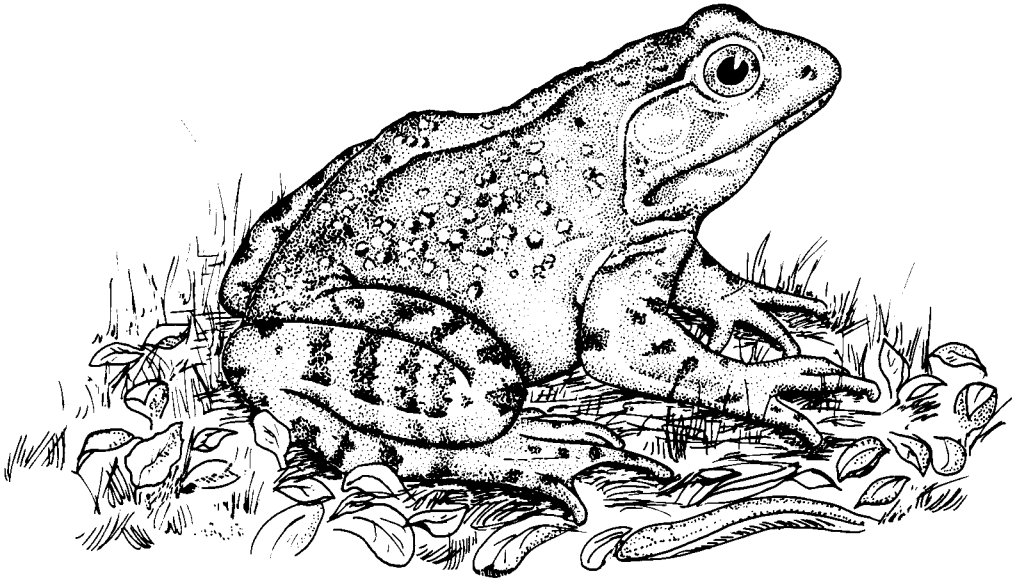


BIOLOGICAL REPORT 82(10.138)
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HABITAT SUITABILITY INDEX MODELS: BULLFROG



U. S. Fish and Wildlife Service

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HABITAT SUITABILITY INDEX MODELS: BULLFROG

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PREFACE

This document is part of the Habitat Suitability Index (HSI) model series [Biological Report 82(10)], which provides habitat information useful for impact assessment and habitat management. Several types of habitat information are provided. The Habitat Use Information section is largely constrained to those data that can be used to derive quantitative relationships between key environmental variables and habitat suitability. This information provides the foundation for the HSI model and may be useful in the development of other models more appropriate to specific assessment or evaluation needs.

The HSI Model section documents the habitat model and includes information pertinent to its application. The model synthesizes the habitat use information into a framework appropriate for field application and is scaled to produce an index value between 0.0 (unsuitable habitat) and 1.0 (optimum habitat). The HSI Model section includes information about the geographic range and seasonal application of the model, its current verification status, and a list of the model variables with recommended measurement techniques for each variable.

The model is a formalized synthesis of biological and habitat information published in the scientific literature and may include unpublished information reflecting the opinions of identified experts. Habitat information about wildlife species frequently is represented by scattered data sets collected during different seasons and years and from different sites throughout the range of a species. The model presents this broad data base in a formal, logical, and simplified manner. The assumptions necessary for organizing and synthesizing the species-habitat information into the model are discussed. The model should be regarded as a hypothesis of species-habitat relationships and not as a statement of proven cause and effect relationships. The model may have merit in planning wildlife habitat research studies about a species, as well as in providing an estimate of the relative suitability of habitat for that species. User feedback concerning model improvements and other suggestions that may increase the utility and effectiveness of this habitat-based approach to fish and wildlife planning are encouraged. Please send suggestions to:

Resource Evaluation and Modeling Section
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BULLFROG (Rana catesbeiana)

HABITAT USE INFORMATION

General

The bullfrog (Rana catesbeiana) is a large, aquatic frog that commonly inhabits permanent bodies of standing or slow-moving water. Bullfrogs may be found in water bodies with swifter currents where slow backwaters are available and may be drawn to such areas in search of prey (Rabeni 1985). Conant (1975) states that the natural range of the bullfrog extends from Nova Scotia to central Florida, west to Wisconsin and across the Great Plains to the Rocky Mountains. Introduction of the bullfrog has been successful in Puerto Rico (Perez 1951), Japan (Telford 1960), Italy (Lanza 1962), Jamaica (Mahon and Aiken 1977), the western United States (Stebbins 1985), and elsewhere.

Most life history events are temperature, rather than photoperiod, dependent. Male choruses (group vocalizations that attract females for mating) generally coincide with air temperatures around 27 °C (Wright and Wright 1949; Howard 1978). Individuals begin hibernating at water temperatures below 16 °C (Willis et al. 1956), and emergence from hibernation in the spring occurs at air temperatures from 19 to 24 °C and water temperatures of about 13 °C (Wright 1914; Willis et al. 1956). Young (smaller) frogs enter and emerge from hibernation sooner than older (larger) frogs. A few large frogs may be seen at air temperatures as low as 5 °C (14 °C water) in the fall.

Bullfrogs are usually found on or near shorelines, but move a number of meters into the water when water temperature is higher than air temperature in the fall (Willis et al. 1956). Males move away from the shore in spring and summer for mating choruses (Howard 1978). Many aspects of bullfrog ecology are reviewed in Bury and Whelan (1984).

Food

Adult bullfrogs are omnivorous carnivores that, generally, will eat anything that can be captured and swallowed (Dickerson 1906). Numerous studies have been published concerning bullfrog diet, and each reflects the opportunistic feeding strategy of the species. Major components of the diet are snails, insects, crayfish, fish, frogs, tadpoles, reptiles, and occasionally mammals and birds, proportions of each depending upon their relative abundance in the particular study area (Korschgen and Moyle 1955; Korschgen and Baskett 1963; Stewart and Sandison 1972; Tyler and Hoestenbach 1979; Corse and Metter 1980).

Larval bullfrogs (tadpoles) are nonselective filter feeders and ingest primarily algae, diatoms, and blue-green algae (Steinwascher 1975; Seale and Beckvar 1980). An exception to this general statement is that bullfrog larvae do not eat Chara, even when it is a dominant growth form (Brown 1972). Some vascular plants may be eaten under starvation conditions (Brown 1972).

