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The declining spadefoot toad *Pelobates fuscus*: calling site choice and conservation

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We investigated whether local biotic and abiotic conditions could explain the occurrence of calling males of the declining spadefoot toad *Pelobates fuscus* in 72 ponds in southern Sweden. The ponds covered the entire distribution range of *P. fuscus* and were monitored during the breeding season in 2000. Calling males were found in 33 ponds, representing ca 50% of all known ponds for the species in Sweden. They had a non-random distribution and a discriminant analysis including 19 environmental variables successfully classified 86% of the ponds as with or without calling males. A stepwise discriminant analysis selected eight of these variables and classified 85% of the ponds correctly. Ponds with calling males were classified mainly on characteristics of the ponds, whereas composition of the terrestrial habitat close to the ponds and traffic load within 500 m had little influence on the distribution of calling males. Ponds with *P. fuscus* were large, permanent and eutrophic with high concentrations of oxygen and high spring temperatures. They also had a high proportion of shoreline with steep banks. Permanent ponds with calling males typically had a low abundance of predatory fish and crayfish; only two of the ponds with *P. fuscus* contained predatory fish. The results of this study indicate that interactions between physical factors (e.g. pond drying) and predation determine the presence of *P. fuscus*. Because *P. fuscus* has specific habitat requirements necessary for its survival and high site fidelity, it is particularly vulnerable to local changes in the condition of its natural breeding ponds. The situation is particularly serious for this species because the majority of the ponds that are within its dispersal range do not seem to be suitable for *P. fuscus* because of physical constraints.

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A major goal of conservation biology is to identify factors affecting the distribution and abundance of species at large scales over long periods of time. Without such knowledge it is impossible to distinguish between natural population fluctuations and actual species declines from anthropogenic or other causes (Pechmann et al. 1991). Although there has been much concern that amphibian populations have been declining globally in recent years (e.g. Houlahan et al. 2001), there is still much uncertainty as to what mechanisms

are responsible for these declines (e.g. Sarkar 1996). The concern has been whether observed declines are due to a combination of local anthropogenic causes and natural population fluctuations, or whether they could be global due to for example increased levels of UV-B radiation or the spread of diseases (e.g. Pechmann and Wilbur 1994, Blaustein et al. 1994, Lips 1998). Due to the frequent fluctuations in abundance of amphibian populations it is important to study processes affecting population dynamics at the local scale so that long-

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term distributions can be predicted (Skelly et al. 1999). Only when we know which factors regulate populations of threatened species can we understand why they decline, or what may limit their distributions, and further expansion. Such knowledge is crucial if conservation measures are to be successful.

Several studies suggest that metapopulation models, in which populations are in sources and sinks within a mosaic of suitable habitats, are appropriate for amphibians (summarised in Pechmann and Wilbur 1994, Marsh and Trenham 2000). In such populations, local extinctions may be balanced by recolonisation events and pose no threat to the metapopulation (Carlson and Edenhamn 2000). However, Blaustein et al. (1994) suggested that the decline of some amphibians in relatively undisturbed areas may be caused by factors related to their recolonisation ability. Many amphibians may be particularly vulnerable to local extinction because their recolonisation ability is poor due to physiological constraints, relatively low mobility and site fidelity. Furthermore, recolonisation may be low if barriers to dispersal exist between extant and extinct groups (Hels 1998). Even though the absence of a species from a habitat may reflect random local extinctions, other processes may cause changes in distribution, and many amphibian extinctions are probably the result from deterministic factors, not stochastic processes (Marsh and Trenham 2000). For example, introductions of predators, changes in water-quality, variations in hydroperiod, increases in traffic volume, and alterations to terrestrial habitats may affect the distribution of amphibians, and subsequently cause localised declines (Fahrig et al. 1995, Gamradt et al. 1997, Bradford et al. 1998, Meyer et al. 1998, Werner and Glennemeier 1999, Skelly et al. 1999, Knapp and Matthews 2000, Snodgrass et al. 2000, Hels and Buchwald 2001). Although the theoretical framework for explaining amphibian population dynamics and declines is poorly developed (Sarkar 1996), some conceptual models of community structure in ponds (e.g. Wellborn et al. 1996) successfully explained amphibian species richness and distribution in South Carolinian wetlands (Snodgrass et al. 2000). These models suggest that community structure in temperate ponds is determined by interactions between physical factors (e.g. pond drying and winter anoxia), predation and the life history characteristics of individual species (e.g. Wellborn et al. 1996). Thus, it is possible that these deterministic factors may be particularly important for the distribution of the amphibians with high site fidelity and limited ability to disperse to new habitats because of physiological constraints.

The aim of this study was to relate physiochemical and biological characteristics of ponds and the surrounding terrestrial habitat to distribution patterns of the declining spadefoot toad *Pelobates fuscus* Laurenti. Specifically, we aimed to identify some of the factors that could explain the decline and absence of this

species from ponds within its natural dispersal range and that may limit expansion of the species.

