Ekológia (ČSFR) Vol. 9, No. 4, 353—360, 1990

FROG DENSITY AND DISTRIBUTION IN A HETEROGENEOUS LANDSCAPE — A MODELLING APPROACH*

JON LOMAN

Department of Animal Ecology, University of Lund, S—223 62 Lund, Sweden

Abstract

Loman J.: Frog density and distribution in a heterogeneous landscape — a modelling approach. Ecology (CSFR), Vol. 9, No. 4, 353—360, 1990.

A model of factors determining frog density and distribution is presented. It considers migrating frog species in a heterogeneous landscape. This situation presents the frog with optimization problems: long and risky migrations may be necessary to utilize the best and least crowded breeding sites and summer habitats. The frogs' options are also dependent on the information available to the frog. Alternative mechanisms that may govern the proposed factors are discussed.

Introduction

Despite of much work on the ecology of frogs there have been few studies that in a comprehensive way address the problem of what determines frog density and distribution in a landscape. Below I discuss the factors that I think proximally constrain fitness of frogs. I then discuss mechanisms which may ultimately govern how frogs åre distributed, given the constraining factors. Though the ideas discussed below have relevance to many frog species, the common frog (*Rana temporaria*) is the species considered (unless otherwise stated) when referring to facts of frog biology.

The purpose of this presentation is to point at how behavioural studies can be put into a context where their importance for the ecology — density and distribution — of a population is evident. I also want to show how this unified approach raises more fundamental issues. I think it should be of value if these were considered by frog researchers.

The model considers a landscape that is composed of a mosaic of breeding ponds, summer habitats (possibly differing in quality) hibernation sites, and

* This paper was presented on VIIIth International Symposium on Problems of Landscape Ecological Research, October 3rd—7th 1988, Zemplínska šírava, CSFR.

waste land. Each habitat is a spot or a coherent area with uniform vegetation (Fig. 1).

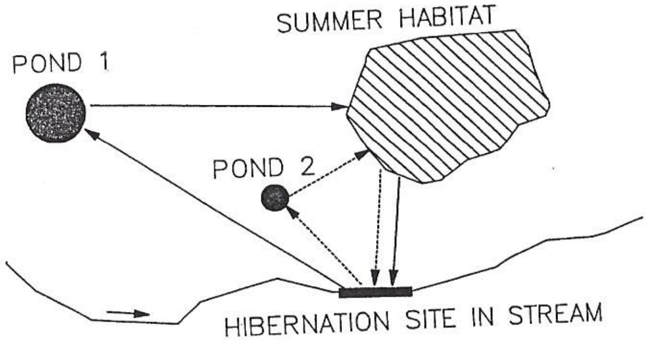

Fig. 1. A simplified frog landscape with two (out of several possible) tactics outlined.

Biotic and abiotic constraining factors

For simplicity, I only consider the female part of the population. The fitness of a female is measured as her expected number of metamorphosed young that reach a summer habitat. This is affected by (Fig. 2):

1. Breeding migration survival. Survival per distance depends on characteristics of the crossed habitat; predator density and cover type. The former may, in turn, be affected by the total number of migrating frogs, a high number attracting predators but also diluting risk for an individual frog (Fig. 3, arrow e. This arrow is also applicable to several other points below).

2. Summer migration survival. See previous point.

3. Number of eggs laid. Their number probably depends on female condition and thus on food availability in the summer habitat. This depends on characteristics of the habitat and the number of competing frogs.

4. Egg survival. This is due to the physical qualities of the pond (risk of drying up in a dry spring) and the presence of egg predators. The latter may be affected by the number of other females and their eggs in the breeding pond. This effect is negative (for a particular female's eggs) if predators are attracted by the presence of many frogs but positive if the effect of a given number of predators in a pond is diluted by many eggs.

5. Larval survival depends on predator density and food availability. Both these factors may be affected in various ways by the number of other larvae in the pond.

6. Dispersal survival. The survival of newly metamorphosed frogs dispersing from the breeding pond to a (late) summer habitat should be affected by characteristics of the crossed habitat (see point 1).

