TERRESTRIAL HABITAT AND ECOLOGY OF FOWLER'S TOADS
(*ANAXYRUS FOWLERI)*

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ABSTRACT

Habitat loss is the primary driver of global amphibian declines and thus preserving habitat is our best hope for preserving species at risk. The habitat needs of amphibians are complex due to terrestrial and aquatic requirements throughout their life history. Many pond breeding amphibians spend the majority of their life cycle within terrestrial environments and thus terrestrial habitats are critical to their persistence. Cryptic and fossorial behavior makes observations of amphibians in terrestrial habitats difficult. Our knowledge of the terrestrial ecology of amphibians is therefore incredibly limited. I review the literature on habitat loss, amphibian declines and terrestrial habitat use by amphibians with specific attention to refuge seeking behavior **(CHAPTER ONE).** I used radio-tracking to investigate the behavior of Fowler's toads (*Bufo fowleri)* in the beach dune ecosystem of Long Point, Ontario. Refuge seeking behavior by these animals is associated with specific components of the dunes and is predictable based on elevation, slope and distance from the lakeshore. Refuge sites placement is not random, but instead represent a trade-off between risk and reward **(CHAPTER TWO)**. Philopatry in Fowler's Toads is driven by fidelity to refugia. These locations are used repeatedly on consecutive days, and even when they are not new sites within 10 meters of the previous day's refuge are most often chosen. Occasionally, however toads relocate their refuge sites as much as 700 m overnight **(CHAPTER THREE).** This contributes to the wide variation in the home range sizes of Fowler's Toads, as does method of calculation and search effort, while there is little apparent influence of intrinsic biological factors. The effect of search effort on range size is reduced in robust location data sets with more than thirty locations for each animal. A minimum home range estimate of 3517m^2 is suggested under the caveat that range sizes may have no hard upper limit **(CHAPTER FOUR).**

RÉSUMÉ

La perte d'habitat est le principal facteur responsable du déclin des amphibiens à l'échelle mondiale. La préservation de leur habitat représente donc le meilleur espoir pour la conservation de ces espèces en péril. Les amphibiens ont des besoins en complexes en matière d'habitat, car leur cycle de vie comprend des exigences terrestres ainsi qu'aquatiques. Plusieurs amphibiens qui se reproduisent dans des étangs passent la majorité de leur vie dans des environnements terrestres, ces derniers sont donc essentiels à leur résilience. Leurs comportements fouisseur et cryptique rendent les amphibiens difficiles à observer dans leurs habitats terrestres. En conséquence, notre connaissance de l'écologie terrestre des amphibiens est très limitée. Je passe en revue la littérature scientifique sur la perte d'habitat, le déclin des amphibiens et l'utilisation d'habitats terrestres par les amphibiens avec une attention particulière à la recherche de refuges **(CHAPITRE UN)**. J'ai utilisé le pistage radioélectrique pour étudier le comportement des crapauds de Fowler (*Bufo fowleri*) dans l'écosystème de dunes de la plage de Long Point, en Ontario. La recherche de refuge par ces animaux est associée à des composants spécifiques des dunes et est prévisible selon l'élévation, la pente et la distance du bord du lac. L'emplacement du refuge n'est pas aléatoire, mais représente plutôt un compromis entre risque et récompense **(CHAPITRE DEUX)**. La philopatrie chez les crapauds de Fowler est due à la fidélité aux refuges. Ces endroits sont utilisés de façon répétée sur plusieurs jours consécutifs ; même lorsqu'ils sont abandonnés, les crapauds choisissent le plus souvent un nouveau site à moins de 10 mètres du refuge de la journée précédente. A l'occasion, cependant, les crapauds peuvent délocaliser leurs sites de refuge jusqu'à 700 m d'une nuit à l'autre **(CHAPITRE TROIS)**. Cela contribue à la grande variation dans le calcul de la taille du territoire des crapauds de Fowler. Les méthodes d'évaluation et l'effort de recherche contribuent aussi à cette variation, alors qu'il y a peu d'influence apparente des facteurs biologiques intrinsèques. De plus, l'effet de l'effort de recherche sur la taille du territoire est réduit lorsque les données de localisation sont robustes et comprennent plus de trente sites par animal. Une estimation de taille minimale du territoire des crapauds de Fowler de 3517 m^2 est suggérée ici, sous la réserve que l'aire totale de répartition peut ne pas avoir de limite supérieure **(CHAPITRE QUATRE)**.