Pelobates fuscus is widely distributed in Europe, but recent investigations have shown that it has declined dramatically in numbers within its northern distribution range, especially in Denmark (Fog 1997, Fog et al. 1997) and Sweden (Berglund 1998). In 1945–1990 it disappeared from 98% of known breeding ponds in Denmark (Fog et al. 1997). Additionally, the distribution of *P. fuscus* in Sweden has been monitored since 1959, and in 1975 it had disappeared from > 90% of its former breeding ponds. In 1993–1997 it was shown that numbers had declined by 99% since 1959 and of 427 ponds where it was present in the 1960s and 1970s, only 60 had calling males in 1993–1997 (Berglund 1998, Fig. 1). Several causes have been suggested, including

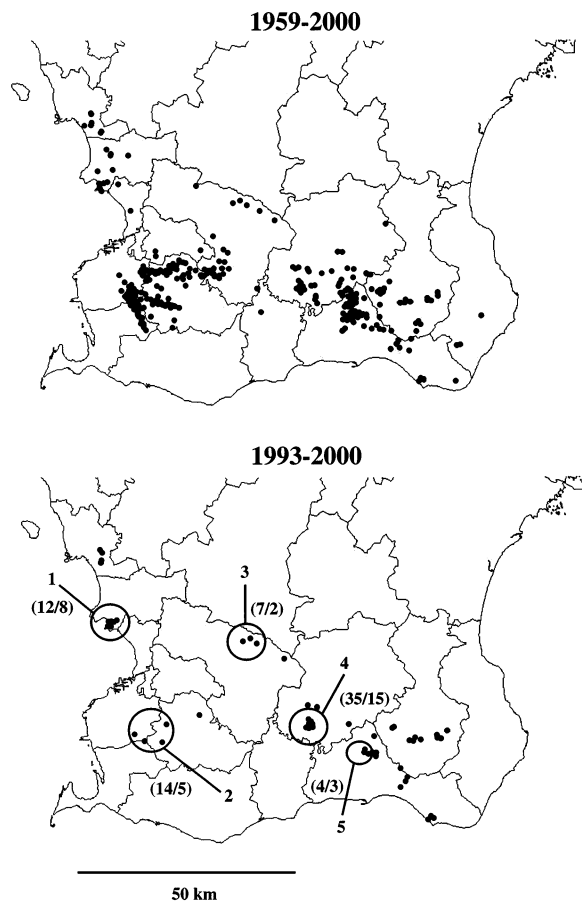


Fig. 1. All known sites (filled circles) with calling males of *Pelobates fuscus* in Sweden between 1959 and 2000 (upper) and 1993 and 2000 (lower). The five areas surveyed in the present study (circles) and the number of sites with and without calling males at those sites are shown. Distribution data for *P. fuscus* was provided by the County Administrative Board of Scania. These data are based on information provided by Berglund and Pröjts (for detailed information of the distribution of *P. fuscus* between 1959 and 1997 see also Berglund 1998).

destruction of breeding habitats and habitat fragmentation (Corbett 1989, Gasc et al. 1997), but changes to breeding habitats and/or surrounding terrestrial habitats are likely contributing factors, since *P. fuscus* has disappeared from several ponds in relatively pristine areas (Berglund 1998). Some of the changes may be fish and crayfish introductions, eutrophication of breeding ponds and intensification of agricultural practices (Corbett 1989, Fog et al. 1997, Berglund 1998). *Pelobates fuscus* occurs at the northern limit of its distribution in Sweden, has high site fidelity, limited dispersal ability, and a long-lived larval stage (Nielsen and Dige 1995, Hels 1998). These characteristics and the predictions from community structure models (e.g. Wellborn et al. 1996) suggest that *P. fuscus* should occur in permanent ponds without larger predators such as fish and crayfish. Low water temperature should also limit the number of ponds suitable for successful reproduction.

In 1999–2000 we surveyed biotic and abiotic characteristics of 33 ponds containing *P. fuscus* (ca 50% of known ponds in Sweden; Berglund 1998), along with 39 other ponds close (50–500 m) to them where *P. fuscus* was absent. Conditions in the surrounding terrestrial environment were also evaluated. A discriminant analysis that included measured environmental variables was then used to differentiate between used and unused ponds.

