Artificial and natural pond use by amphibian larvae on the National Bison Range, Montana, USA.

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Abstract. As destruction of amphibian wetland habitat continues at an unprecedented rate, artificial ponds are increasingly important to amphibian conservation ecology. However, artificial tanks have not yet been examined for their value as habitat substitutes for reproducing amphibians in these changing landscapes. This study assessed amphibian larvae presence and habitat preference in 13 natural ponds and 14 artificial tanks in one season on the National Bison Range, MT, USA. It sought to determine which amphibians were breeding in natural ponds and artificial tanks, whether differences in biotic and abiotic habitat variables exist between natural ponds and artificial tanks, and what habitat factors best predicted amphibian larval presence. The Long-toed salamander, *Ambystoma macrodactylum*, was the most abundant and widely dispersed amphibian larvae on the Bison Range and was the only amphibian to exploit both natural ponds and artificial watering tanks. Pacific Treefrogs (*Hyla regilla*) were found in healthy numbers in several natural ponds, but Columbia Spotted Frogs (*Rana luteiventris*) did not appear to be either abundant or wide spread. Distance to the nearest water body with amphibian larvae, pond depth, and pond size were the best predictors of presence of *A. macrodactylum* and *H. regilla*. Artificial tanks tended to be smaller in circumference, pond area, and water depth than natural ponds. Tanks also supported less aquatic vegetative cover, were set higher off the ground, and were significantly further away from the next water body with amphibian larvae than natural ponds. The same results were found for ponds without larvae present as compared to those with them present. Conservation and management recommendations are also suggested for consideration of the National Bison Range.

Key Words: artificial tanks and ponds, amphibian larvae, breeding habitat preference, amphibian conservation, National Bison Range, Montana

Introduction

In light of the global amphibian decline phenomenon of the last decade, as well as the reduction by half of natural wetlands in the United States since European settlement, investigation of and conservation of amphibians and their habitats have never been more pressing issues (Halliday 2005; Stevens et al. 2002; Tiner 1984). From such concerns conservation biology has taken a prominent place on agendas of ecological research and includes the restoration and creation of ecosystems which will support viable populations of organisms, especially those listed as threatened or of special concern (Petranka, Kennedy, & Murray 2003). Possible threats to many species' survival range from urbanization and predation to fragmentation and destruction of suitable habitat (Fellers & Drost 1993; Stebbins & Cohen 1995; Reaser and Pilliod 2005). In the face of these changing landscapes, there have been worldwide efforts to protect remaining habitat for wildlife, which encompasses restoration of the especially vulnerable wetland systems, and many encouraging reports have already been touted for amphibians in renovated habitats in Europe (Pavignano et al. 1990; Joly and Grolet 1996; Denton et al. 1997; Baker and Halliday 1999), Australia (Letnic and Fox 1997), Costa Rica (Heinen 1992), and the United States (Bunnell and Zampella 1999, Funk and Dunlap 1999, Monello and Wright 1999).

Even so, there rests an assumption that with new additions of habitat to an area, the amphibians associated with these habitats will quickly move in and establish themselves there. This assumption may be complicated, however, by amphibians' fairly limited ability to disperse across large areas (Sinsch 1990; Driscoll 1997; Semlitsch 1998) as well as by the reduction of suitable corridors to new habitats due to dispersal barriers like roads, spatial isolation from source populations (Fahrig et al. 1995, Hitchings and Beebee 1997, Lehtinen et al. 1999, Lehtinen and Galatowitsch 2001), and the high occurrence of natal pond fidelity found in many pond-breeding amphibians, all of which may decrease their chances of migrating to new habitats (Sinsch 1997).

Colonization of new ponds, whether natural, restored or constructed, becomes especially important when viewed from the perspective of amphibian metapopulations, which are divisions of a larger population into subpopulations in a given area (Molles 2005). The implications of this perspective are that amphibian populations increase their level of fitness through the exchange of individuals between ponds and metapopulations and also that this biological fitness is threatened by declines in the number of adjacent breeding habitat and by increases in the quantity of dispersal barriers between these nearby ponds (Bradford et al. 1993, Semlitsch and Bodie 1998, Kolozsvary and Swihart 1999). The end result is often that such wetlands become isolated, species immigration and emigration rates drop, and local populations may suffer in terms of biological diversity and abundance, possibly even to the point of extirpation (MacArthur and Wilson 1963).

However, when appropriate terrestrial corridors do exist between wetlands, wildlife populations may more easily and readily pass between them and thus help secure future persistence of their species. This has been supported by numerous studies of both reptiles (Gibbons et al. 1983; Burke et al. 1995; Seigel et al. 1995; Buhlmann and Gibbons 2001) and amphibians (Scott 1994; Findlay et al. 2001; Lehtinen and Galatowitsch 2001; Newman and Squire 2001). Some drier habitats, such as that of the western United States, may offer greater resistance to overland migration of amphibians due to the semi-arid environment and in these cases artificial ponds may hold an even greater importance in serving as corridors or even breeding ponds for certain amphibian communities.