CONTRIBUTIONS OF AUTHORS

CHAPTER ONE

I surveyed the literature with advice and editorial support from Dr. Green.

CHAPTERS TWO, THREE AND FOUR

I collected the data, with the field assistance of Jessica Middleton, and analyzed the results. The final versions of each manuscript have been prepared with editorial support from Dr. Green.

CHAPTER ONE: Introduction and Literature Review

Habitat Loss and Extinction

Over the last two hundred years human impacts on the natural world have intensified dramatically, leading to rates of biodiversity loss that are approaching extinction rates experienced during historical mass extinction events (Wake and Vredenburg, 2008; Barnosky et al., 2011). Anthropogenic habitat loss, degradation and fragmentation are primary drivers of biodiversity loss (Harrison and Bruna, 199; Fahrig, 2001; Brooks et al., 2002). Due to complex habitat requirements, amphibians are at particularly high risk for extinction resulting from habitat alteration, and are currently threatened on a global scale (Houlahan et al., 2001; Stuart et al. 2004; Storfer, 2003; Bradford, 2005).

Habitat loss has multiple dimensions. First, it results in a reduction in absolute area of landscape able to sustain populations and individuals and, in so doing, alters the composition of a landscape and shifts the relative proportions of habitat components (e.g. forest vs. grassland). This affects both the abundance and diversity of species (Rosenweig, 1995; Tilman et al., 1994) in the habitat that remains. A second aspect of habitat loss is fragmentation, which results in the subdivision of remaining habitat into isolated patches. These are separated by spaces typically referred to as matrix (Wiens, 1996), which may well be habitat for a second suite of species and influences the exchange of individuals between patches (Gustafson and Gardner, 1996). Although habitat loss is clearly a concern for the persistence of species and the preservation of biodiversity (Tilman et al., 1994) the relative importance of fragmentation and connectivity is a topic of much debate (Lefkovitch and Fahrig, 1985; Harrison and Bruna, 1999; Fahrig, 2001). In model ecosystems fragmentation has been shown to negatively affect the diversity and abundance in much the same way habitat loss does (Gonzalez et al, 1998). A third aspect of habitat loss is degradation, or the reduction of habitat quality within an existing patch. Often fragmentation leads to degradation, as the ratio of edge to interior habitat rises, leading to alterations in the community structure within the remnant habitat (Harrison and Bruna, 1999).

Patterns of Habitat Fragmentation and Scale

Patterns of landscape structure drive ecological processes (Turner, 1989). Habitat fragmentation leads to four categories of landscapes based on the size of remaining patches and the distance between these patches (Fig. 1). Most simply, the environment consists of habitat and non-habitat (matrix). Patches of habitat may be either large or small and distances between patches may likewise be either large or small. If each organism perceives the environment at a spatial scale influenced by its perceptual abilities and movement capabilities (Wiens, 1989; Wiens and Milne, 1989; Levin, 1992) then the effects of post fragmentation landscape structure depend upon the scale at which a resident organism within this landscape operates. The potential of a patch to support an individual depends upon how much habitat that individual needs, which may be considered in terms of carrying capacity (Hutchison, 1978; Botkin, 1990; Sayre, 2008) from the perspective of the landscape, or critical patch size (Skellam, 1951) from the perspective of the organism. Large patches are those which contain enough resources for an individual to survive without having to leave the patch and small patches do not. Proximal patches are those which can easily be navigated by regular movements and are within the perceptual range of individuals in neighboring patches, while distant patches have neither of these qualities, though may be reached through improbable movement events. In scenario ***A*** in this conceptual model, patches (Fig. 1) are large and inter-patch distances are small. In these situations the effects of fragmentation on resident animals should be minimal, though if the boundary between habitat and matrix is unlikely to be crossed it may lead to isolation of sub-populations and genetic structure. In scenario ***B***, patches are large as are inter-patch distances. These situations should be typified by infrequent movement between patches and are landscapes that fit the meta-population framework (Levins, 1969; 1970; Hanski, 1998; Hanksi and Ovaskainen, 2000). In scenario ***C***, single patches are insufficient to support an individual, but movement between patches is easy and thus sufficient resources can be acquired to survive within the landscape through resource complementation (Dunning, 1992) and we expect a high degree of functional connectivity (Belise, 2005). Individuals in these landscapes will use more space than those in **A** or **B** as a considerable amount of matrix will be travelled through, or otherwise occupied, in the process of acquiring adequate resources. Scenario ***D*** is the only landscape in which individuals cannot survive. A single patch contains insufficient resources and no complementation can take place as the remaining patches are outside the perceptual range of the resident.