Material and methods

Natural history

Pelobates fuscus inhabits regions with warm climate and sandy soils in Sweden and its distribution range is therefore restricted to Scania in the south of the country (Gasc et al. 1997, Berglund 1998, Fig. 1). Adults are nocturnal and spend most of their time during the day in burrows. Reproduction starts in the beginning of April and ends in May. A female lays ca 2000 eggs in a string, which is often wrapped around submerged macrophytes at a depth of 10–40 cm (Strijbosch 1979, Fog et al. 1997). Embryos hatch after ca 7 d, and the newly hatched larvae need a temperature of above 15°C to develop normally and subsequently to metamorphose (Jensen 1992). Although *P. fuscus* is relatively small (maximum length ca 8 cm), tadpoles grow to a length of 15 cm. The larval stage is long compared to that of other amphibians in Sweden and lasts for 3–4 months depending on water temperature and food abundance. In some years with cold summers, tadpoles may spend the entire winter in ponds and metamorphose the following summer. Adults spend most of their terrestrial life close to the breeding pond and rarely disperse > 500–1000 m from it (Nöllert 1990, Nielsen and Dige 1995, Hels 1998). In late autumn (October–November) *P. fuscus* start to hibernate in

burrows where they spend the winter (Cedhagen and Nilson 1991, Fog et al. 1997).

Selection of study ponds

In 1999 and 2000 we surveyed 72 ponds in Scania. Ponds were chosen in five different areas (Fig. 1) because our intention was to include ponds encompassing the entire distribution range of *P. fuscus* in Sweden. Most ponds in the west and east of Scania were located close to urban areas, whereas ponds in the centre of Scania were located in less populated areas. The selection of ponds was based on the results of a survey of *P. fuscus* calling males conducted in 1993–1997 (Berglund 1998) and our own survey of area 4 in 1999. Our aim was to include at least one pond in an area with *P. fuscus* and to include all other ponds within 500 m of it. These latter ponds could have had calling males previously (i.e. before the survey in 1993–1997), or they could be ponds whose status as a breeding pond for *P. fuscus* was unknown. Since our aim was to determine the characteristics of potential breeding and non-breeding ponds we did not want dispersal barriers to confound our survey. Therefore, a selected group of ponds within an area had no apparent dispersal barriers between them (e.g. larger roads or ditches) and we thus assumed all ponds were accessible to *P. fuscus*.

Habitat description

Between 12 May and 7 June 2000, we characterised 19 biological, chemical and physical parameters of the 72 ponds. Data on crayfish abundance (July–September) and fish abundance (June–July) were obtained in 1999 (area 4) and in 2000 (areas 1–3, and 5). Crayfish > 6 cm total length were quantified using baited cylindrical traps as described by Nyström et al. (1996) and expressed as number of crayfish caught per trap. A trap attracts crayfish from an area of ca 12 m² (Abrahamsson and Goldman 1970), and traps were put in the littoral zone at a distance of 10 m. Between one and 15 traps were used in each pond depending on pond size. In large ponds at least 100 m of the circumference was surveyed for crayfish. To determine the abundance of fish, the littoral zone was electrofished (Brönmark and Edenhamn 1994). In some ponds where the abundance of fish was high only 25–50% of the circumference was electrofished, however, in most ponds without fish all (or at least 100 m) of the circumference was electrofished. Depending on the size of the pond and fish abundance, the time spent electrofishing varied between 1 and 30 min. Fish caught were identified to species and weighed. The abundance of fish in each pond was expressed as fish biomass (g wet weight) per minute fished.

Water temperature, oxygen saturation and pH were measured 10 cm below the surface in all ponds between 3 May and 12 May. Since it was not possible to sample all ponds on the same day, we reduced the influence of variation in weather conditions between sampling days by sampling around noon on sunny days and on the same day within each of the five study areas. At the same time, a sample was taken for later analysis of total nitrogen and total phosphorus concentration. N and P were analysed on a Technicon Auto Analyser II, according to Swedish standards (SS 028127 and SS 028131). Two measurements of water temperature were made (one in the southern part of the pond and one in the northern part), with the mean value being used in analyses. Maximum depth, pond area, the proportion of shoreline with steep banks, macrophyte cover and canopy cover were also estimated. Pond area was calculated from estimates of length and width, while the proportion of shoreline with steep banks was estimated by determining water depth with a measuring stick 0.5 m from the shore every twelve meters. If the depth exceeded 40 cm the shoreline was considered to be steep. Vegetation cover was estimated from the shore and proportions of emergent, floating-leafed and submerged macrophytes were recorded. Since adult *P. fuscus* are typically found close to their breeding pond most of the year, we estimated proportions of cultivated fields, pasture and forest within 250 m of a pond in the field. During hibernation and migration a small proportion of the adults may, however, be found up to 500–1000 m from a pond and the proportion of sandy soils and traffic load was therefore estimated within 500 m from a pond. Proportion of sandy soils was determined from geological maps (1:50 000). Traffic load within 500 m of a pond was provided by the Swedish National Road Administration. Data were obtained in 1995–1998 and these measurements reflect the traffic load in our study areas in 2000 (von Schantz pers. comm.). Two-way traffic load was measured annually and expressed as the number of vehicles per day (± 8 –12% error rate).