A study done by Petranka, Kennedy, and Murray (2003) on amphibian response to restored wetlands in southern Appalachia discerned that "amphibians rapidly exploit newly created ponds with reduced levels of competitors and predators" (p. 1039), implying an increasing value of artificial wetlands in variable environments for pond-breeding salamanders and frogs. In a similar study by Monello and Wright (1999) in the eastern Palouse bioregion of northern Idaho, they found that several of the most common western amphibian species (Long-toed Salamander, *Ambystoma macrodactylum*; Columbia Spotted Frog, *Rana luteiventris*; and

Pacific Treefrog, *Hyla regilla*) were able to successfully exploit artificial ponds (permanent water impoundments damming water runoff) for reproductive purposes. This area has experienced extensive wetland degradation while at the same time more than 1500 artificial ponds have been constructed and appear to be having substantial influence in terms of amphibian conservation (Black et al., *in press*). The most important factors explaining amphibian preference for these artificial ponds were determined to be positively correlated to distance to grassland and/or forest and to presence of emergent vegetation but negatively correlated to distance from cultivated lands. Pond age also appeared to be important for breeding R. *luteiventris*, a species being intimately observed due to declines in its close relative, the Western Spotted Frog, *R. pretiosa* (Stebbins and Cohen 1995).

Other studies have delved into how amphibians use a variety of manmade ponds, which range from ponds associated with timber harvesting (Jeffries 1991, McAlpine 1997) to drainage ditches in peat-mined bogs (Mazerolle 2004) to bomb craters (Warwick 1949). These types of investigations on amphibians have even stretched to include assessments of pond communities in artificial, outdoor tanks but only in their value as temporary habitat for amphibians in ecological research, not as possible habitat substitutes in modernized landscapes (Rowe and Dunson 1994). While this option of artificial tank-ponds has been explored for breeding waterfowl in irrigation facilities (Sánchez-Zapata et al. 2005), its investigation of amphibian populations is both lacking and fundamental to their conservation at a time when these populations seem to be suffering.

In order to investigate such an alternative, this study seeks to assess any significant differences in certain abiotic and biotic factors between "natural" ponds and "artificial" tanks thought to have important implications for amphibian reproduction and survival. The purpose of this study is to ascertain answers to the following inquiries: which amphibians are producing successful juvenile populations on the National Bison Range, Montana; whether these amphibians are reproducing in artificial watering tanks; whether artificial watering tanks differ from natural ponds in habitat variables important to amphibian reproduction; and which factors determine breeding habitat preference for these amphibians.

Materials and Methods

This study was conducted on the National Bison Range, located in Sanders and Lake Counties, Moiese, MT, USA (Appendix 1). Established in 1908 the National Bison Range is a nearly 19,000 acre (7689 hectare) National Wildlife Refuge administered by the U.S. Fish and Wildlife Service and is designed to protect American bison (*Bison bison*) and breeding bird populations. The Bison Range consists of mainly native Palouse prairie grassland, which is the land type surrounding most of the ponds used for this research. ("GORP – National Bison Range, MT") Over the course of this study, two general types of water bodies were sampled, artificial tanks and natural ponds, all between 6 July and 11 July 2006. For the purposes of this investigation, artificial ponds were defined as concrete or fiberglass watering tanks fed by springs, which were provided for purposes of watering large ungulates, such as bison, deer, bighorn sheep, and elk. Natural ponds included spring-fed pools and ditch plugs, which are springs or creeks that were historically dammed or developed to form small bodies of standing water. While these ditch plug ponds have actually been constructed by humans, the majority of them were created as part of the Bison Range's Spring and Pond Development Project 170 between 1953 and 1959 and over the past 47 to 53 years have evolved the appearance of and composition of nearly any natural spring-fed pond on the property (Refuge Narrative Reports, 1953-1959).

This study consisted of sampling fourteen artificial tanks on the National Bison Range: eleven rectangular concrete tanks with circumferences ranging from 7.8 meters to 11.6 m and three polygonal fiberglass tanks that ranged from 10.05 m to 15.1 m. Mean artificial tank circumference was 10.96 m (+/- 1.53m Standard Deviation), mean tank depth was 0.46 m (+/- 0.07 m SD), and mean tank surface area was 5.18 m^2 (+/- 4.27 m^2 SD). Thirteen natural ponds were sampled in this study: eleven ditch-plug ponds and two natural spring-fed ponds; all will be referred to as "natural ponds." All natural ponds had a silty-mud bottom and ranged in circumference from 20 m to 105 m. Mean natural pond circumference was 58.88 m (+/- 24.43 m), mean pond depth was 0.96 m (+/- 0.62 m), and mean pond surface area was 220.48 m^2 (+/- 124.5). As part of this project, a systematic formula for naming each water body was determined to be necessary. Each natural pond was named N (natural), then DP or S (ditch plug or spring), and given a number. Artificial ponds were classified as A (artificial), then C or F (concrete or fiberglass), and numbered. The actual numbering sequence was an arbitrary decision, but it was necessary to use and initiate a standardized naming system for mapping, reporting, and tracking purposes. Artificial tanks and natural ponds were chosen on the criteria of general accessibility and pond condition, which were *excellent* or *good*, although one pond, NDP6, was listed as *fair*, based on an internal FWS survey performed by Eva Paredes in 2003.

The following abiotic habitat variables were measured at each pond or tank: elevation, maximum pond depth, pond circumference, pond surface area, pH, surface and mean water temperature, and approximate percent aquatic vegetative cover. Mean water temperature was determined after sampling by measuring the bottom temperatures in eight natural ponds and averaging this with the corresponding original surface temperature, which was taken at one to two points per pond at the time of sampling. Temperature and pH were measured with an HI

98129 Waterproof pH, EC/TDS & Temperature Meter while elevation was determined with a Garmin etrex GPS unit and topographic maps. Distances from the nearest road and distances to the nearest vegetative cover (e.g. shrubs and trees) were measured using a Bushnell Laser Rangefinder Sport 450. Distances to the nearest water body (pond or tank) with a breeding amphibian population and to the nearest natural pond with larvae were determined from topographic maps (USGS Ravalli Quadrant, MT; 7.5 minute series). Distances accounted for elevation movement and linear movement between ponds.