The ecological consequences of each of these categories of fragmentation patterns can only be appreciated when we have an understanding of both the types of environments which are important to the resident animal (i.e. what type of habitat does it require) and the spatial scale at which it interacts with its environment (i.e. how often and how far does it move). Measuring both qualitative and quantitative aspects of habitat use are then critical to understanding the consequences of habitat fragmentation.

Habitat Use

Habitat selection by animals can chiefly be inferred based on their occupancy of one form of habitat or another (Neu et al., 1974; Aebischer, et al., 1993). The use-availability paradigm (Thomas and Taylor, 2006) assumes that the proportion of time spent-within a particular habitat type should correlate with both the availability of habitat elements and the degree of preference by an individual for each habitat element. Thus, when rare habitat elements contain the majority of animals most of the time, the animals arguably are selecting that habitat and are not randomly distributed spatially. The evidence for this may be via direct observation, indirect observation (e.g. tracks or scat), radio-telemetry or radio-tracking. This approach is refined further when multiple spatial scales are investigated concurrently (Johnson, 1980). The placement of a home range within a landscape and the placement of an animal within a home range may both provide valuable information regarding habitat selection. In the first case we gain information about what types of habitat available within the landscape are important to the individual and influence its placement of home range. In the second case we gain information about which habitat elements within the home range are important. This all assumes that occupied locations serve some ecological function and that occupancy is not a trivial.

Use-availability models of habitat selection may be criticized because they do not consider that habitat preference may shift with habitat availability through functional responses (Myerstaud and Ims, 1998). Use-availability models assume that we can accurately describe habitat categorically in a fashion that is meaningful to the organisms we are studying. However, defining what habitat is available is problematic and the definitions radically affect the interpretation of occupancy data (Beyer, et al., 2010). This may be less of an issue for organisms that perceive the environment in ways and at scales similar to us, but most animals do not. Use-availability models also assume that time of residency within a habitat is positively correlated with value. This may not always be the case. For example, residency time in a high quality foraging patch may be less than in a lower quality patch.

Multivariate characterizations of the environment are an alternative to categorical descriptions of habitat. Maximum entropy analysis (Phillips et al., 2006; Phillips and Dudick, 2008; Elith et al., 2011) allows the distribution of organisms to be modeled based on environmental predictors and can serve as a method for conducting multivariate analysis of habitat use across spatial scales. This approach makes use of presence-only data and compares the probability density of environmental factors at these sites with a background sample of sites which are presumed to represent locations where the organism is absent (Elith et al., 2011). Comparing these distributions allows the probability of presence to be estimated based on each environmental factor and thus provides insight into the drivers of organism distribution within a landscape.

Home Range: Space Use and Spatial Requirements

The extent of habitat an individual needs in order to survive is a fundamental ecological question. The answer usually invokes the concept of the "home range" (Burt, 1943). However, no general consensus exists with regard to what a home range is (Obsorn, 2004) or whether home ranges exist at all (Gautestad and Mysterud, 1995). The idea of an animal having a home range stems from observations that animals generally do not wander randomly but instead remain in or return to a "home region"

(Seton, 1909). Burt (1943) formalized the term “home range” as being “the area, usually around a home site, over which the animal normally travels in search of food”. This leaves open the definition of what constitute normal movements (Cooper, 1978, White and Garrott, 1990). Burt (1943) was unclear on this matter as he also proposed that the home range is “the area traversed by an individual in its normal activities of food gathering, mating and caring for the young”, therefore including reproduction and parental care as behavioral components of a home range. This definition blurs the distinction between reproductive behavior, which contributes to the persistence of a population, and foraging behavior, which contributes to the survival of an individual. This distinction is likely to be of considerable consequence to animals such as aquatic insects or aquatic-breeding amphibians whose life-histories feature discrete larval and adult life stages that are largely or exclusively committed to either feeding and growth or to reproduction, and inhabit spatially distinct and qualitatively divergent environments.