Pelobates fuscus survey

During the breeding season, male *P. fuscus* were counted by two groups of people using stereo hydrophones. The hydrophone has a filter unit that only lets through frequencies between 250 and 1000 Hz; these frequencies are then amplified to reduce disturbances from sounds other than those from calling *P. fuscus*. Calling males were monitored from dusk until 0200 h, during the peak of the calling period. The hydrophones were lowered into the pond 10 cm below the surface for 1 min at 10 m intervals. During a period of 40 d, starting 20 April, each of the 72 ponds was checked at least once. If no males were detected even after three

visits we inferred the pond was not a breeding pond for *P. fuscus*.

Data analysis

Nineteen quantitative habitat variables were first included in a direct discriminant function analysis and then in a stepwise discriminant analysis (e.g. Dillon and Goldstein 1984) to characterise ponds occupied by calling males of *P. fuscus*, and to identify which habitat parameters were most important in determining pond choice. We followed the analytical protocol of Marnell (1998), whereby the direct method included all 19 environmental variables (the independent variables in the analysis) to discriminate between ponds used or not used by calling males of *P. fuscus* (the dependent variable). Additionally, the forward stepwise method was used to determine those habitat variables which were most significant (the default F-value to enter the model was 4 and the default remove value was 3.9) in determining pond choice by *P. fuscus*.

The analyses were conducted using SYSTAT 10.0 with the validity of the discriminant function being estimated using jackknife classification. This involved allocating each pond to its closest group (in this case ponds with or without calling males) without using that pond to help determine the group centre (Manly 1994). To meet the assumptions of the analyses, data in proportions were arc sine transformed prior to analysis and other data (except pH) were natural log-transformed.

Results

The first calling male was recorded on 20 April and the last on 15 May. A total of 429 calling males were heard in 33 of the 72 ponds investigated. The numbers of *P. fuscus* counted at these positive ponds varied between 1 and 80, with a mean of 13 males per pond. Calling males were found in ponds located in urban areas with a high traffic load, as well as in ponds located in forest, pasture and in areas with cultivated fields. However, calling males did not occur in ponds with canopy cover exceeding 75%. Even though the physical, chemical and biological characteristics varied greatly between ponds with calling males (Table 1), a direct discriminant function analysis using 19 environmental variables successfully classified 86% of the 72 ponds in the correct category (Wilks $\lambda = 0.42$, $p < 0.001$). Classification success was higher for ponds with *P. fuscus* (91%) than for ponds without *P. fuscus* (82%); only three of the ponds with calling males were misclassified (Table 2). Although there was some degree of overlap, the group centroids also indicated that ponds with and without calling males differed with respect to their average score

Table 1. Mean values of 19 environmental variables in ponds with (N = 33) and without (N = 39) *Pelobates fuscus*. Ranges are given in parentheses. The most important environmental variables identified by the stepwise discriminant analysis used to discriminate between ponds with and without *P. fuscus* are shown in bold.

Variable	Ponds with <i>P. fuscus</i>	Ponds without <i>P. fuscus</i>
Maximum depth (m)	1.5 (0.5–3.5)	1.2 (0.1–3.5)
Area (m²)	1128 (43–5170)	952 (12–4992)
% shoreline with steep banks	30 (0–100)	22 (0–100)
Temperature (°C)	18.0 (15.3–21.5)	17.1 (13.1–20.7)
Total phosphorus (µg l⁻¹)	272 (29–1540)	160 (23–2240)
Total nitrogen (mg l ⁻¹)	2.06 (0.44–7.8)	1.77 (0.38–6.3)
% oxygen saturation	112 (29–195)	95 (30–218)
pH	7.6 (4.9–10.1)	7.7 (5.85–9.26)
Fish (g min⁻¹)	0.4 (0–9.8)	5.6 (0–66.9)
Crayfish (numbers/trap)	0.2 (0–5.2)	1.71 (0–20)
% submerged macrophyte cover	25 (0–100)	25 (0–100)
% floating-leaved macrophyte cover	19 (0–75)	20 (0–100)
% emergent macrophyte cover	31 (0–95)	29 (0–100)
% canopy cover	10 (0–75)	15 (0–90)
% cultivated fields (within 250 m)	40 (0–100)	30 (0–100)
% forested area (within 250 m)	15 (0–60)	20 (0–60)
% pasture area (within 250 m)	40 (0–95)	40 (0–95)
% area with sandy soils (within 500 m)	70 (0–100)	65 (0–95)
Traffic load (vehicles d ⁻¹ within 500 m)	930 (0–7320)	430 (0–7320)