Water

Standing water is required for all stages (i.e., egg, larvae, and adult) of bullfrog life history. For eggs, water must be between 15 and 32 °C for development to occur (Moore 1942). The "adaptive temperature" for embryos is given as 24.3 °C by Bachman (1969). Similarly, Ryan (1978) measured the temperature within 62 egg masses in a New Jersey pond and found the mean to be 23.8 °C (SE = 4.3). Hatching is severely disrupted at pH readings below 4.3. This is probably due to changes in osmotic potential across the egg membrane, and the same phenomenon probably accounts for reduced viability of eggs in water with high salinity (Gosner and Black 1957; Mahon and Aiken 1977; Dunson and Connell 1982).

Bullfrogs are larvae from 79 days (Corse and Metter 1980) to 3 years (Brattstrom 1962), depending on food availability (Corse and Metter 1980) and temperature (Moore 1942). Larval temperature preferences generally increase with acclimation (Hutchison and Hill 1978). Lucas and Reynolds (1967) found that the preferred temperature of Wisconsin bullfrog larvae was 24 °C in May, 28 °C in June, and 30 °C in July, and that such differences were due to developmental stage, not season.

Constant water level is beneficial to larvae (McAuliffe 1978). As water level falls, available habitat decreases, hence, intraspecific competition and predation increase. Similarly, cannibalism of larvae by adult bullfrogs increases as population density increases. Frequent water level fluctuations, such as in flood control reservoirs, can be detrimental to bullfrog breeding, because eggs laid in a suitable site at one water level may be left on land when water level is dropped. Similarly, frogs hibernating in mud may be exposed to air and desiccated or frozen if water level drops in winter. Larvae tend to congregate in shallow, unshaded water with minimal current where solar radiation raises the temperature.

Adult bullfrogs require standing water but can migrate to other ponds if water level drops considerably (Raney 1940; Schroeder and Baskett 1968; Stewart and Sandison 1972). Stable water levels are also important because drops in water level result in exposed banks without cover and drying of backwater areas that normally serve as refugia (McAuliffe 1978). Bullfrogs generally inhabit larger and deeper bodies of water than other frogs (Dickerson 1906; Moore 1942; Moyle 1973; Conant 1975), and eutrophic waters are generally preferred, although exceptions to these generalities are frequent. Eutrophic waters may be favored because of the abundance of algae as food for larvae, abundance of aquatic vegetation as cover for larvae and adults, abundance of prey animals living in and feeding on the aquatic vegetation, and mud bottoms for hibernating and escape. Additionally, since bullfrog eggs are deposited as a film on the surface of the water, low dissolved oxygen of eutrophic waters will not affect bullfrog eggs to the extent that it affects frogs that

lay their eggs in clumps, e.g., Rana pipiens, R. sylvatica, (Moore 1940). Water bodies should have both deep and shallow areas (Dickerson 1906; Moore 1942); however, ponds in Kentucky with good bullfrog populations had a maximum depth of 80 cm (Viparina and Just 1975; Cecil and Just 1979). Hibernation in water that is too shallow can result in freezing of animals in the bottom mud (Manion and Cory 1952).

Cover

Availability of overhead cover for protection and escape from predators is an important factor influencing the quality of an area as bullfrog habitat. Indeed, Cecil and Just (1979) concluded that population size for R. catesbeiana in permanent ponds is not controlled by food availability but by predation. Larvae rely on aquatic vegetation for cover (Brown 1972). Aquatic vegetation, logs, stumps, and brush are also important as cover for adults (Raney 1940; Currie and Belles 1969; Brown 1972; Moyle 1973; McAuliffe 1978). Adults often retreat to deep water when disturbed (Raney 1940; Smith 1961).

Many descriptions of bullfrog habitat have emphasized the importance of heavily vegetated banks (Dickerson 1906; Raney 1940; Wright and Wright 1949; Wiewandt 1969; McAuliffe 1978). Bullfrogs spend much of their time sitting on the shoreline and utilize such vegetation for concealment from predators. Willis et al. (1956) studied movements of bullfrogs and found that no specific cover types were preferred, a finding congruous with observations of bullfrogs using vegetation, overhanging banks, muskrat (Ondatra zibethica) burrows, stumps, logs, branches, and other debris as shoreline cover. Thrall (1971) found young bullfrogs using pits in the mud of bare pond banks as cover. Apparently, the frogs dug these themselves, because pits were not found at nearby ponds with vegetated banks. In contrast, Moyle (1973) found bullfrogs most abundant in waters devoid of surrounding vegetation. His study, however, dealt with mountain streams and probably reflects a need for solar radiation to warm the water, overshadowing a need for shoreline cover.

Reproduction

R. catesbeiana is a "warm-adapted" species (Bachman 1969). Eggs will not hatch and larvae will not develop below 15 °C (Moore 1942; Viparina and Just 1975). The critical factors necessary for breeding are permanent, calm water and air temperatures above 27 °C (Wright and Wright 1949; Howard 1978). (Of course, water temperature is the primary factor; however, only air temperature data are available in the literature). Therefore, earliest spring breeding dates vary from February along the Gulf of Mexico coast to May in northern parts of the bullfrog's range (Willis et al. 1956).

Males establish territories a few meters from shore and call at night to females that stay near the shore and approach selected males to mate (Emlen 1968; Wiewandt 1969). Small males often do not call but stay near calling males and attempt to mate with females that calling males attract (Howard 1978). Sites defended by males are used as oviposition sites and the largest males defend the best oviposition sites (Howard 1978). Each female may produce 10,000 to 20,000 eggs (Wright 1920); thus, populations can be maintained or

ponds repopulated if only a few frogs breed (Wiewandt 1969; McAuliffe 1978). Emlen (1977) has presented evidence that female bullfrogs can produce two clutches in a season; however, the usual number is one.

Interspersion

All habitat requirements for bullfrogs are usually found within and around a single pond. Emigration to other ponds, however, is common (Raney 1940; Wiewandt 1969). Corse and Metter (1980) found that virtually all bullfrogs in a pond in Missouri dispersed from their natal pond within 1 to 2 days after metamorphosis. And, bullfrogs have been observed on land by others in situations that suggest emigration (Bohnsack 1952; Schroeder and Baskett 1968). Such movements between ponds may be important for reestablishing populations in ponds that periodically dry up (Cohen and Howard 1958; Wiewandt 1969; Tyler and Hoestenbach 1979). Territoriality is apparent only during the breeding season (Blair 1963). Because only males defend territories, and males that cannot establish and defend a territory usually become satellites, it is not thought that such behavior limits population density.