Jewell (1966) attempted to overcome the conceptual problems of home range, especially the issue of which movements comprise the home range and which do not, by proposing that animals have a “life-range” which includes all locations it occupies in its lifetime. Life range, as a concept, is valuable in illustrating the scale, or range of scales that individuals operate on. A life range may include many home ranges, “areas with a certain productivity that meet the energy requirements of the individual that occupies it” (Jewell, 1966), either overlapping or joined by dispersal paths. However, the length of a lifetime is highly variable and determined by numerous stochastic as well deterministic factors. Thus the life range is highly contingent upon life span.

Beyond the conceptual issues regarding exactly what a home range is there are numerous methodical issues. The calculation of home range areas relies on animal location data, represented as a two dimensional pattern of points. Two general classes of approach exist, those relying on the statistical distribution of locations and non-statistical methods. Early methods, predating computing, are generally non statistical in nature, including the creation of Minimum Convex Polygons (Mohr, 1947), although new non statistical methods do arise, most recently the use of localized convex hulls

(Getz and Wilmers, 2004). Statistical methods, including harmonic mean (Dixon and Chapman, 1980) and kernel density estimates (Worton, 1989) are computationally intensive but can provide utilization distributions, quantifications of the intensity of use of areas. A host of other methods have been used to date (reviews in: Worton, 1987; Harris et al., 1990; Laver and Kelly, 2008). No consensus exists as to which methods are most appropriate, though there is evidence that some degree of taxon specificity may exist (Row and Blouin-Demers, 2006). Methods which compute utilization distributions can provide a quantitative means to sort "normal" from unusual locations (Dixon and Chapman, 1980; Worton, 1989; Kenward et al., 2001). Applying a number of statistical and non statistical methods in parallel reduces the likelihood that a single method inappropriate to the species in question is used, and allows for greater flexibility in making comparisons between studies and taxa, a common macro-ecological theme.

Further debate concerns the number of locations required to achieve reliable estimates of spatial utility (Beckoff and Mech, 1984; Seamen et al., 1999) and the length of time that must pass between successive relocations of the same individual (Swihart and Slade, 1985; Fieberg, 2007). These are related issues as the number of relocations can artificially be inflated at the expense of independence of observations.

Given its widespread application and the variety of methods used for its calculation, it is unlikely that everyone using the term "home range" is doing so in the same fashion. Since we are chiefly interested in understanding the spatial scale at which organisms operate, we will employ an inclusive interpretation of the home range concept, approaching the life range concept of Jewell (1966). Our interests are in terrestrial habitat use so in the course of data collection we will include any locations of animals which are made in terrestrial habitats outside of the breeding season, thus providing an estimate of seasonal range, which we shall refer to as home range throughout.

Habitat Use in Terrestrial Amphibians

For most species of amphibians, life on land makes up the larger portion of an individual's existence, with adults returning to aquatic habitat solely for breeding. These animals forage, migrate, disperse and seek refuge terrestrially. We cannot ignore terrestrial ecology when considering the biology of nearly every amphibian species (Stewart and Pough, 1983;Harper and Semlitsch, 2007; Patrick et al., 2008). However a tendency towards nocturnal activity and daytime crypsis in the terrestrial environment has made this aspect of their lives a challenge to study and, consequently, the terrestrial ecology of amphibians is poorly understood and has not been studied as extensively as breeding and larval ecology (Semlitsch, 2003). It is nevertheless vitally important to address amphibian population ecologies in terrestrial habitats (Storfer 2003; Trenham and Shaffer, 2005) especially since changes in terrestrial landscapes, including habitat loss, are a primary driver of amphibian declines worldwide. (Stuart et al. 2004; Storfer, 2003; Bradford, 2005).