The relative abundance of each amphibian species' larvae was determined in each pond. Larvae sampling was accomplished by dip-netting in a general zigzag pattern across a natural pond. For the artificial tanks, larvae numbers and species were usually determined by a combination of sight and dip-netting due to the small size of the tanks. To standardize sampling effort across different sized ponds/tanks, a standard was created such that one dip-net was scooped for each meter of circumference of a water body (e.g. 57 points would be dip-netted for a pond 57 meters around). This technique appeared to sample thoroughly the relative abundance of the larval populations while being the most efficient and consistent method of sampling.

Data was analyzed using JMP IN 5.1 to perform linear regressions and Analysis of Variance (ANOVA) to determine if significant differences existed between the abiotic and biotic variables characterized for the artificial and natural ponds, for ponds with amphibian larvae present or absent, and for only the artificial and natural ponds with amphibians present. The statistical computing program R (R Development Core Team 2006) was also used to create a classification and regression tree to determine the significance and rank the importance of the following data variables against presence and absence of *Hyla* and *Ambystoma* in ponds: surface temperature, depth, circumference, distance to nearest amphibian population, and pond type.

Results

Amphibian presence

Twenty-seven ponds and tanks were sampled on the National Bison Range (Appendix 1). Of those water bodies, 13 held amphibian larvae, which included ten natural ponds (2 springs and 8 ditch-plugs) and three artificial tanks (2 concrete and 1 fiberglass). In these 13 water bodies, three hundred fifteen amphibian larvae were found. The following species of larvae were discovered in the ponds and tanks: the Pacific Treefrog (*Hyla regilla*), the Long-toed Salamander (*Ambystoma macrodactylum*), and the Columbia Spotted Frog (*Rana luteiventris*). *Ambystoma macrodactylum* were the only larvae present in tanks while *H. regilla* and *R. luteiventris* were additionally detected in natural ponds (Table 1). *Rana luteiventris* was only located in two ponds but both times co-occurred *H. regilla*. *Ambystoma macrodactylum* appeared with *H. regilla* in five ponds. *Rana luteiventris* was only found together with *A. macrodactylum* once, and all three of these species' larvae were encountered in a single pond, Natural Spring 2 (NS2). The most abundant larval species found on the National Bison Range was *A. macrodactvlum*, with 201 larvae occurring in 12 of the 13 ponds and tanks that held larvae (Table 1). Total relative abundance of amphibian larvae was regressed against each habitat variable to determine if any factors predicted abundance but no significant results were found, indicating larval abundance within these ponds is random.

Amphibian breeding habitat preference

The R program Classification and Regression Tree (Ripley 2006) created a dichotomous key of the most important variables in predicting probability of presence/absence of ambystomids and hylids in water bodies. Variables used for this analysis were chosen based on possible biological importance to amphibians, especially factors shown to be significant in previous analyses, and on personal observations noted by the researcher. They included pond surface temperature, depth, circumference, distance to next closest amphibian population, and pond type. Relative frequency of presence or absence of amphibians is used as an estimate of probability of occurrence. For *A. macrodactylum* distance to next closest water body with larvae was the best predictor of their presence: if ponds are less than 387.7 m away, then there is a 76.9% probability of finding ambystomids there and within that distance, salamanders are in water with temperatures less than 20.95°C 87.5% of the time and in ponds with temperatures over 20.95° 60% of the time. When ponds with larvae are greater than 387.7 m away from a pond, ambystomids will only be present 16.67% of the time and within that, they are unlikely be found in artificial tanks (0% probability) and only in natural ponds 40% of the time (Table 2).

On the other hand, hylid presence was predicted by pond depth. They should be absent in ponds less than 0.575 m deep and they have a 60% probability of appearing in ponds deeper than 0.575 m. Within that 60% probability, *Hyla* should be present 100% of the time in ponds that are less than 254.7 m from the next breeding pond with larvae, but only in ponds further than that from other larvae 20% of the time (Table 2).

In support of the above results, *A. macrodactylum* and *H. regilla* presence and absence were analyzed separately against each of the habitat variables in order to further explore predictors of presence in ponds and the following results were biologically significant for *Ambystoma*: ponds with larvae had a larger circumference (ANOVA; F=5.15, df=26, P=0.0321) and were closer in distance to the next pond with larvae (ANOVA; F=8.31, df=23, P=0.0086, excluding pond NDP8 as an outlier; Fig. 1). Percent aquatic vegetative cover was nearly significantly higher in water bodies with *Ambystoma* larvae (ANOVA; F=3.14, df=26, P=0.0885) and distance from the ground nearly significantly lower (ANOVA; F=3.81, df=26; P=0.0624).

For *Hyla*, the following habitat factors were the most successful predictors of presence: greater pond depth (ANOVA; F=7.59, df=26, P=0.0108), greater circumference (ANOVA; F=20.95, df=26, P<0.0001), pond area (ANOVA; F=10.15, df=24, P=0.0041), lower distance from ground (ANOVA; F=7.70, df=26, P=0.0103), and closer distance to the next non-tank with amphibian larvae (ANOVA; F=4.47, df=23, P=0.0076, excluding pond NDP8 as an outlier). Interestingly, *Hyla* distance to the next closest pond or tank with larvae was not significant (ANOVA; F=2.70, df=23, P=0.1133), which is probably related to the complete absence of *Hyla* from tanks.

