of terrestrial amphibians in the oak-hornbeam forests in a wet year of 1967. In August 1967, when young of the year had already dispersed in forests, mean densities of amphibians were 2186 ind ha^{-1} (SD=429, min–max 1603–2552) and the mean biomass 11.56 kg ha^{-1} (SD=1.9, min–max 8.3–13.3). In July 1999, capturing of amphibians in the mixed coniferous and alder-ash forests near Lake Łuknajno (Masurian Lakeland, NE Poland) yielded 82–90 ind ha^{-1} and 0.7–0.9 kg of total biomass ha^{-1} (M. B r z e z i ń s k i , unpubl. data). Thus, the abundance of amphibians recorded by us in oak-lime-hornbeam forests of the BNP in very dry years was 40 to 60 times lower than those reported from Niepołomice Forest, and 4 to 8 times lower than that found in the Masurian Lakeland. These three studies elucidate the range of variation in amphibian densities in the temperate forests of Central Europe.

In Białowieża Primeval Forest, this study has so far been the only attempt to estimate the densities of terrestrial amphibians by capturing them on quadrats. However, counts of amphibians on transects (one-meter wide) were conducted in BPF in the summer seasons of 1955, 1957, 1981–1985, 1995–1996, and 1998 (B a n n i k o v & B e l o v a 1956, B a k h a r e v 1986, P i k u l i k et al. 1987, 2001; in all cases only overwintering individuals, and not the youngest current-year cohort, were counted). The mean indices of amphibian abundance (weighted by proportional availability of various forest habitats) varied from 3.5 individuals per 1 km of the transect in 1957 to 24 individuals in very wet years of 1984 and 1985 (total precipitation in April–June 323 and 267 mm, respectively). Our data from quadrats can be compared with the above mentioned indices by recalculating the number of amphibians trapped during the first census on the first day in the summer trapping series, and the area of the quadrats into the length of a 1-m wide transect. Such rough estimation yielded an average of 0.6 amphibians km^{-1} in 1993 and 0.7 in 1994. Thus, the maximum numbers of terrestrial amphibians recorded in wet summer seasons (1984–1985) were again at least 40 times higher than the lowest numbers counted in very dry years (1993–1994).

Indeed, in the entire data set available from the BPF, total April–June precipitation over two years (the year, when the census was done, and the previous year) was a crucial factor

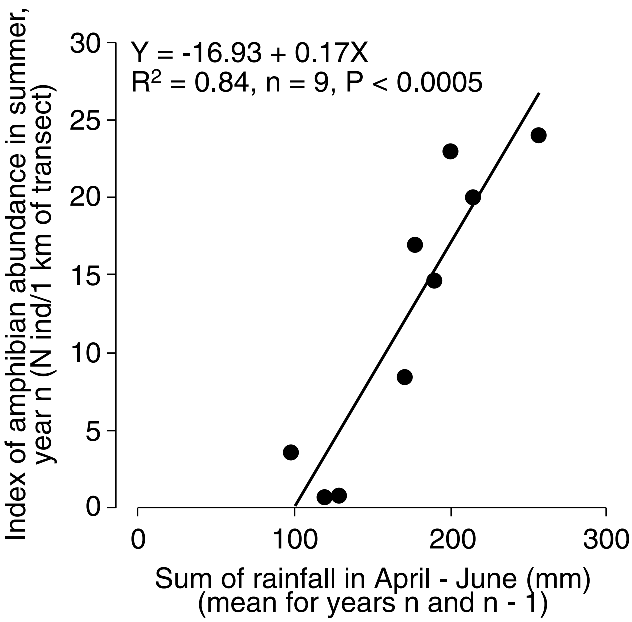

Fig. 3. Indices of summer abundance of terrestrial amphibians (frogs and toads, the youngest current-year cohort not included) in the Białowieża Primeval Forest in relation to the total rainfall in April-June (averaged for the year of census and the previous year). Data from: Bannikov & Belova (1956), Bakharev (1986), Pikulik et al. (1987, 2001), and this paper.

shaping the abundance of terrestrial amphibians, and the mean values for April–June explained 84% of variation in their numbers from year to year (Fig. 3). The strong positive correlation between amphibians and two-year average rainfall most probably reflects the fact that precipitation acts through changes to both the density and activity of amphibians. Rainfall of the previous year, when majority of the censused frogs hatched and metamorphosed, affects the numbers of frogs. Rainfall in the year of the census changes the activity of frogs and, thus, their detectability by surveyors. As suggested by this study, the impact of precipitation on true numbers is heavier, because the larval stages of amphibians are not able to cope with pond desiccation in dry years.

Acknowledgements

We are grateful to E. Bujko for his help in the field, K. Zub and M. Rabczuk-Orzechowska for their preparing the map and figures. We sincerely thank A. Bobiec (Białowieża) for kindly lending us the equipment for water pH measurements. The study was financed by the grant KBN 4 4416 91 02 from the Committee for Scientific Research (Poland) and the budget of the Mammal Research Institute. Comments and criticisms by two anonymous reviewers are gratefully acknowledged.

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