profiles (Fig. 2, Table 1). Moreover, the jackknife method classified 76% of the ponds correctly (Table 2). In order to determine the individual contributions of environmental variables to the overall discrimination, and to determine the minimum number of variables that needed to be entered into the discriminant function, a stepwise forward discriminant analysis was conducted. When eight of the 19 original variables were used, the analysis classified 85% of the ponds correctly (Wilks $\lambda = 0.48$, $p < 0.001$). The jackknife method classified 79% correctly. Characteristics of the ponds rather than terrestrial habitat variables influenced the distribution of calling males (Table 1, 3). Ponds with calling males of *P. fuscus* were large, permanent and eutrophic with high concentrations of oxygen and high spring temperatures. They also had a high proportion of shoreline with steep banks. During our survey, six ponds dried out in July, and calling males were never observed in these temporary ponds. Permanent ponds with calling males typically had a low abundance of predatory fish and crayfish. Fish was the first factor selected to be included in the stepwise discriminant function (Table 4) and fish were found in 14 ponds. Of the 33 ponds with calling males only two contained fish (one pond with crucian carp *Carassius carassius* (L.) only, had one calling male, and one pond with stickleback *Pungitius pungitius* (L.) only, had 50 calling males). The fish ponds contained several species of predatory fish. Crucian carp was the most frequently occurring species and was found in nine of the ponds, but other predatory fish including pike *Esox lucius* L., perch *Perca fluviatilis* L., roach *Rutilus rutilus* L., sticklebacks and the exotic rainbow trout *Oncorhynchus mykiss* (Rich.)

were also found. Five of the ponds with fish also contained crayfish. Calling males were not found in ponds with high densities of the exotic signal crayfish; *Pacifastacus leniusculus* (Dana) (i.e. catches of ≈ 10 crayfish per trap or more), but were found in one pond with the native noble crayfish *Astacus astacus* (L.) (5.2 crayfish per trap). Crayfish occurred in eight ponds (two ponds contained the native noble crayfish and six ponds contained the exotic signal crayfish). In these ponds, their density estimated as catch per unit effort ranged between 1.43 and 20 crayfish per trap.

Discussion

The results of this study indicate that the declining *P. fuscus* has specific habitat requirements, associated particularly with the conditions of the pond, and that these requirements probably preclude *P. fuscus* from colonising most habitats that are otherwise within its dispersal range. Furthermore, the distribution of *P. fuscus* in ponds could be predicted from the conceptual model of Wellborn et al. (1996), where the distribution of aquatic species in temperate regions is determined by hydroperiod and the presence of large predators such as fish. Several other studies suggest that other European species of amphibians select breeding habitats based on characteristics of the terrestrial as well as the aquatic environment (Beebee 1985, Loman 1988, Ildos and Ancona 1994, Marnell 1998, Vos and Chardon 1998). Other studies also indicate that traffic mortality has a significant effect on the local density and distribution of anurans (Fahrig et al. 1995, Vos and Chardon 1998, Hels and

Table 2. Classification matrix and jackknifed classification matrix showing the observed and predicted presence/absence of calling males of *Pelobates fuscus* in 72 ponds using direct discriminant function analysis. Percentage correctly classified ponds are given.

Model prediction	True distribution		Classification success (%)
	Absent	Present	
Absent	32	7	82
Present	3	30	91
Total	35	37	86

Model prediction	True distribution		Jackknifed classification success (%)
	Absent	Present	
Absent	29	10	74
Present	7	26	79
Total	36	36	76

Buchwald 2001). Neither characteristics of the terrestrial habitat nor traffic load had any significant influence on the distribution of calling males in our survey. However, we aimed specifically to identify some of the factors that could explain the absence of *P. fuscus* from ponds within its natural dispersal range. Thus, ponds with *P. fuscus* were never > 500 m from ponds without *P. fuscus* and dispersal barriers such as roads with high traffic load were absent. Consequently, there was considerable overlap in the characteristics of terrestrial habitat surrounding the ponds as well as in the influence of traffic. Moreover, average traffic load in our study areas was comparatively low (Table 1). For example, daily, two-way traffic load on roads within 500 m of 51 of the 72 ponds survey was 50 vehicles or less. At this low traffic load the probability of *P. fuscus* of being killed on the road is low whereas at a traffic load of 3200 vehicles d^{-1} , 10% of the adult population of *P. fuscus* was estimated to be killed annually (Hels and Buchwald 2001). Nevertheless, our results suggest that without conservation measures being put in place to improve current and former breeding ponds, the distribution of *P. fuscus* is not likely to increase.

The mechanisms behind the decline of *P. fuscus* are difficult to determine precisely for several reasons. Firstly, the major decline of *P. fuscus* occurred before 1975, and was focused mainly in urban areas and areas with a high proportion of cultivated fields with less sandy soils (Berglund 1998). Most of the ponds with calling males found in our study were not in such areas, and our analysis reflects mainly factors affecting the distribution of *P. fuscus* in the relatively pristine areas with low traffic load (area 4, Fig. 1). Secondly, we found only eight ponds that were known to have calling males before 1993–1997, and still had calling males. Nevertheless, the results of our study can be considered with respect to local factors that may limit the expansion and distribution of rare species with physiological and ecological constraints.