Toads of the family Bufonidae, with a few noteworthy exceptions, have aquatic larvae but tend to be highly terrestrial as adults. The over 500 species in 35 genera included in this cosmopolitan family (Vitt and Caldwell 2009) exhibit a wide range of behavioral ecologies. The most atypical Bufonids include the Plump toads (genus *Osornophyrne*) which develop directly into adults from terrestrially deposited eggs, two species each from the genera *Nectophrynoides* and *Nimbaphrynoides* which give birth to live young (viviparity), the Asian tree toads (genus *Pedostibes*) which are entirely arboreal and the Peat Swamp toad (*Pseudobufo subasper*) which is chiefly aquatic. A handful of species are adapted to sand dune environments and regularly burrow into sandy substrates when these are available. These include the Natterjack toad (*B. calamita*) in Europe (Beebee 1983) and Fowler's Toad (*Anaxyrus fowleri*) in North America (Harding and Holman, 1992). Relative to the rest of the genus these two species have been studied extensively (Clarke 1974; Beebee, 1983; Breden, 1987, 1988; Green, 1989; Miaud et al., 2000; Miaud and Sanuy, 2005; Smith and Green, 2004, 2006). In sandy sites animals are free to burrow into the ground at any location where bare substrate is available. On beaches and dunes abundant sand may free individuals from constraints on the choice of refuge sites, provided the natural dune environments are left relatively undisturbed by humans.

Terrestrial refuge site choice in amphibians

Terrestrial refuge sites for anuran amphibians vary considerably between species, between allopatric populations, between sympatric individuals, across seasons and over the lifetimes of individuals (Schwarzkopf and Alford, 1996; Griffin and Case, 2001; Yu et al., 2010). Retreat areas may range from cover objects such as logs, rocks, downed wood or leaf litter on the ground to deep, underground burrows. Many species considered to be terrestrial and fossorial have morphological adaptations that enable them to dig and create their own burrows (Emerson 1976; Hillman et al. 2009). In some cases, individuals will take refuge opportunistically in burrows dug by other animals (Denton and Beebee, 1993; Griffin and Case, 2001; Bossert et al., 2003).

The characteristics typical of terrestrial refuge sites for amphibians have been described for a handful of species in a few locations over relatively short periods of time (Table 1). For most species, though, detailed studies of this aspect of natural history are lacking and reported mainly as anecdotal information in older literature, such as Dickerson (1907).

For amphibians, hydroregulation often supercedes thermoregulation in importance and locations that prevent dehydration are occupied preferentially, even when outside of optimal thermal bounds (Tracy et al., 1993; Oromi et al., 2010). Experimental manipulations in the wild (Cohen and Alford 1996) and in the lab (Hoffman and Katz 1989) exploring choice of refuge site and burrowing behavior by frogs or toads have shown the importance of local temperature and soil moisture on the expression of burrowing and refuge seeking. Laboratory maintained Green toads (*Bufo viridis*) were far more likely to bury themselves entirely when exposed to 24° C temperatures relative to 18° C (Hoffman and Katz, 1989). Full burrowing behavior continued for weeks after returning toads to 18° C conditions. Cane toad preference for artificial shelter sites correlated directly with soil moisture content and temperature at these shelters (Cohen and Alford, 1996). Artificial shelters were most often used on hot days and moist shelters were most preferred. The notion that shelter sites provide homeostatic refugia which protect individuals from extremes of heat and drought is well supported (Denton and Beebee, 1993; Pinder et al., 1992; Oromi et al., 2010). For ectotherms, occupying locations which allow an individual to operate close to its thermal optimum can have profound effects on short term performance (e.g. digestion, metabolic rate), and ultimately fitness (growth and reproduction) (Bush, 1963; Lillywhite et al., 1973; Tracy and Christian, 1986; Huey, 1991; Tracy et al., 1993).

Home Range Studies in terrestrial amphibians

Significant advances in the miniaturization of radio transmitters have made extensive studies on the movements of amphibians other small animals possible (Harris et al., 1990). Home range estimates for a number of amphibian taxa are now available, though great variation exists both within species and between species (Table 2).