Abiotic factors of natural and artificial ponds

In terms of habitat variables, artificial tanks tended to differ from natural ponds only in size-related characteristics and percent aquatic vegetative cover, which was significantly greater in natural ponds than in artificial tanks (ANOVA; F=5.15, df= 26, P=0.0322; Fig. 2). Artificial tanks had smaller circumferences than natural ponds (ANOVA; F=43.15, df=26, P<0.0001), shallower depths (ANOVA; F=8.89, df=26, P=0.0063), smaller surface area (ANOVA; F=38.97, df=24, P<0.0001), and were located higher above the ground (e.g. amphibians would have to climb up the sides of the tanks in order to reach the water) (ANOVA; F=81.61, df=26, P<0.0001). Artificial tanks did not differ significantly from natural ponds in surface temperature, mean temperature, or pH (Table 3).

A week after sampling was completed, it appeared that the average temperature of the entire pond might have been a factor in determining presence of larvae, rather than just surface temperature. Bottom and surface temperatures were measured at eight natural ponds but insignificant results yielded nothing of interest. One natural pond, NDP6, was completely dry at that time.

Artificial ponds were significantly further away than natural ponds from the next closest water body with a larval amphibian population (ANOVA; F=5.45, df=23, P=0.0291). The mean distance from an artificial tank to the closest amphibian larvae was 1041.04 m (+/- 1062.14 m SD) while for natural ponds this mean distance was only 319.26 m (+/- 139.37 SD). One natural pond, NDP8, was 3314.6 m from the closest amphibian population and was excluded as an outlier from these tests. Distance from each water body sampled to the nearest non-tank with amphibian larvae, or to the most likely source pond, was also significantly greater for artificial tanks (ANOVA; F=6.62, df=23, P=0.0173).

The same statistical comparisons were made for tanks and natural ponds with amphibian larvae present as compared to those without larvae, and all of the same variables were found to be significant as before (percent aquatic vegetative cover, circumference, depth, pond surface area, distance from ground, distance from nearest amphibian larvae, and distance from nearest non-tank with larvae) (Table 4). When only ponds and tanks with larvae present were considered (excluding ponds with zero larvae), tanks with larvae were found at a significantly higher elevation (ANOVA; df=12, P=0.0457), had a smaller circumference (ANOVA; df=12, P=0.0054), smaller pond surface area (ANOVA; df=11, P=0.0104), and were higher above the ground (ANOVA: df=12, P<0.0001). Considering only water bodies with larvae present, tank distance from nearest pond with larvae tended to be greater than that of natural ponds but only with a borderline significance (ANOVA; F=4.70, df=11, P=0.0554).

Pond type and amphibian presence

Each pond was also classified as Natural-Present, Natural-Absent, Artificial-Present, and Artificial-Absent to determine differences in habitat variables by pond type (natural or artificial) in combination with presence or absence of larval amphibians. Natural-Absent ponds, or those natural ponds lacking larvae, had significantly higher surface water temperatures than Artificial-Present ponds (ANOVA; F= 3.26, df=26, P=0.0398; Fig. 3). Natural-Present ponds were significantly deeper than the Artificial-Absent ponds (ANOVA; F=5.38, df=26, P=0.0059; Fig. 4) and had larger circumferences (ANOVA; F=18.8, df=26, P<0.0001). Additionally, Artificial-Absent ponds were situated significantly further away than Natural-Present and Artificial-Present ponds from the next closest larval population (ANOVA; F=5.11, df=23, P=0.0087; Fig. 5) as well as further than Natural-Present ponds to the next closest larvae in a natural source pond (ANOVA; F=4.60, df=23, P=0.0132). NDP8, a Natural-Present pond was excluded as an outlier from the data in the previous two tests.

Discussion

Amphibian presence and habitat preference

While it is difficult to make a direct connection between presence of a reproducing population and an increase in adult populations, which is the best measure of wetland restoration success (Pechmann et al. 2001; Petranka et al 2003), successful reproduction of juvenile amphibians indicates positive movement toward amphibian conservation. An integral part of this equation is the persistence of healthy metapopulations that can travel between ponds and colonize new habitat via functioning terrestrial and aquatic corridors (Morreale et al. 1984, Burke et al. 1995, Lovich 1990).

Based on the results of this study, there seem to be several stubbornly persistent, if not thriving, amphibian breeding populations on the National Bison Range. As the most abundant and widespread amphibian on the National Bison Range, *Ambystoma macrodactylum* larvae seem to be surviving with some degree of success in a variety of wetland environments, which include ditch-plug ponds and natural springs as well as concrete and fiberglass tanks. *Rana luteiventris* larvae do not appear to be either abundant or widely dispersed on the Bison Range as only twelve total larvae and eight adults were caught at two of twenty-seven sites. However, this may be due to juvenile dispersal by *R. luteiventris* prior to sampling because all of the immature *Rana* larvae caught were actually nearly fully metamorphosed and the rest of the cohort may have already left the area. *Hyla regilla*, on the other hand, seems to have a fairly healthy breeding population at several natural ponds and appears to be more abundant and well dispersed than *R. luteiventris*. While there were a few ponds in which *H. regilla* were also nearly metamorphosed, these juveniles were obviously still abundant in and around the pond.