Special Considerations

Bullfrogs hibernate during cold winter months. Both adults and larvae spend the winter buried in soft mud at the bottom of permanent wetlands, although adults have been reported to hibernate on land (Bohnsack 1952). Soft mud pond bottoms that remain below ice level and are oxygenated throughout the winter may be important in this regard (Manion and Cory 1952).

HABITAT SUITABILITY INDEX (HSI) MODEL

Model Applicability

Geographic area. The model presented here has been developed for use in the midwestern United States. Within other areas of the geographic range of *R. catesbeiana* in North America (Figure 1), caution should be used when applying the model. The model may require modifications when applied in the northern extremes, throughout the southeastern United States (i.e., ice-free climates), or in areas of the range where the bullfrog did not originally occur, but has been introduced.

Season. Bullfrogs are year-round residents within their habitats; hence, this model is intended to assess an area's ability to support bullfrogs during all seasons. Variables should be measured during the summer, except for an assessment of ice depth as described below.

Cover types. The model may be used to evaluate bullfrog habitat quality in and around permanently or semipermanently (containing standing water year-round during most years) flooded, riverine, lacustrine, or palustrine wetlands as defined by Cowardin et al. (1979).

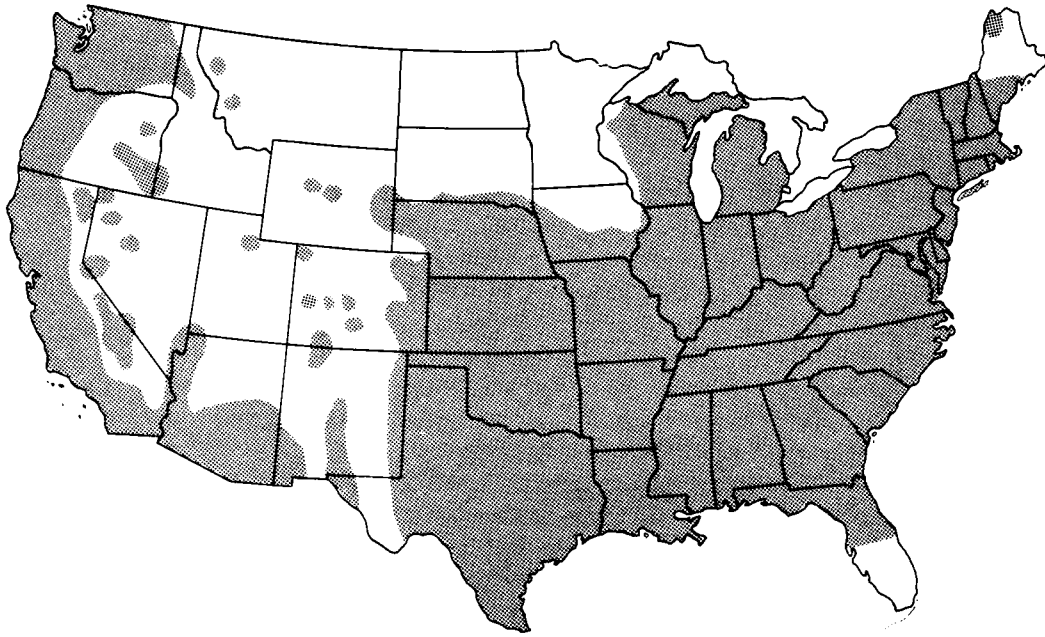


Figure 1. Geographic range of *Rana catesbeiana* within the continental United States (after Conant 1975 and Stebbins 1985).

Minimum habitat area. No information is available to quantify this value. However, the senior author has observed several adult and larval bullfrogs at the University of Missouri's Ashland Wildlife Research Area near Ashland, Missouri, living in a permanent pond with a diameter of approximately 1.5 m. This single observation has limited value, but in general, bullfrogs seem to occur in permanent wetlands at least several meters in diameter.

Conversely, a much larger (approximately 20 m diameter) ephemeral wetland at the Harry S. Truman State Park (Missouri) contained no frogs or tadpoles. Hence, the size and depth of a wetland may influence desiccation and winter ice thickness rather than indicate spatial requirements of the species.

Verification level. Sensitivity analyses were performed to indicate if the influence of each variable on model output was appropriate to the variable's assumed biological significance in determining bullfrog habitat suitability. The model was evaluated at various sites throughout Missouri, Kansas, and Nebraska during May 1984. Twenty-nine sites were surveyed and variables contained in an earlier version of this model were quantified at each. An estimate of bullfrog population densities at each site was also made. The results of this work and the senior author's impressions of bullfrog-habitat relationships were employed to revise the model to more accurately portray our interpretations of bullfrog habitat suitability.

The model is a set of hypotheses describing assumed bullfrog-habitat relationships, but no attempt has been made to address all causal relationships affecting population densities. The standard of comparison for this model is bullfrog use of a site, as reported in the literature, and as interpreted from limited observations of bullfrog populations at the 29 surveyed sites. Potential model users should realize that the demographic histories of surveyed populations in Missouri, Kansas, and Nebraska were unknown. Without such information, it is impossible to evaluate correspondence between model output and habitat-use patterns at locations that were not surveyed, or at survey sites in other years.

Constructive reviews of an earlier draft of this model were provided by Drs. T.S. Baskett and R.B. Bury. Modifications suggested by these reviewers have been incorporated into the model where possible, and their assistance is gratefully acknowledged. Use of the reviewers' names, however, does not necessarily imply that they concur with each section of the model, or the entire model.

Model Description

Overview. This model assumes that food, winter cover availability, and water characteristics associated with reproduction and migration are the primary factors determining habitat suitability for bullfrogs. The following sections provide documentation of the logic and assumptions used to extrapolate variables and suitability index relationships from information on bullfrog habitat use and life history features presented in the Habitat Use Information section and surmised from the 1984 application of an earlier version of this model. Specifically, these sections address: (1) identification of habitat-related variables, (2) definition and justification of suitability levels for each variable, and (3) descriptions of the assumed relationships between variables.