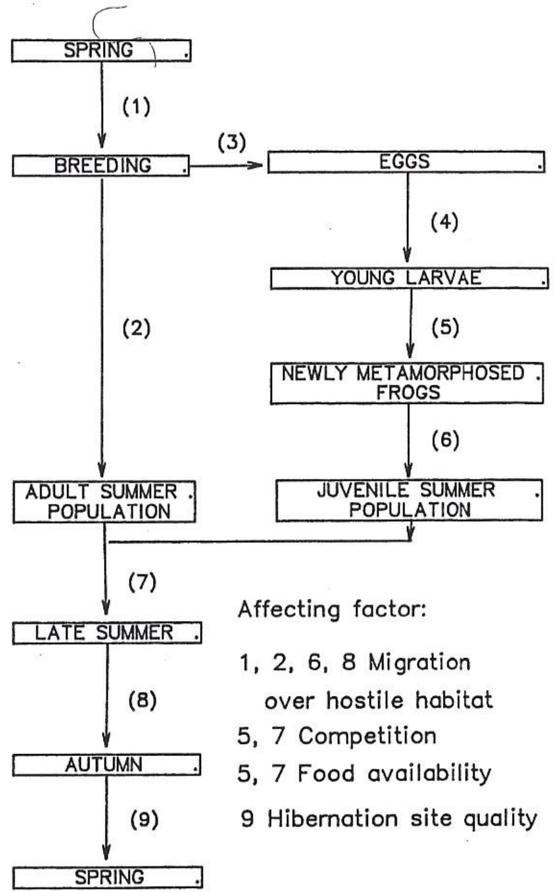

Fig. 2. The frog seasonal cycle as envisaged in this presentation. The numbers refer to processes described in the section "Biotic and abiotic constraining factors". The boxes symbolize numbers of frogs in different categories, development stages or seasons.

7. Survival in summer habitats. This depends on the characteristics of the summer habitat, e. g. cover type and predator density. Survival may also depend on food availability. Both predator density and food may, in turn, depend on frog density (and thus on the movements and survival of other frogs).

8. Hibernation migration survival. This depends on predator density and cover type in the crossed habitat. See point 1.

9. Hibernation survival. Apart from yearly variation, due to winter weather conditions, this depends on the quality of the hibernation site.

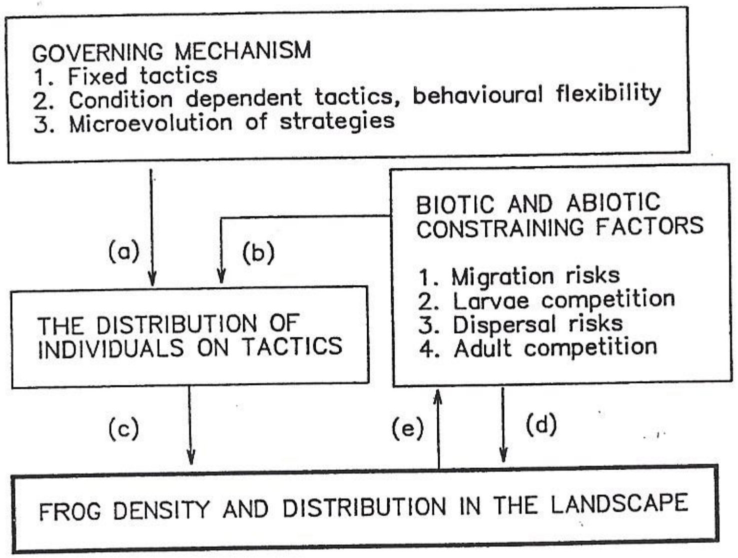

Fig. 3. An outline of the interaction between constraining factors, governing mechanisms, and strategies that determine frog density and distribution in a landscape.

Frog tactics

A set of rules that determine which summer habitat, which hibernation site and which breeding pond a frog will utilize is a tactic. One tactic may consist of breeding in pond i ($i = 1, 2, 3, \ldots, P$), spending the summer in habitat patch j ($j = 1, 2, 3, \ldots, S$), and hibernating at site k ($k = 1, 2, 3, \ldots, H$). P, S, and H are the total number of ponds, summer habitats and hibernation sites in the landscape, respectively. Altogether there are $P * S * H$ different tactics possible.

Governing mechanism

Given the factors listed above, that I assume influence survival and reproductive success in frogs, I will discuss three mechanisms that may explain the distribution of frogs in a landscape. I will treat them as alternatives, in the real world it may well be that they somehow operate in combination. These mechanisms determine, together with the factors discussed above, the individual frog's tactic (Fig. 3, arrows a and b). The tactics of all frogs and the constraining factors determine the total density and distribution of frogs in the landscape (Fig. 3, arrows c and d).