Neither *H. regilla* nor *R. luteiventris* seem to be utilizing the artificial tanks for reproductive purposes, which could be because the tanks do not offer the dense floating and emergent vegetation preferable as refugia for juveniles (Reaser 1997a) or as enticement to breeding adults (Nussbaum et al. 1983); because they lack the shallows of lentic habitat for egg deposition (Reaser and Pilliod 2005) or could be too high off the ground for anurans to access. In the case of *H. regilla*, they are not attracted to breed in ponds less than 0.575 m deep, even if they are natural ponds, but none of the tanks were this deep. The importance of pond depth could be a measure of how ephemeral a pond is.

Ambystomids, on the other hand, are known as opportunistic breeders and exploit a number of different permanent and temporary water habitats, which include disturbed and human-influenced areas (Pilliod and Fronzuto 2005) and helps explain their presence in the artificial watering tanks on the National Bison Range. Salamander larvae presence in tanks is also accounted for by the ability of adults to migrate along riparian corridors to colonize nearby tanks. They may be better adapted than anurans to climb into and out of concrete and fiberglass tanks with brush or branches to assist them in and out of the tanks. Tank AF1 had a branch wired to the fencing surrounding it and which reached the fiberglass tank bottom. It was placed there by the Bison Range maintenance crew to assist animals out of the tank that fall in and are unable to grip the slippery fiberglass surfaces. This tank was the only fiberglass tank with amphibian larvae and the only tank with such a set-up. At least one of the concrete tanks that held ambystomid larvae had a large wild rose bush growing next to and hanging over the tank, which might aid adult salamanders in their access of the tank for breeding. Other concrete tanks into which adults might have been able to climb either lacked both sufficient aquatic vegetation and the associated invertebrate pray for larval ambystomids or were greater than 500 m from the next closest pond with larvae (Fig. 4 and Fig. 5).

Amphibian dispersal

Ambystoma macrodactylum on the Bison Range appear to prefer to breed in ponds that are within approximately 390 m of other salamander populations, indicating their limited dispersal ability and relatively small home range size (Sheppard 1997). Juveniles do tend to migrate further than adults, with a home range of up to 281.6 m^2, as estimated in Sheppard's study, which may explain the relatively wide dispersal of ambystomids compared to anurans on the National Bison Range. While desiccation is a concern for most amphibians, these salamanders have even been observed venturing across mountain ridges in the Bitterroot Mountains of Western Mountain, and at a greater frequency than across valley bottoms (Tallmon et al. 2000). This again highlights their ability to colonize of a variety of habitats spread across the Bison Range. *Ambystoma macrodactylum* likely exist in a series of possible metapopulations along Pauline Creek (NDP1-5, AF1, and AC1), along Elk Creek (NDP9 and NS2), along Triskey Creek (NDP7, AC2, and NS1), and the isolated pond NDP8. In order to colonize new habitats, the adults appear to be utilizing both natural ponds and tanks along these creeks and riparian corridors for reproduction and to further their dispersal.

Rana luteiventris may be unable to produce larger numbers of larvae in more widely spread habitat due to possible predation of larvae by *A. macrodactylum* larvae and adults (Munger et al. 1997b) and the importance of pond age to *R. luteiventris* reproduction, which implies either preference for older ponds or poorer dispersal ability than *H. regilla* and *A. macrodactylum* (Monello and Wright 1999). Another study cited adult *R. luteiventris* migrating up to 560 m between breeding ponds (Bull and Hayes 2001) but this species was not found in great enough abundance in this study to support or refute the above studies.

Hyla regilla have shown preference for natural ponds within approximately 254 m of the nearest pond with an amphibian population and at least three possible metapopulation clusters seem to exist in the six ponds with hylids on the Bison Range. These clusters of metapopulations consist of ponds NDP1, NDP2, and NDP3 in one cluster; NDP7 as the second cluster; and NDP9 and NS2 in the third cluster. Evidence of these metapopulation clusters is supported by the ponds within each cluster being only between 130 and 490m apart and observations of breeding males moving at least 400 m to adjacent ponds (Shaub and Larsen 1978).

Artificial and natural ponds

Based on the abiotic and biotic factors of the artificial tanks and natural ponds examined on the National Bison Range, artificial tanks tend to be smaller and support less aquatic vegetative cover than the natural ponds. As a result, artificial tanks seem to be inadequate for anuran reproduction and sometimes insufficient for salamander reproduction as well. The height of the tanks may also be a deterrent to possible amphibian colonizers since only 49 larvae of one species were observed in tanks and 276 larvae of three species were in natural ponds. Artificial and natural ponds do not differ in water temperature or pH and should not because all water bodies, natural and artificial, are supplied by the same system of natural springs on the Bison Range.

Artificial tanks were more isolated from other water bodies that supported reproducing amphibian populations but also tended to be more isolated from other water bodies in general. This was most likely a conscious decision on the part of the National Bison Range managers because the tanks were installed to provide a water source for the large game animals on the Range and would be more likely placed in an area which lacks other functioning water bodies, particularly non-tank, or natural, ponds.

When pond type is taken into consideration with larval presence or absence, natural ponds that lacked larvae tended to have warmer surface temperatures, lower water levels, and smaller circumferences than natural ponds with larvae, indicating a higher degree of seasonal temporality and a shorter hydroperiod. These traits would discourage amphibian breeding due to the threat of the pond drying out and larvae desiccating before metamorphosis (Semlitsch and Wilbur 1988). The tanks receive a constant stream of spring water throughout the summer, making them less ephemeral and desiccation less of a threat to amphibians using them.