Study species

Fowler's toad (*Anaxyrus fowleri*) is a valuable model species for studying anuran terrestrial ecology. Adults are highly terrestrial, relying on sand dunes for the daytime refuge sites and seasonal hibernacula required to complete their life cycle. Adults seek out ponds, wetlands and ephemeral pools for breeding shortly after spring emergence from deep within the dunes (Green, 1989). Reproductive behavior typically lasts two to three weeks (Green, 1989). Calling males attract males and females alike to breeding sites, allowing the formation of large breeding aggregations. Eggs are fertilized externally and left to develop without parental care. Tadpoles hatch from eggs after 2-7 days and metamorphose into land dwelling toadlets after a further 30 – 40 days (Harding, 1997). The remainder of an individual's life is largely spent exclusively on dry land as mating is the sole obligate aquatic act. Adults rely on fresh water, absorbed through special patches on skin on the ventral surface of the pelvic area, for daily hydration. Typically toads emerging from daytime refuge sites make their way more or less directly to water. Toads make use of water as a means to escape from predation by jumping into water and swimming away when threatened.

In Canada, Fowler's Toads are restricted to dune and beach habitats along the north shore of Lake Erie (Green, 1989). This handful of isolated populations is at the northern limit of the species' range and therefore are of great interest in an evolutionary context (Smith and Green 2004). The endangered status of this species in Ontario (COSSARO, 2010) and Canada (COSEWIC, 2010) makes it an important target for research, especially as population viability models predict extirpation from Canada within 50 years. Although some fragments of the Canadian population are entirely contained with habitat protected by Provincial Parks or Federal Wildlife Areas, about half of the shoreline within the extremely restricted range of these animals is privately owned (COSEWIC, 2010). In order to best protect the Canadian populations of Fowler's Toad from localized extinction we need to better understand how these animals interact with the terrestrial environment.

Currently we are able to define terrestrial habitat requirements adequately on a landscape scale. Fowler's Toads live mainly on the beach. However, most observations of these animals take place in the evening when they are active and generally spend time within a few meters of the Lake Erie shoreline. Although we do know that these animals dig into the sand during the daytime, as do many other Bufonid toads, we do not know, on a finely grained toad-sized scale, which sort of locations within the beach and dune ecosystem are most important to these animals with respect to refuge seeking behavior. With this knowledge we may be able to forestall or reverse their decline. This may be achieved by engaging in a campaign of targeted habitat protection initiatives, habitat rehabilitation through the creation of suitable terrestrial habitat and public education to inform private landowners how to best balance their desires to manage their properties as they wish with the needs of the toads.

Methods used to study refuge site selection and movement behavior

Radio-tracking has been used successfully to locate individual frogs and toads in their cryptic refuge sites (Oromi et al. 2010; Indermaur et al. 2009a,b ;Schwarzkopf and Alford 1996 ; Spieler and Linsenmair 1998). Radio tracking may also be used to quantify movements rather than habitat use *per se* (i.e. Constible et al., 2009) or may be used to assess habitat use at a larger scale than the refuge site (Watson et al., 2003).

The attachment or implantation of a radio transmitter in a toad and frog yields valid data only if it has negligible effect on the behaviour and ecology of the animals. This requires the ratio of transmitter mass to body mass to be below about 5-10% (Rowley and Alford, 2007). This is supported by most research (i.e. Indermaur et al., 2008).

Radio-tracking provides an opportunity to study choice of refuge sites and movement ecology while minimizing the confounding effects associated with directly observing animal behavior. Toads can be found without disturbing them. Therefore the observed location of an animal is a result of choices it made at an earlier time while free from human interference. Radio tracking solves many problems in the study of terrestrial amphibians. Historically no reliable means to collect data on these cryptic and fossorial animals existed. Thus rare opportunistic observations served as the entire basis for our understanding of these behaviors and the associated habitat. Radio tracking allows us to be systematic in our study of terrestrial amphibians and switch from an anecdotal and observational framework to a quantitative and statistical one. We consider the intersection of the two modes quantitative natural history.