Food component. Variables selected to characterize food availability are often associated with cover availability. For example, it is not known whether bullfrog populations in areas having excellent cover thrive because of the protection cover provides from predators, or because prey items are usually found in such cover. Although bullfrogs are dietary generalists, adults feed on animal life and larvae feed primarily on phytoplankton. Because animal prey abundance is difficult to assess, it is assumed that prey availability will be commensurate with cover availability for adult bullfrogs. Therefore, the variables included in the food component are assumed to quantify cover for both bullfrogs and their prey, as well as food availability for tadpoles.

Both shallow and deep water are required by bullfrogs. Some shallow water around the edge of a wetland is desirable to provide warm (due to solar radiation) water for tadpoles and adults and an area for growth of aquatic vegetation. Also, shallow water is required for many prey items. Deep water (>1.5 m) should be located relatively close to shore so that adults and tadpoles can use such areas for escape and hibernation.

It is assumed that the relationship between the availability of both shallow and deep water can be represented by a determination of the mean distance from shore at which water depth >1.5 m occurs (SIV1, Figure 2). Based on field observations of various midwestern wetlands, the optimal distance from shore for water depth >1.5 m is assumed to range from 10 to 20 m. Distances <10 m are assumed to have a decreased value because of a reduced littoral zone. No habitat value exists if a mean water depth >1.5 m is reached <1.0 m from shore. Suitability is assumed to decrease between 20 and 30 m because of increased travel distances required to reach water >1.5 m in depth.

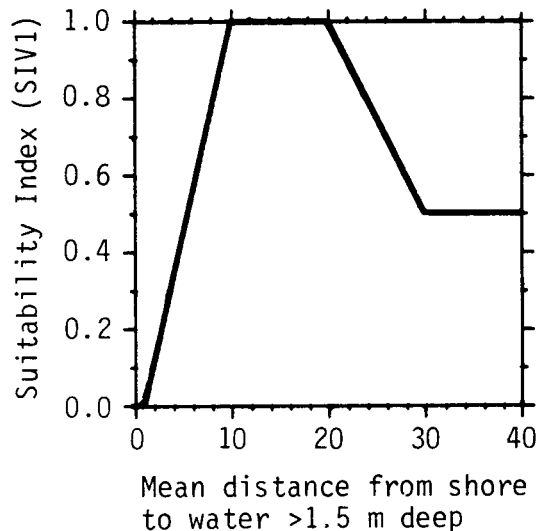


Figure 2. The assumed relationship between the mean distance to deep water and suitability index values for bullfrog food requirements.

Some users may wish to redefine the above relationships. The maximum depth of ponds in Kentucky supporting bullfrog populations was 80 cm (Viparina and Just 1975; Cecil and Just 1979).

Aquatic vegetation, both emergent and submergent forms, provides escape cover, ambush cover, and hiding cover for bullfrogs. Such vegetation also is employed by prey items and provides attachment sites for egg masses. Hence, it is assumed that this type of cover improves habitat suitability for bullfrogs unless vegetation becomes so dense that it impedes locomotion. This variable may have its greatest effect on habitat suitability in relatively shallow water, because this is where most foraging, sunning, and escape behavior occur.

It is assumed that the relationship between aquatic vegetation and hiding cover for both bullfrogs and their prey can be characterized by a measure of the percent canopy cover of aquatic vegetation (both emergent and submergent hydrophytes) occupying the littoral zone (water <1.5 m deep) (SIV2, Figure 3). Optimal conditions are assumed to exist when canopy cover ranges from 55% to 80%. Suitability is assumed to decrease to 0 when no aquatic vegetation is present, and to 0.2 at 100% canopy cover. The assumption that aquatic vegetation density affects habitat suitability is derived from literature sources; specific values are derived from field observations in midwestern wetlands.

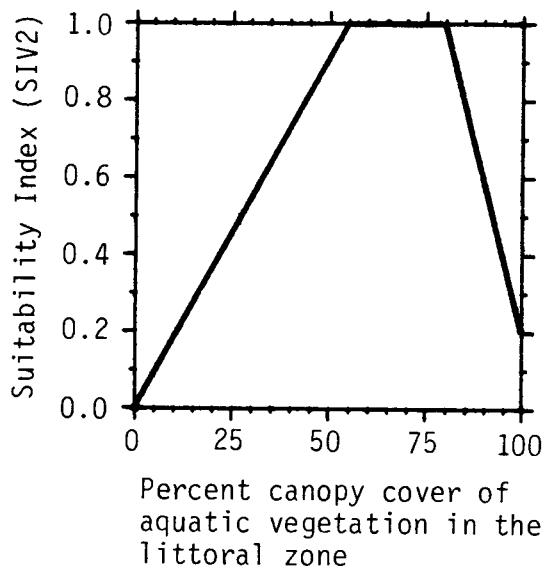


Figure 3. The assumed relationship between percent canopy cover of aquatic vegetation in the littoral zone and the food suitability of a wetland for bullfrogs.

Adult bullfrogs usually sit directly along the land-water interface. Shoreline vegetation may provide both concealment for bullfrogs and their prey. Bullfrogs are rarely found along sections of shoreline devoid of cover unless no shoreline with cover is available. Shoreline cover is defined as vegetation, debris, or overhanging banks sufficient for frog concealment. A direct linear relationship is assumed between percent of shoreline with cover and habitat suitability (SIV3, Figure 4).

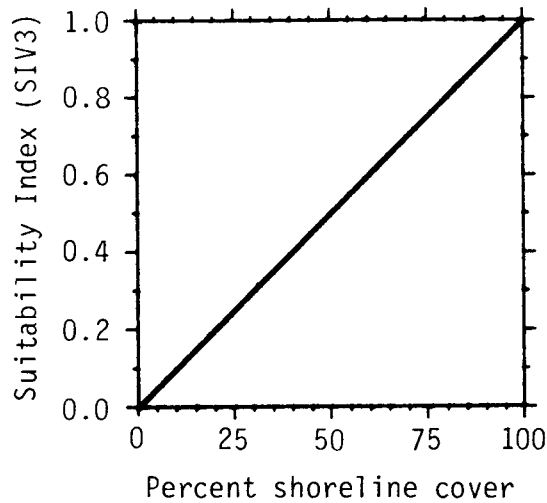


Figure 4. The assumed relationship between percent shoreline cover and food suitability of a wetland for bullfrogs.