Pond choice by male *P. fuscus* in relation to abiotic factors

Our results indicate that *P. fuscus* is limited to large permanent ponds with high spring temperatures. These ponds also have high concentrations of phosphorus, high oxygen concentrations and a shoreline with a high

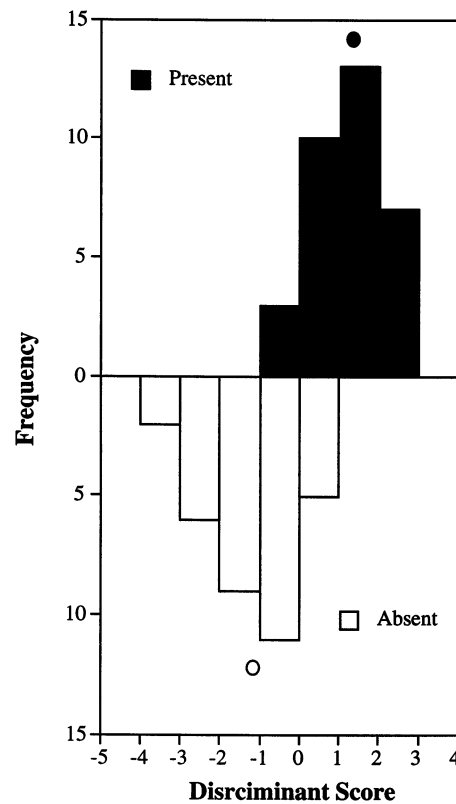


Fig. 2. Discriminant grouping patterns of ponds with (N = 33) and without (N = 39) calling males of *Pelobates fuscus*. The filled (+ 1.270) and open circles (- 1.705) indicate discriminant scores of group means.

Table 3. Standardised canonical discriminant function coefficients for 19 environmental variables used in a direct discriminant analysis, and eight variables selected using the stepwise forward option (a dash indicates the variable failed to enter the model). The dependent variable in the analyses was the presence/absence of calling males of *Pelobates fuscus*.

Variable	Direct method	Stepwise method
Maximum depth	0.524	0.397
Area	0.361	0.441
% shoreline with steep banks	0.663	0.464
Temperature	0.594	0.626
Total phosphorus	0.620	0.549
Total nitrogen	0.059	–
% oxygen saturation	0.591	0.471
PH	–0.216	–
Fish (catch per unit effort)	–0.932	–0.886
Crayfish (catch per unit effort)	–0.363	–0.354
% submerged macrophyte cover	0.298	–
% floating-leaved macrophyte cover	0.046	–
% emergent macrophyte cover	0.241	–
% canopy cover	–0.007	–
% cultivated fields (within 250 m)	0.055	–
% forested area (within 250 m)	–0.158	–
% pasture area (within 250 m)	0.283	–
% area with sandy soils (within 500 m)	–0.392	–
Traffic load (within 500 m)	–0.248	–

proportion of steep banks. Strijbosch (1979), who studied *P. fuscus* in the Netherlands, obtained similar results and found that adults select the most eutrophic and well oxygenated breeding habitats and suggested that it was important for species whose larvae grow to a large size at metamorphosis to breed in productive waters. In our survey, many of the selected ponds were man-made, and in agricultural areas with no shading trees or major inflows of cold water from springs. Thus, ponds with low spring temperatures (< 15.3°C), the limit for normal tadpole development (Jensen 1992), were not used by *P. fuscus*. Similarly, the pool frog *Rana lessonae* Camerano exists on the northern fringe of its distribution in Sweden and occupies ponds with high spring water temperatures (Sjögren 1994), and also selects warmer areas within a breeding pond for oviposition (Sjögren et al. 1988). High temperature may have positive effects on the development rate of most amphibians in temperate regions (e.g. Berven and Gill 1983), but high temperatures may be critical for the survival of species near their thermal distribution limits. Although some of the unoccupied ponds in this study had low temperatures because of inflows of ground water, the low temperatures of other ponds appeared to be associated with high canopy cover. Canopy cover was negatively correlated with water temperature in our study ($p < 0.001$, $r = -0.56$) and ponds with canopy cover exceeding 30% always had temperatures < 16°C. Werner and Glennemeier (1999) considered that forest canopy cover affected the distribution and survival of *Rana pipens* (Schreber) and *Bufo americanus* (Holbrook) through its negative effects on temperature, oxygen concentration and the absence of high quality food sources such as algae. They concluded that pond succession may have had a major impact on the long-

term species distributional patterns of amphibians in E. S. George reserve in Michigan. Skelly et al. (1999) also proposed that forest succession via its effects on canopy cover and hydroperiod affected the dynamics and distribution of amphibians in Michigan. Although high canopy cover may preclude *P. fuscus* from inhabiting some of these habitats because of low temperature, low oxygen concentrations may also be detrimental, particularly during winter if tadpoles fail to metamorphose before winter. We found dead tadpoles of *P. fuscus* in some of our crayfish traps possibly because oxygen concentration was low at the sediment surface. Normally, *P. fuscus* can use atmospheric oxygen in ponds during summer, but we predict that winter anoxia may be an important mortality factor for tadpoles, particularly in years with cool summers and cold winters.