Conservation and management recommendations

In conclusion of this study, it is recommended that if the National Bison Range managers are interested in increasing the dispersion, abundance, and species richness of the amphibian species present, they should increase the number and quality of ditch-plug ponds and fiberglass tanks ideally within 300 m, but no more than approximately 500 m, of existing amphibian populations. In addition, since fiberglass tanks have replaced concrete tanks, new fiberglass tanks should be placed as low into the ground as possible, with a branch or wooden board placed into the tanks reaching to the bottom and attached to the posts around them to allow adult amphibians to climb into and out of them. Also, to improve adult amphibian habitat surrounding the existing tanks, especially for salamanders, a wooden board could be placed on the wet ground next to overflowing concrete tanks to offer cover.

Because the fiberglass tanks have larger circumferences, as more are installed, amphibians should be more encouraged to utilize them for breeding or at least as relief from desiccation during dispersal along terrestrial corridors. In order to ensure stable amphibian populations and promote increases, especially in ranid populations, it is recommended that these ponds and tanks be monitored annually or bi-annually for abundance and identification of reproducing amphibian populations between the beginning of June and the first week of July. The number of natural wetlands and artificial tanks sampled on the Bison Range should also be expanded to include any other possible amphibian populations present.

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Tables

Table 1. Amphibian larvae species richness and abundance at ponds and tanks with larvae.

Pond Type	**Pond Name**	**Number of *R. luteiventris***	**Number of *H. regilla***	**Number of *A. macrodactylum***	**Total Larvae**
Natural	NDP1	0	1	7	8
Natural	NDP2	0	27	10	37
Natural	NDP3	0	4	20	24
Natural	NDP4	0	0	5	5
Natural	NDP5	0	0	44	44
Natural	NDP7	0	62	38	100
Natural	NDP8	0	0	5	5
Natural	NDP9	7	3	0	10
Natural	NS1	0	0	19	19
Natural	NS2	5	5	4	14
Artificial	AC1	0	0	1	1
Artificial	AC2	0	0	28	28
Artificial	AF1	0	0	20	20
	Total:	**12**	**102**	**201**	**315**

Table 2. Classification and Regression Tree: dichotomous key generated which shows the most significant priorities in habitat variables for presence of *Ambystoma* and *Hyla* larvae. Numbered in rank order of importance. Possible habitat variables include pond surface temperature (°C), pond depth (m), pond circumference (m), distance to closest amphibian larvae population (m), and pond type (natural/artificial). Bold numbers in parentheses indicate relative frequency (probability) of larvae presence.

Classification and Regression Tree	
Node), split, n, deviance, y-value, (y-probability)	*denotes terminal node
***Ambystoma* presence or absence**	***Hyla* presence or absence**
1) root 25 34.620 FALSE (0.5200 0.4800)	1) root 25 27.550 FALSE (0.76 0.24)
2) **dist_amph. < 387.7 m** 12 14.050 TRUE (0.2308 **0.7692**)	2) **depth < 0.575** m 15 0.000 FALSE (1.00 **0.00**)*
4) **pond_temp < 20.95°C** 8 6.028 TRUE (0.1250 **0.8750**)*	3) **depth > 0.575** m 10 13.460 TRUE (0.40 **0.60**)*
5) **pond_temp > 20.95°C** 5 6.730 TRUE (0.400 **0.600**)*	6) **dist_amph.** < 254.7 m 5 0.00 TRUE (0.00 **1.00**)*
3) **dist_amph > 387.7 m** 12 10.819 FALSE (0.8333 **0.1667**)	7) **dist_amph.** > 254.7 m 5 5.004 FALSE (0.80 **0.20**)*
6) **Pond_Type: Artificial** 7 0.000 FALSE (1.00 **0.00**)*	
7) **Pond_Type: Natural** 5 6.730 FALSE (0.600 **0.400**)*	

Table 3. A summary of the means of abiotic habitat variables and biotic factors characterizing natural ponds and artificial tanks, with p-values (ANOVA). Significant values in bold. * denotes exclusion of pond NDP8 as a possible outlier.

Variable measured	Natural Pond	Artificial Tank	P-value
Elevation (ft)	3365.69	3316.14	0.746
Surface Temperature (°C)	22.87	20.84	0.2658
pH	8.28	7.97	0.2315
Pond Depth (m)	**0.96**	**0.46**	**0.006**
Circumference (m)	**53.88**	**10.96**	**0.0001**
Pond Surface Area (m^2)	**220.48**	**5.18**	**0.0001**
Distance from Road (m)	206.25	136.12	0.946
Distance from Cover (m)	45.25	87.75	0.094
Distance from Ground (m)	**0.00**	**0.36**	**0.0001**
Percent Aquatic Vegetative Cover	**76.69**	**47.64**	**0.0322**
Distance from Nearest Amphibian Larvae Found (m) *	**319.26**	**1041.04**	**0.0291**
Distance from Nearest Natural Pond with Amphibian Larvae Present (m) *	**500.65**	**1335.55**	**0.0173**

Table 4. A summary of means of abiotic habitat variables and biotic factors characterizing ponds and tanks with amphibian larvae present against those where larvae were absent, with p-values (ANOVA). Significant values in bold. * denotes exclusion of pond NDP8 as a possible outlier.