The last variable included in the food component is a measure of food availability for the larval stage of the bullfrog life cycle. This variable attempts to quantify phytoplankton abundance using a Secchi disk. It is assumed that a mean Secchi disk depth ranging from 100 to 300 cm corresponds to optimal phytoplankton abundance for larval bullfrogs (SIV4, Figure 5). It is assumed that too little phytoplankton (high water transparency) will not provide sufficient food for tadpoles and that too much phytoplankton (low water transparency) will be associated with algal blooms. Blooms typically have high proportions of cyanophyta, which can secrete toxic substances. However, too little or too much phytoplankton are not thought to be limiting. Water transparency should be measured in midsummer to minimize the influences of other suspended particles, such as silt.

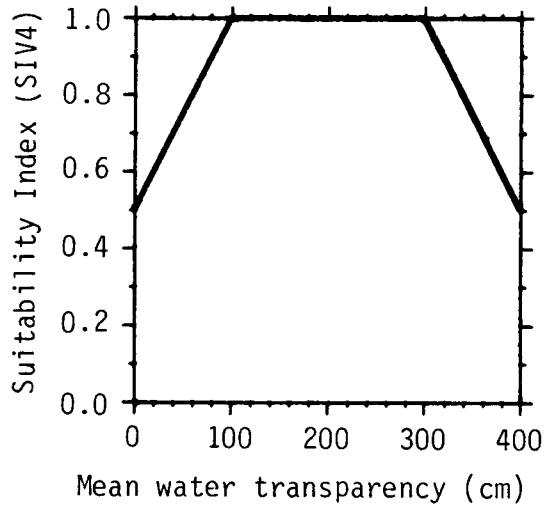


Figure 5. The assumed relationship between mean water transparency and food suitability for larval bullfrogs.

A value for the food component (SIF) is obtained by combining suitability indices SIV1 through SIV4, as shown in equation 1. Suitability indices are combined with an arithmetic mean because frogs may still occupy sites that exhibit 0 suitability for any of the identified variables.

$$SIF = \frac{SIV1 + SIV2 + SIV3 + SIV4}{4} \quad (1)$$

Winter cover component. No characterization of year-round habitat would be complete without an attempt to address the suitability of a wetland in terms of winter survival for bullfrogs. Bullfrogs overwinter by hibernating in the bottom substrates of permanent wetlands. The bullfrog literature provides only limited general descriptions of winter hibernation requirements.

We have elected to address this aspect of the bullfrog's biology as winter cover needs, and describe two variables that can be used to assess sites at a level of resolution representing presence versus absence.

Water depth sufficient to prevent a wetland from freezing completely to its bottom is assumed to be necessary for winter survival of hibernating bullfrogs. This depth will vary with local conditions and must, therefore, be determined for each wetland in an evaluation area. We suggest that the relationship can be characterized with a binary variable (SIV5) providing values of either 1 or 0, depending upon the following conditions:

If winter water depth is greater than maximum ice depth then SIV5 = 1

If winter water depth is less than maximum ice depth then SIV5 = 0

Composition of a wetland's bottom substrate is assumed to influence the bullfrog's abilities to burrow into the bottom for hibernation. We have assumed that the composition of the bottom substrates, as they relate to winter cover suitability, can be represented by particle size. Of all potential sized particles available, fine silt was selected to represent our interpretation of an ideal substrate for burrowing (a 63-micron sieve allows passage of fine silt but not larger particles, such as sand, gravel, etc.). Although bullfrogs may not require 100% silt for optimum conditions, a linear relationship (0 to 100) is assumed between the percent of the substrate composed of silt (or finer particles) and the suitability of the substrate for burrowing by bullfrogs (SIV6, Figure 6).

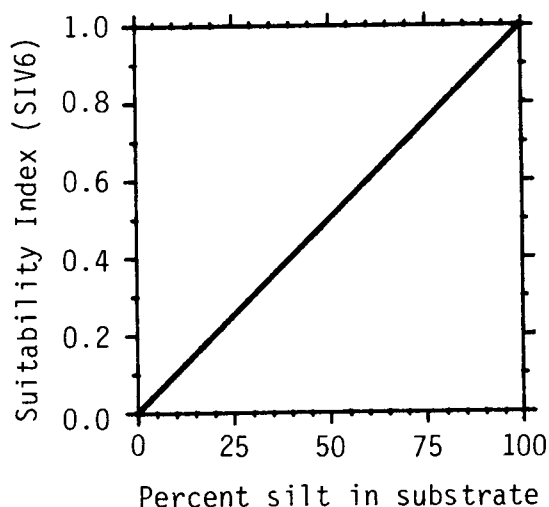


Figure 6. The assumed relationship between silt in the substrate and the suitability of a wetland for winter cover for bullfrogs.

It is assumed that the suitability of a wetland as winter cover for bullfrogs can be expressed as the product of the suitability indices for winter water depth (SIV5) and the percent silt in the bottom substrates (SIV6). The suitability index for winter cover (SIWC) can be determined by using equation 2.

$$\text{SIWC} = \text{SIV5} \times \text{SIV6} \quad (2)$$

Reproduction component. Variables describing habitat suitability for bullfrog reproduction address water characteristics required for successful breeding and hatching of eggs, and include current velocity, pH, temperature, and water level constancy.

Bullfrogs are not found in streams with a strong current, although the relationship between habitat suitability and current velocity has not been systematically quantified. Values used in the suitability index graph for this variable (SIV7, Figure 7a) have been drawn from observations of bullfrog abundance in various streams in Missouri and Kansas and from literature sources. The relationship is based on the hypothesis that bullfrogs preferentially inhabit wetlands with still or slow-moving water and that habitat suitability decreases as current velocity increases.

Hydrogen ion concentration (expressed as pH) also affects bullfrog habitat suitability. Gosner and Black (1957) and Dunson and Connell (1982) found severe inhibition of hatching at pH readings of approximately 3.9-4.0 [high salinity (~0.250 gm/100 cc H₂O) would produce the same effect] and about 50% of eggs did not hatch at pH of 4.1-4.3 (Gosner and Black 1957). Hatching occurs normally at pH 5.9. The relationship in Figure 7b (SIV8) uses the above information to assume a linear increase in hatching from pH 4 to 5.5. Maximum hatching is assumed to occur from pH 5.5 to 8.5 and a decrease in hatching is assumed to be caused by high pH's.