Genetically fixed tactics

If these tactics are genetically fixed and completely inherited one may consider each tactic a strategy in the sense of Dominey (1984). All frogs with one strategy constitute a closed population, a deme, and one can study its population dynamics and possible population density equilibria. The total density and distribution of frogs in a landscape is in this case the sum of its parts, these populations. Different closed populations may compete if they jointly utilize one summer habitat. The different population equilibria may thus be studied using the theory for competing species.

Several populations may thus spend the summer in a single summer habitat patch or at one hibernation site. However, if several populations, in this sense, breed in the same pond this mechanism runs into conceptual problems or problems with realism. What happens if frogs from different populations mate?

A model that is basically similar to this has been used by Lundberg & Alerstam (1986) to predict the global distribution of migrating bird species.

Condition-dependent tactics

If a frog's tactic is formed by it successively *choosing* different habitats (e. g. depending on the current distribution of other frogs) this tactic is a part of a conditional strategy, *sensu* Dominey (1984). If all frogs somehow could perceive what other frogs were doing or intended to do, one would expect them to be distributed so that they all had the same fitness. Such a situation should be considered within the framework of game theory (Maynard Smith & Price 1973) or Fretwell's (1972) theory of the "ideal free distribution".

Evolution of strategies

If frogs cannot perceive the relevant information of other frogs' whereabouts and a tactic is genetically fixed but subject to intrademe variation and evolution, one would expect a balanced polymorphism to settle. This situation can be considered within the framework of "evolutionary stable strategies" (Maynard Smith, 1976).

Discussion

Available information

1. Spacing. Do frogs react to the presence of other frogs when settling in a summer habitat and choosing breedings ponds? I have previously shown (Lo-

man, 1981) that the presence of other frogs does affect their summer distribution. However there is no information suggesting whether large breeding aggregations are avoided due to high frog density.

2. Movement pattern. Do movements take place as assumed by the model? Is it sufficient to consider one summer habitat only or do frogs use a succession of habitats during one summer? The fact that at least some frogs stay in restricted home ranges for long periods, also returning to the same home range in successive year has been shown (Haapanen, 1970).

3. Hibernation. Does winter mortality contribute significantly to overall mortality and are suitable hibernation sites in short supply? Large aggregations of hibernating frogs have been observed both in streams and in heaps of debris (T. Madsen, pers comm). This suggests that such sites are valuable enough to warrant long migrations.

4. Predation. In a study area in southern Sweden there is evidence that a large part of total mortality is due to predation (Loman, 1984). If this is generally true one would expect the cover of a habitat to be important for its suitability.

5. Food, growth, and reproduction. There is a positive correlation between female size and number and size of eggs (Barker, Jørgensen, 1981). If growth rate depends on feeding rate, which seems most likely, there is a direct link between summer habitat quality and number of eggs laid. However, as frogs are iteroparous the relation is complicated by the fact that frogs potentially have the options to convert energy directly into eggs or to grow fast and, probably, be in a better position to lay a large clutch in later years. A model that completely predicts the optimum choice of a frog must take life time reproductive success into account.

6. Breeding migration mortality. Frogs may move extensively, Heusser (1968) has shown that common toads *Bufo bufo* may move as far as 3 km (although 1 km is more normal) to the breeding pond. Studies of the importance of traffic mortality for the common toad have been made (van Gelder, 1973). There are data suggesting that the degree of isolation is one factor that determines the choice of breeding ponds *or* the average density of frogs in a landscape (Wederkinch, 1988; in press, Loman, 1988).

Suggested field work and conclusions

Further work should be conducted along two lines. First we need more data on the importance of the factors constraining frog population dynamics. Such studies concern predation rates, the relation between food availability and reproduction and larval competition in natural populations. Given the importance of migration mortality and breeding site competition, all mechanisms make certain predictions with respect to frog distribution in landscape. Such studies give clues to the importance of these factors.

Second we need data that allow us to evaluate the relative importace of the suggested mechanisms. The mechanisms imply different basic facts, the relative importance of which can be studied.