Variable measured	Larvae Present	Larvae Absent	P-value
Elevation (ft)	3410.38	3274.64	0.3727
Surface Temperature (°C)	20.49	23.05	0.1547
pH	8.13	8.11	0.963
Pond Depth (m)	**0.962**	**0.458**	**0.006**
Circumference (m)	**48.38**	**16.07**	**0.001**
Pond Surface Area (m^2)	**186.9**	**36.1**	**0.0039**
Distance from Road (m)	176.2	225.7	0.691
Distance from Cover (m)	54.9	209.07	0.138
Distance from Ground (m)	**0.096**	**0.27**	**0.0256**
Percent Aquatic Vegetative Cover	**75.53**	**48.71**	**0.0495**
Distance from Nearest Amphibian Larvae Found (m) *	**221.72**	**1138.58**	**0.0039**
Distance from Nearest Non-tank with Amphibian Larvae Present (m) *	**403.33**	**1432.88**	**0.0022**

Figures

Figure 1. Graph of ANOVA displaying ambystomid presence (p) and absence (a) as determined by distance (meters) to the nearest water body with a larval amphibian population. Excludes pond NDP8 as a possible outlier. 95% Confidence Interval. P=0.0086.

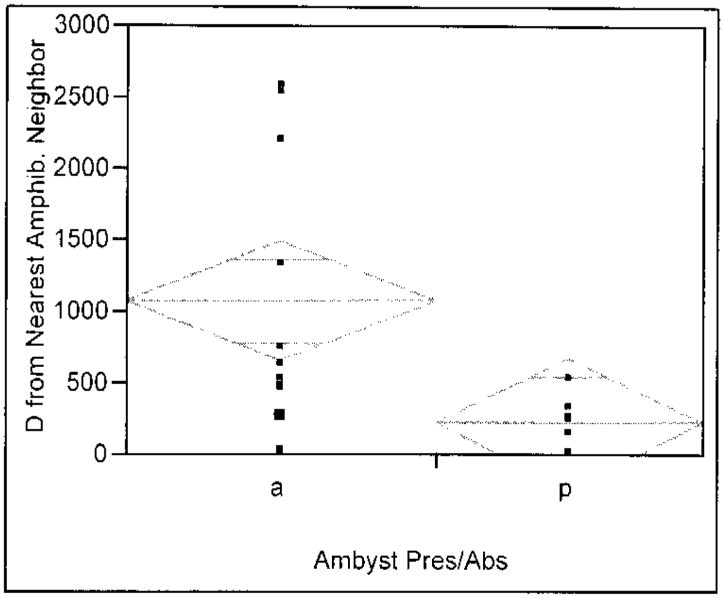


Figure 2. Graph of ANOVA showing differences in percent aquatic vegetative cover in artificial tanks and natural ponds. 95% Confidence Intervals. P=0.0322

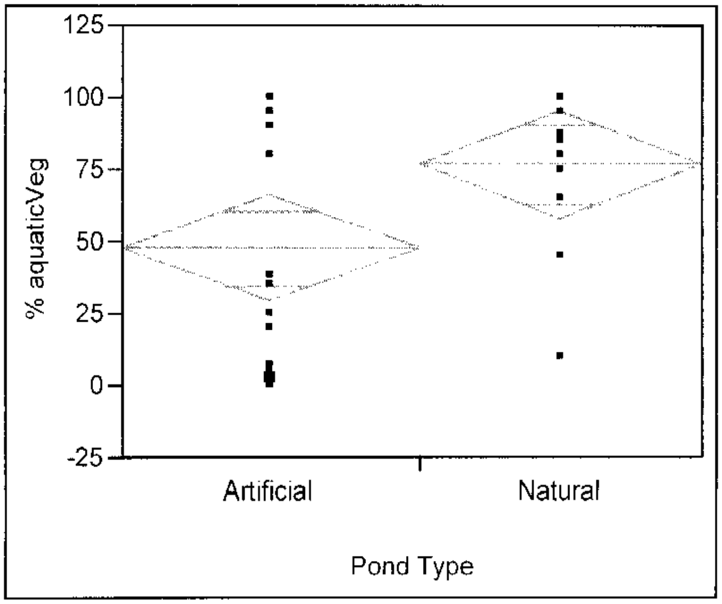


Figure 3. Graph of ANOVA with Tukey's HSD post-hoc showing differences in surface temperature (°C) in artificial ponds with amphibian larvae absent (AA), artificial ponds with larvae present (AP), natural ponds with larvae absent (NA), and natural ponds with larvae present (NP). 95% Confidence Intervals. P=0.0398