Because bullfrogs are aquatic ectotherms, water temperature directly affects activity and metabolic rates. Water temperature also influences hatching of eggs. The relationship between mean water temperature (measured at mid-depth during summer) and habitat suitability (SIV9, Figure 7c) is derived from data presented in Moore (1942) and Bachman (1969). Development was abnormal at 14 °C, and the minimum temperature at which normal development occurred was 15 °C, although developmental rate was approximately eight times slower at 15 °C than at 30 °C. At 34 °C eggs were killed in the blastula stage and 24.3 °C was determined to be the "adaptive temperature."

Frequent large fluctuations in water level can be detrimental to bullfrog populations by leaving eggs or hibernating frogs above water level, thereby inducing desiccation. Also, large water level fluctuations in riverine habitats may indicate flooding and associated excessive current velocity, which could wash eggs, tadpoles, and adults out of the area. Infrequent fluctuation in water level of ≤2 m per year is regarded as normal. More frequent fluctuations of such a magnitude could result in detrimental effects as described above, although these are not seen as strictly limiting (SIV10, Figure 7d).

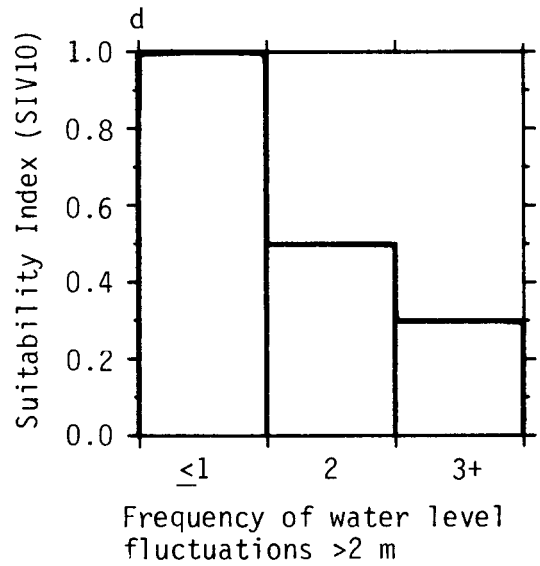
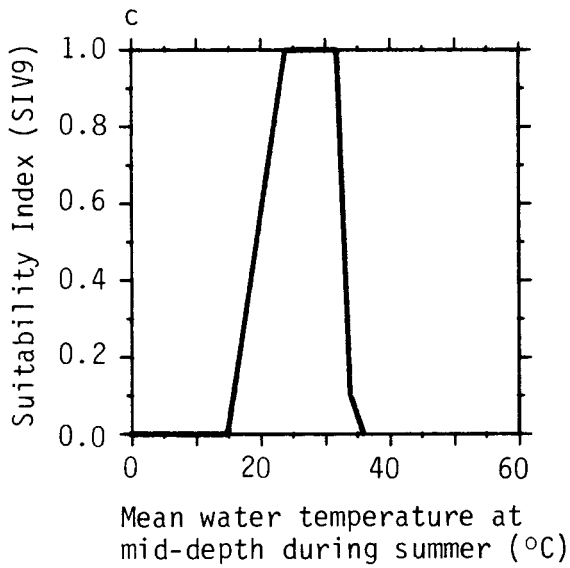
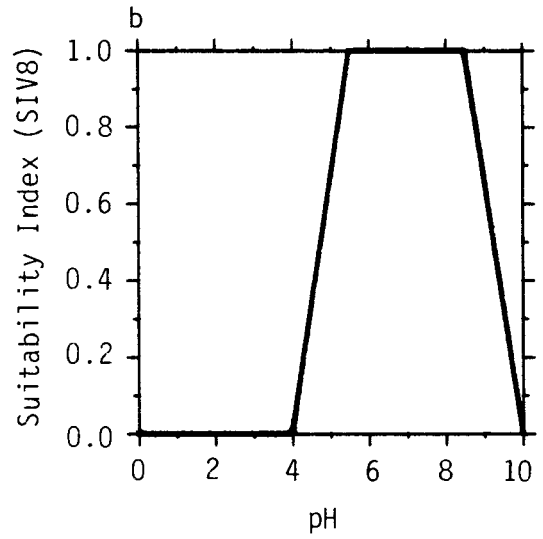
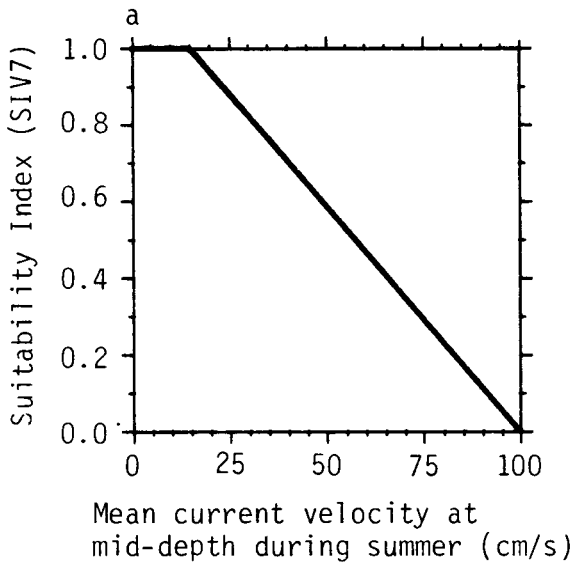


Figure 7. Relationships between water characteristics affecting reproduction of bullfrogs and habitat suitability indices.

A value for the reproduction component (SIR) is obtained by combining SIV7 through SIV10, as shown in equation 3. A geometric mean is used because a value of 0 for any variable would render a wetland unsuitable for bullfrogs.

$$SIR = (SIV7 \times SIV8 \times SIV9 \times SIV10)^{1/4} \quad (3)$$

Interspersion component. When wetlands are permanently flooded and exhibit some level of suitability as bullfrog habitat, all requirements for each life history stage are usually found within a single contiguous wetland. However, in semipermanently flooded wetlands, adult bullfrogs may need to migrate to other aquatic sites to avoid desiccation. In such situations, alternative permanently flooded wetlands should be nearby, since bullfrogs will desiccate enroute if the migration is too long. Also, young bullfrogs may disperse after metamorphosis and would face the same restrictions. Although Willis et al. (1956) reported movements of 0.16 to 2.8 km for a small proportion of tagged bullfrogs, it is assumed that the bullfrog's saltatorial locomotory pattern and high rate of water loss places limits on migration. Hence, a linear decrease in habitat suitability is assumed as distance to permanent water increases (Figure 8). If the wetland under evaluation is permanently flooded, SIV11 is designated as 1.0. However, since it is not known how far bullfrogs can migrate, this variable is not treated as exclusionary. The suitability index derived from Figure 8 will equal the interspersion component value (SII) if the permanent water exhibits values >0 for SIF, SIWC, and SIR.