1. Are migration tendencies inherited? One could, e. g., capture female and male frogs that leave a breeding pond in a certain direction for their summer habitat, let them mate and raise their offspring. Will it tend to migrate in the same direction the parents? The preferred migration direction can be tested in areas of the type used by Ferguson et al. (1968). If there is such a correlation between parent and offspring it makes the evolution of this character — summer habitat choice — possible, something required by the last mechanism.

2. The first mechanism requires that a frog returns, for each breeding season to the pond where its parents bred. This pattern should be described.

3. An experiment where frogs are removed from a breeding pond could determine if other frogs perceive this and react by moving in to this pond instead of breeding in a neighbouring pond. Such processes are expected if the second mechanism is important.

This purpose of this model has been to point to the value of the proposed studies and put them into a unified context.

Acknowledgements

This study has been supported by the National Swedish Environment Protection Board.

References

Barker Jørgensen, C., 1981: Ovarian cycle in a temperate zone frog, *Rana temporaria*, with special reference to factors determining number and size of eggs. J. Zool., *195*, p. 449—458.

Dominey, W. J., 1984: Alternative mating tactics and evolutionary stable strategies. Am. Zool., *24*, p. 385—396.

Ferguson, D. E., McKeown, J. P., Bosarge, O. S., Landreth, H. F., 1968: Suncompass orientation of bullfrogs. Copeia, 1968, p. 230—235.

Fretwell, S. D., 1972: Populations in a seasonal environment. Princeton University Press, Princeton N. J.

Gelder, J. J. van., 1973: A quantitative approach to the mortality resulting from traffic in a population of *Bufo bufo* L. Oecologia, *13*, p. 93—95.

Haapanen, A., 1970: Site tenacity of the common frog (*Rana temporaria* L.) and the moor frog (*Rana arvalis* N.). Ann. Zool. Fenn., 7, p. 61—67.

Heusser, H., 1968: Die Lebensweise der Erdkröte *Bufo bufo* (L.). Rev. Suisse Zool., *75*, p. 927—982.

Loman, J., 1981: Spacing mechanism in a population of the common frog *Rana temporaria* during the non-breeding period. Oikos, 37, p. 225—227.

Loman, J., 1984: Density and survival of *Rana arvalis* and *Rana temporaria*. Alytes, *3*, p. 125—134.

Loman, J., 1988: Breeding by *Rana temporaria*; the importance of pond size and isolation. Memoranda Soc. Fauna Flora Fenn., *64*, p. 113—115.

Lundberg, S., Alerstam, T., 1986: Bird migration patterns: Conditions for stable geographical population segregation. J. Theor. Biol., *123*, p. 403—414.
Maynard Smith, J., 1976: Evolution and the theory of games. Am. Scientist, *64*, p. 41—45.
Maynard Smith, J., Price, G. R., 1973: The logic of animal conflicts. Nature, *246*, p. 15—18.
Wederkinch, E., 1988. Population size, migration barriers, and other observations of *Rana dalmatina* populations near Køge, Zeeland, Denmark. Memoranda Soc. Fauna Flora Fenn., *64*, p. 101—103.

Received 7. 7. 1989

Loman J.: **Hustota žab a jejich rozdělení v heterogenní krajině — modelový přístup.**

V práci je předložen model faktorů určující hustotu žab a jejich rozdělení. Model uvažuje migraci žabích druhů v heterogenní krajině. Tato situace představuje žábu s optimalizačními problémy: dlouhé a riskantní migrace mohou být nezbytné k využití nejlepších a nejméně zaplněných míst k plození i letních stanovišť. Možnosti volby jsou také závislé na informaci, která je žábám dostupná. Jsou diskutovány alternativní mechanismy, které mohou ovládat navržené faktory.

Ломан Й.: **Плотность лягушек и их распределение в гетерогенном ландшафте — модельный подход.**

В работе представлена модель факторов определяющая плотность лягушек и их распределение. Модель говорит о миграции видов лягушек в гетерогенном ландшафте. Эта ситуация представляет лягушкы с оптимализационными проблемами: длительные и рисковые миграции могут быть необходимыми для использования самых лучших и менее всего заполненных мест с целью плодиться, и для летних местонахождений. Возможности выбора находятся в зависимости от информации, которая является для лягушек доступной. Дискутируются альтернативные механизмы, которые могут владеть предлагаемыми факторами.