Another factor that may limit the breeding success of *P. fuscus* is low pH. Low pH has important ecological effects on amphibians through complex interactions with other physical, chemical and biological paramete-

Table 4. Significance between groups (ponds with or without calling males of *Pelobates fuscus*) and environmental variables that were selected to enter the discriminant function using the stepwise forward option. The selected variables had the strongest positive (+) or negative (–) association with choice of ponds by calling males.

Variable	Wilks λ	p
Fish (–)	0.8971	0.0060
Maximum depth (+)	0.7411	0.0000
Temperature (+)	0.6597	0.0000
Crayfish (–)	0.5992	0.0000
Total phosphorus (+)	0.5580	0.0000
% oxygen saturation (+)	0.5261	0.0000
% shoreline with steep banks (+)	0.5087	0.0000
Area (+)	0.4757	0.0000

ters. Some species are relatively sensitive to acidity, others exhibit considerable tolerance, and acid tolerance of amphibian embryos varies from population to population (reviewed in Pierce 1993). Nevertheless, we found calling males in water with pH ranging from 4.9 to 10.1, five ponds having pH < 6.2. Even though it is only five ponds, these ponds represent ca 10% of all the known positive ponds of *P. fuscus* in recent years. pH does not seem to be a major factor affecting pond choice by males, but if ponds are vulnerable to acidification from acid rain, the reproductive success of *P. fuscus* may be low. Strijbosch (1979) found calling males in ponds ranging from pH 3.9 to 6.3, but egg-masses of *P. fuscus* deposited in acid waters were often decomposing due to infestations of *Saprolegnia*. We have found no experimental studies of pH tolerance of *P. fuscus* and such studies must be conducted in order to assess the effects of acidification on the reproductive success of this species.

Pond choice by male *P. fuscus* in relation to the presence of fish and crayfish

Even though *P. fuscus* occupied permanent ponds, very few of these ponds had calling males when predatory fish and crayfish were abundant. However, one pond with sticklebacks only contained 50 calling males. Like the vulnerable tree frog *Hyla arborea* L. which often co-occurs with *P. fuscus* (e.g. in 13 of 15 ponds in area 4), the presence of small fish such as sticklebacks likely does not affect their distribution (Brönmark and Edenhalm 1994), whereas larger predatory fish have negative effects on both species. Thus, even though ponds are numerous in some areas within the distribution range of *P. fuscus* (e.g. area 2, Fig. 1), the majority of these contain fish (e.g. Brönmark and Weisner 1996). Numerous studies have shown that predatory fish can limit the distributions of palatable amphibians by consuming eggs and larvae (Gamradt and Kats 1996), by deterring oviposition (Holomuzki 1995), or by acting as barriers to dispersal (Bradford et al. 1993). The effects of predatory crayfish on the distribution of amphibians are less well known and are likely to be more complex than those of predatory fish (e.g. Nyström 1999). Spread of the exotic red swamp crayfish *Procambarus clarkii* Girard had negative effects on newts *Taricha torosa* (Rathke) in Californian streams through the consumption of eggs and larvae, and this aggressive crayfish also drove newts onto land so they were unable to reproduce (Gamradt and Kats 1996, Gamradt et al. 1997). Up to 1996 it was estimated that > 1000 ponds in southern Sweden had been stocked with the exotic signal crayfish, mainly for culture purposes (Anon. 1999). These stockings began in the late 1970s and culminated at the beginning of the 1990s. Thus, the decline of *P. fuscus* began before most signal crayfish

populations were established. Nevertheless, experimental studies have shown that dense populations of signal crayfish may affect the survival of amphibians by consuming eggs, by consuming and injuring tadpoles and by altering habitat by consuming macrophytes (Axelsson et al. 1997, Nyström 1999, Nyström et al. 2001).

Unpalatability and chemically mediated predator avoidance are common features of amphibians that co-exist with larger predators such as fish (Kats et al. 1988). *Pelobates fuscus* larvae are readily consumed by fish (rainbow trout) and signal crayfish, but do not respond strongly to chemical cues released by these predators (Åbjörnsson and Nyström unpubl.). These results, and the distribution data obtained in this survey suggest that *P. fuscus* is not well adapted to survive in habitats with these predators. Furthermore, experimental studies have shown that when both fish and crayfish are present they almost eliminate amphibians such as the widely distributed *Rana temporaria* (L.), even though it responds behaviourally to these predators (Nyström et al. 2001).