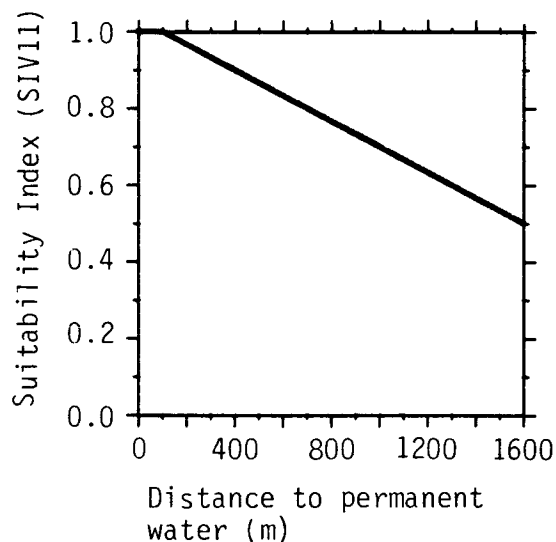


Figure 8. Relationship between distance to permanent water and habitat suitability for the bullfrog.

HSI determination. Because of the limited mobility exhibited by most bullfrog populations, we have assumed that year-round habitat suitability is a reflection of the characteristics of individual wetlands, or those in close proximity to permanent water. We have assumed that within a wetland (or within a short distance), food (SIF), winter cover (SIWC), and reproductive (SIR) requirements must be met. Limitations in one component are assumed to be compensated for by other components, but a 0 value for food, winter cover, or reproduction indicates an unsuitable wetland in terms of year-round habitat for bullfrogs. Permanent water is assumed critical not only in terms of habitat suitability, but for basic survival of bullfrog populations. Because of this assumed importance, the interspersion index (SII) is used to penalize a semipermanently flooded wetland (Cowardin et al. 1979) that is not located within 100 m of permanent water that exhibits some habitat value for bullfrogs (i.e., SIF, SIWC, and SIR of the permanent wetland must each be >0). These assumed relationships are described in equation 4.

$$HSI = (SIF \times SIWC \times SIR)^{1/3} \times SII \quad (4)$$

Application of the Model

Summary of model variables. Eleven habitat variables are used in this model to determine food, winter cover, reproduction, and interspersion values for the bullfrog. Relationships between habitat variables, model components (life requisites), and overall HSI values are summarized in the flow diagram presented in Figure 9.

Figure 10 provides definitions and suggested measurement techniques for each of the 11 variables in this model. Care and judgment must be exercised in determining when to measure variables. Variables involving water depth and velocity should be measured during average midsummer conditions (i.e., not after heavy rains or during severe drought). Similarly, temperature should be measured at mid-day during seasonable weather.

Because bullfrog habitat may be extremely heterogeneous with regard to suitability, it may be necessary to determine several HSI values for various parts of the evaluation area. This would be necessary if variables (other than those that have mean values) have different values in different areas of a single location (e.g., a lake, pond, swamp, or section of stream). Similarly, if the permanently or semipermanently flooded wetland under consideration is large, and the area in which maximum water depth is greater than maximum ice depth is small, this should be considered. For example, Manion and Cory (1952) found that all frogs killed by freezing were in the shallow half of a pond while those in the deep half survived. The pond was only 23 m by 6 m in size.