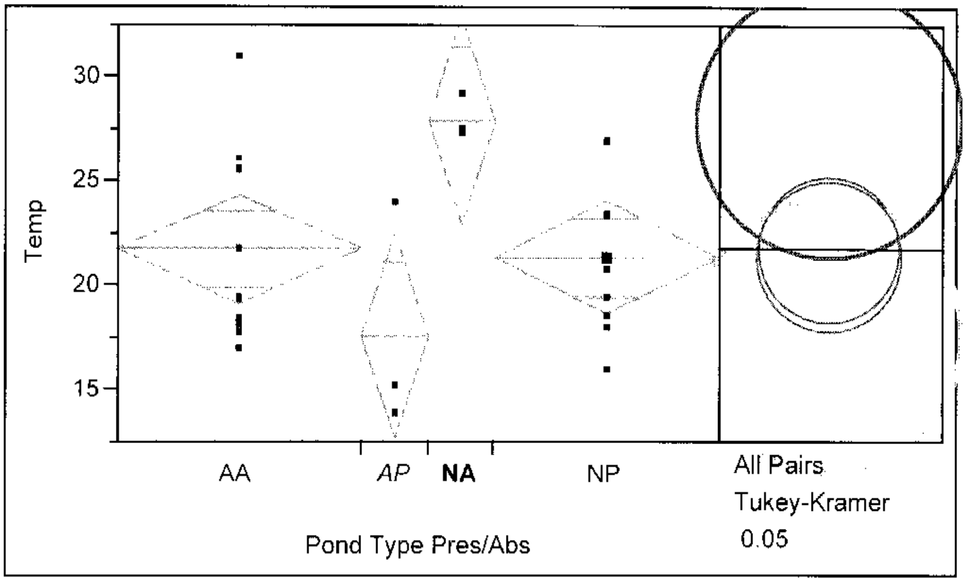


Figure 4. Graph of ANOVA with Tukey's HSD post-hoc exhibiting differences in pond depth (meters) for artificial ponds with amphibian larvae absent (AA), artificial ponds with larvae present (AP), natural ponds with larvae absent (NA), and natural ponds with larvae present (NP). 95% Confidence Intervals. P=0.0059.

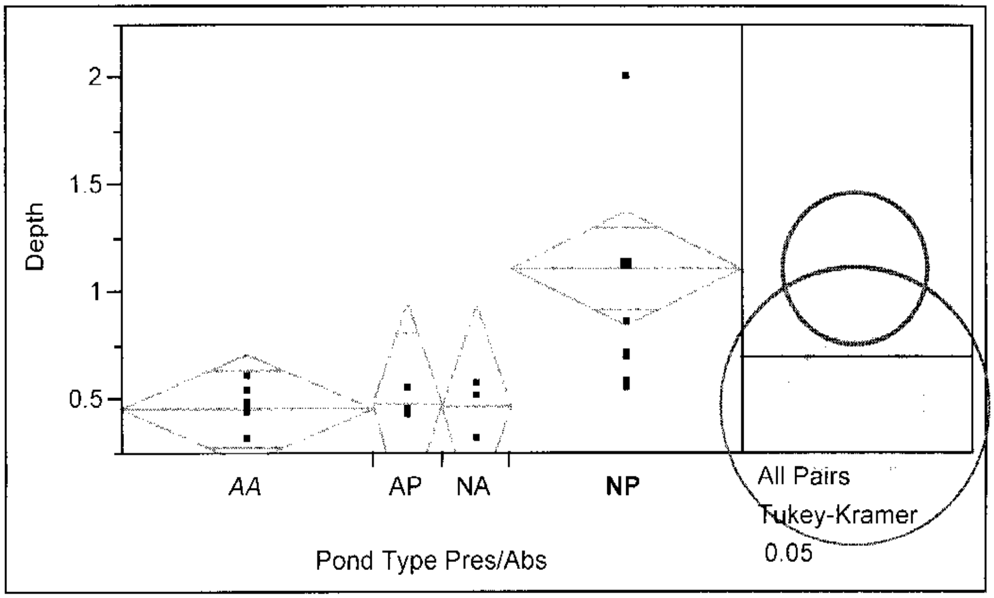
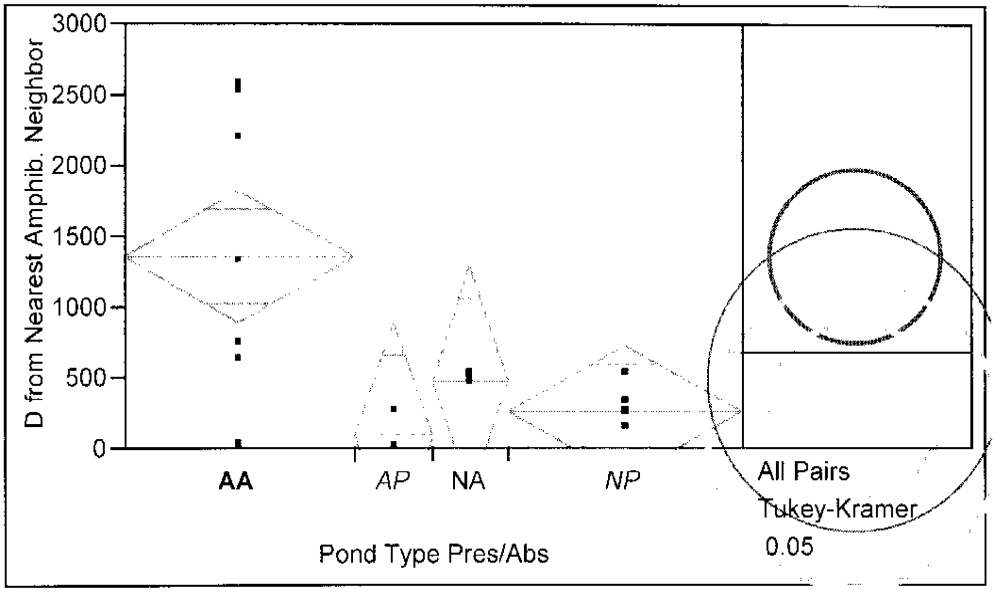


Figure 5. Graph of ANOVA with Tukey's HSD post-hoc showing differences in distance (meters) to the next closest pond with amphibian larvae for artificial ponds with amphibian larvae absent (AA), artificial ponds with larvae present (AP), natural ponds with larvae absent (NA), and natural ponds with larvae present (NP). Excludes pond NDP8 as a possible outlier. 95% Confidence Intervals. P=0.0087



Appendix

Appendix 1. Map of the natural ponds and artificial tanks sampled on the National Bison Range, Sanders and Lake Counties, MT, USA.