Distribution of amphibians and conservation of *P. fuscus*

The mechanisms affecting the distribution of *P. fuscus* cannot be determined from a descriptive study such as ours and the hypotheses proposed in this study need to be evaluated experimentally. It is not clear how *P. fuscus* select breeding ponds, but several amphibians do so using biotic and abiotic cues. The use of such cues often results in avoidance of shallow waters and ponds with predators (e.g. fish), and the selection of water bodies with high temperatures (Sjögren et al. 1988, Bradford 1989, Crump 1991, Resetarits and Wilbur 1991, Hopey and Petranka 1994, Holomuzki 1995, Spieler and Linsenmair 1997). Our results indicate that *P. fuscus* may belong to this group. Of the 72 ponds examined, 39 had calling males between 1959 and 1982, but only 31 had calling males between 1993 and 1997 (Berglund 1998). Thus, *P. fuscus* has probably disappeared from a further eight potential breeding ponds, since we did not record them there either. Even though the reason for absence from these ponds may be factors that were important in the past, and the characteristics of the ponds could have changed, it may be representative to examine these particular ponds. Today, four of them contain predatory fish and two of these also have crayfish. Two of the ponds are now much shallower than they were ca 20 yr ago (Berglund pers. comm.) and were almost dry at the beginning of June in 1999 and 2000. We surveyed 32 ponds that had not been identified as positive ponds before, despite being within the potential range of dispersion of *P. fuscus*, but calling males were found in only seven of them. Four of these ponds are fishless permanent ponds that have

been restored successfully in recent years (enlarged, deepened, removal of canopy cover), to make them more suitable for *P. fuscus*. These observations indicate that fish and crayfish introductions, as well as changes in hydroperiod, may drive local populations extinct and prevent recolonisation even though they are close to ponds with established *P. fuscus* populations.

Habitat relationship models can be used to predict the presence/absence of a species, and they can also be used to direct conservation effort by examining particular sites that are not correctly classified (e.g. Morrison et al. 1992). However, if prediction errors are not placed in an ecological context the results of a model may be misleading (Fielding and Bell 1997). In our study, discriminant analysis was more successful at predicting the presence of *P. fuscus* (91% success) than its absence (82% success). Errors made in predicting the presence of rare and endangered species are often considered to be problematic in conservation biology because they may indicate that the predictive model did not include a vital parameter. On the other hand, falsely predicting the absence of a species could indicate that animals were not correctly sampled, the species in question does not occupy all suitable habitats, or the model overemphasised the value of some environmental parameters (Morrison et al. 1992). Hence, ponds falsely predicted to have *P. fuscus* might be potential breeding sites of high quality. The distribution and population densities of rare species of amphibians such as *Hyla arborea* and *P. fuscus* have been monitored successfully in Swedish ponds by counting the number of calling males (Brönmark and Edenharn 1994, Berglund 1998). Unfortunately, because *P. fuscus* males attract females by calling from the bottom of a pond, their calls can be hard to detect in deep water making the species difficult and time consuming to survey. However, even individuals calling from the bottom of relatively deep ponds (≈ 4 m) up to 20 m away can be detected using the hydrophone we used (Falk and Sterner 1999). Moreover, its stereophonic nature makes it possible to locate the direction and distance of males, and with experience it is also possible to distinguish the number of calling males. Thus, it is highly unlikely that we have classified sites with calling males as sites without calling males.

All seven ponds that were classified as containing *P. fuscus*, but where *P. fuscus* was in fact absent, were permanent ponds with relatively high oxygen concentrations and high spring temperatures. However, two of the ponds contained low numbers of predatory fish and one contained signal crayfish, making them less suitable as breeding ponds for *P. fuscus*. Two further ponds that were misclassified as *P. fuscus* ponds were restored in the year before our survey and have the potential to become breeding ponds for *P. fuscus*. Only three of 33 ponds with *P. fuscus* were classified as not containing it, indicating that our model included the most important environmental variables for determining the presence of

the species. Two of these misclassified ponds had low oxygen concentrations (29 and 65% saturation respectively) and one was permanent but relatively shallow (0.7 m).

The landscape in Scania has been transformed from an area dominated by pasture, small scale farming and numerous wetlands in the 1950s to an area with large scale agriculture, forest plantations and urbanisation, but relatively few ponds. These changes have undoubtedly contributed to the dramatic decline of *P. fuscus* (Fog et al. 1997, Berglund 1998). Even though many habitats have been destroyed completely, our survey indicates that some factors associated with this decline may be due to altered conditions within the ponds. Factors identified in this study as precluding *P. fuscus* from expanding are decreasing water levels, low water temperature, low oxygen concentration and the presence of fish and/or crayfish. These results are in agreement with the predictions of conceptual models with respect to community structure in ponds across a permanence gradient (Wellborn et al. 1996). Presently, an expansion of the distribution of *P. fuscus* in southern Sweden is very unlikely, since most of the ponds within its distribution range provide unsuitable habitats. Because it recolonises restored ponds (Fog 1997) it may be necessary to intensify the restoration of ponds in order to prevent extinction of this species. In order to maximise restoration success, future studies of *P. fuscus* should investigate reproductive success in relation to the environmental factors identified in this survey as potentially limiting for its distribution, especially temperature, pH, eutrophication and oxygen concentration. In addition, it is important to evaluate experimentally how biotic interactions (e.g. inter and intraspecific competition and predation) affect the reproductive success of *P. fuscus*.

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