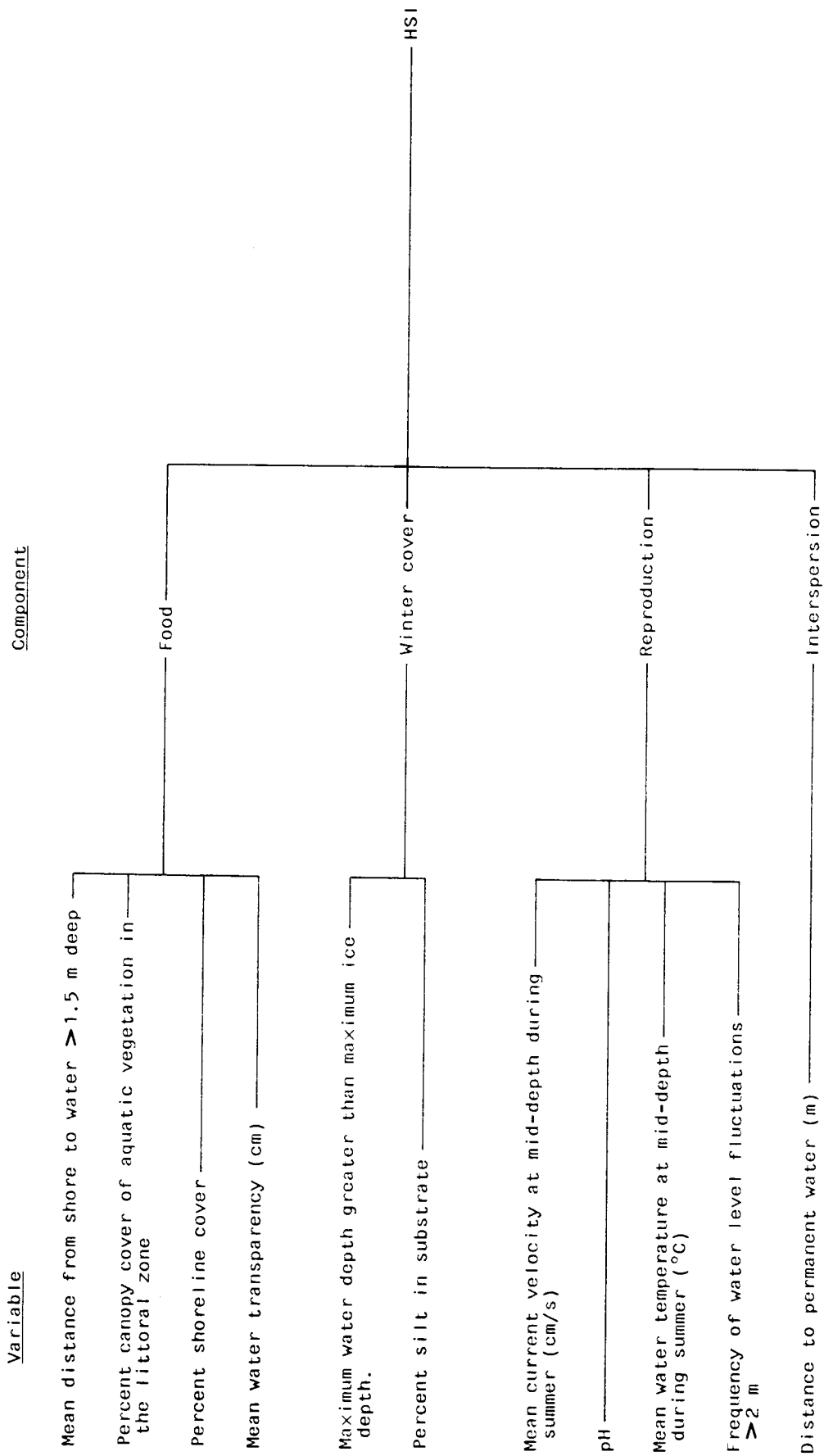


Figure 9. Relationships of habitat variables to components of the HSI model for the bullfrog (*Rana catesbeiana*).

Variable (definition)

Suggested measurement technique

Mean distance from shore to water >1.5 m (4.9 ft) deep.

Weighted line with gradations marked along it. Drop to bottom at various points along shore to find points at which water becomes >1.5 m (4.9 ft) deep.

Percent canopy cover of aquatic vegetation in the littoral zone (the percent of the aquatic substrate in the littoral zone that is shaded by a vertical projection of submergent and emergent vegetation).

Emergent vegetation can be observed from the shore but submergent vegetation distribution will be more difficult to assess. If water is clear, submergent vegetation may be mapped from a boat. Otherwise, wading and a tactile survey may be required. A convex polygon may be drawn around vegetation patches to segregate vegetation vs. no vegetation areas.

Percent shoreline cover [the percent canopy cover of overhanging shrubs, tree crowns, woody downfall, herbaceous vegetation, and debris within 1 m (3.3 ft) of a wetland's shore].

This variable can be measured by pacing off the total shoreline distance and dividing this value into total shoreline distance with cover adequate for concealment of bullfrogs (assessed visually).

Mean water transparency (cm) [the average depth at which a weighted white disk 20 cm (8 inches) in diameter disappears from view].

Standard methods for Secchi disk use are covered in Lind (1979).

Maximum water depth greater than maximum ice depth.

Establish where deepest water areas are within wetland during summer. Return when ice is thickest (or sample throughout winter) and determine ice thickness by drilling a hole with an auger.

Figure 10. Definition of variables and suggested measurement techniques.

Variable (definition)

Suggested measurement technique

Percent silt in substrate
(silt is defined as material
0.004-0.06 mm in diameter).

A spring loaded dredge (see Lind 1979) may be lowered on a line for sampling from deepest water areas within wetland. Samples should be thoroughly dried, then sifted through a 63-micron sieve. Weight of material passing through the sieve should be divided by the total sample weight to obtain a percent value.

Mean current velocity at mid-
depth during summer (cm/s).

Speed of a neutrally buoyant
object.

pH

Negative log of the hydrogen ion
concentration in the water as
measured with pH meter or pH paper.

Mean water temperature at
mid-depth during summer (°C).

Temperature can be accurately
measured with a thermometer.

Frequency of water level
fluctuations >2 m (6.6 ft).

Determine annual frequency from
water records, interviews with
residents, frequent measurement
over a number of years.

Distance to permanent water (m).

Records, interviews, or observation
over a number of years to determine
permanency of vicinal wetlands.
Pace or measure distances between
wetlands. If the wetland under
consideration is permanent,
distance = 0.

Figure 10. (Concluded)

Model assumptions. Output from this model should be interpreted as an indication of the ability of an area to support bullfrogs. The model does not predict population density in an area because more factors influence population density than habitat suitability. For instance, McAuliffe (1978) found that the factor having greatest effect on bullfrog populations in Nebraska ponds was the extent of predation by man. Hence, many areas that may be deemed excellent habitat for bullfrogs by this model, may actually have relatively sparse bullfrog populations as a result of nonhabitat influences.

Most relationships proposed in the model are not empirically derived. They are based on inferences drawn from the literature, supported by what empirical data is available, and the impressions and data obtained from application of an earlier version of this model in Missouri, Kansas, and Nebraska during May 1984. Therefore, personal judgment should be used in determining the applicability of this model. Model users should be aware that bullfrogs are not necessarily desirable species in all regions currently occupied, especially in the western United States. Bury and Whelan (1984) reviewed several studies documenting the reduction or elimination of native species by bullfrogs.

Potential users may wish to make some modifications before using the model. For example, 1.5 m was selected as a reference point in SIV1 because it fit our objectives in the sites surveyed in 1984. Bullfrog populations occur in wetlands with maximum depths <1.5 m, and some users may wish to modify SIV1 to more accurately characterize local conditions. SIV4 assumes a relationship between water transparency and algae abundance, but the values presented in Figure 5 may be inappropriate for some localities within the model's assumed area of applicability. Silt was selected to represent the suitability of bottom substrates for burrowing, but other sized particles may have suitability, and some percent composition <100% silt may represent optimum conditions. The relationship between current velocity and suitability should be carefully scrutinized before being incorporated into an assessment of habitat. Inherent in SIV7 is the assumption that still- or slack-water areas are available for bullfrog use in areas of higher velocities, and judgment must be used when evaluating wetlands for this variable. Other assumptions may be inappropriate and the model should be evaluated carefully in its entirety before use.

SOURCES OF OTHER MODELS

No other published habitat models concerning the bullfrog (*Rana catesbeiana*) are known. The Pennsylvania Game Commission (P.O. Box 1567; Harrisburg, PA 17105-1567) developed a bullfrog habitat model in 1980, but the model was not published.

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