Location of Field Work and Research Objectives

Long Point, Ontario, provides an ideal location for investigating the terrestrial ecology of Fowler's Toads in the wild (Green, 1989; Green, 2005; COSEWIC, 2010). The sand spit that comprises Long Point extends more than 35 kilometers from base to tip, the entire length made up a thin strip of lakeshore, beach and dune interface flanked by wetlands and marshes. Human disturbance is minimal in the majority of locations though there are many cottages and roads at the western base of Long Point where it joins the mainland Studies of Fowler's Toad movements clearly support the argument that the forty plus kilometers of linear beach habitat should not constrain toads in their movements, except when approaching the tip (Clarke, 1974; Smith and Green, 2006). This allows us to assume that habitat selection by toads in this environment is not constrained by lack of suitable habitat (habitat degradation) or by lack of connectivity between habitat patches (habitat fragmentation).

The dune ecosystems along the north shore of Lake Erie are highly dynamic (Gelinas and Quigley, 1973; Stenson, 1996). Winter storms sculpt new dune faces and alter beaches and vegetation structure on an annual basis. During the summer, fluctuations in water level can greatly affect the shape and area of beach available for toads to use. High winds can create waves large enough to have powerful erosive impacts on standing dunes and present a real threat to toads, whether active or dormant. For toads in this environment, choosing refuge sites which are likely to be impacted by waves is a dangerous proposition. Further, snakes, which are the primary predators of toads, tend to avoid the barren beach environment, instead staying within the vegetated dune tops and dune faces. Thus pressure from predators may drive refuge site placement towards onto the beach and towards the waterline. At the same time, access to fresh water for hydration is critical and minimizing the distance an individual has to travel to reach water could influence growth and survival. The refuge site to water's edge distance may be of great importance in the ecology of Fowler's Toads. Refuge site placement, in relation to the shoreline, should represent a trade-off between decreasing probability of death or transportation by catastrophic wave action and increasing energetic costs associated with daily commuting from refuge to hydration source and vice versa. Safety from waves can likely be achieved through distance from lake edge or elevation above waves in tall dunes.

In CHAPTER TWO we test the hypothesis that if proximity to the waterline represents a trade of between risk and reward, and microhabitat characteristics affect the quality of refuge sites, then the refuge sites of Fowler’s Toads should be distributed non-randomly in the dune ecosystem.

In CHAPTER THREE we test the hypothesis that Fowler’s Toads exhibit fidelity to particular refuge sites on a daily time scale. If the distance between refuge locations on successive days is less than the distance between refuge sites and evening activity locations then we can say that toads return to a central nest area on a daily time scale.

In CHAPTER FOUR we quantify home ranges for Fowler’s Toads. We also investigate the relationship between home range size and biological (sex and body size) and methodological (search effort) factors. If intrinsic biological factors play a role in driving home range sizes then we expect that we should be able to detect this relationship provided we can control for variation in sampling effort.

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Table 1. Examples of burrowing behaviour in anuran amphibians

Species		Locality	observation	reference
Cane toad	*Bufo marinus*	northern Australia	underground burrows or above ground grassy sites as refuge sites	Schwarzkopf and Alford 1996
Crowned Bullfrog	*Hoplobactrachus occipitalis*	Ivory Coast	refuge in crevices beneath rocks, underneath shrubby vegetation, in patches of grass and underwater in ephemeral pools or ponds	Spieler and Linsenmair, 1998
Natterjack toad	*Bufo calamita*	Britain	dug extensive and deep burrows in sandy substrates	Denton and Beebee, 1993
Natterjack toad	*Bufo calamita*	Spain	on clay substrates were less able to burrow and more likely to rely on naturally occurring crevices for refuge	Miaud and Sanuy, 2005
Common toad	*Bufo bufo*	Britain	tended to remain near the surface, hiding in vegetation or beneath logs, occasionally taking advantage of rabbit holes	Denton and Beebee, 1993
Asiatic toad	*Bufo gargarizans*	southwestern China	sought out vegetated areas to take shelter, relying heavily on the presence of broad leaved agricultural crops when available	Yu et al., 2010
Burrowing Toad	*Rhinella fernandezae*	Argentina	select burrow sites based on the presence of broad leaved vegetation and soil hardness	Sanchez et al. 2010
Arroyo toad	*Bufo microscaphus californicus*	California	burrow into sandy substrates, sometimes horizontally into sandy riverbanks. Refuge sites in most commonly associated with coastal sage, oak and agricultural vegetation	Griffin and Case, 2001

Table 2. Estimated home range size for terrestrial anurans.

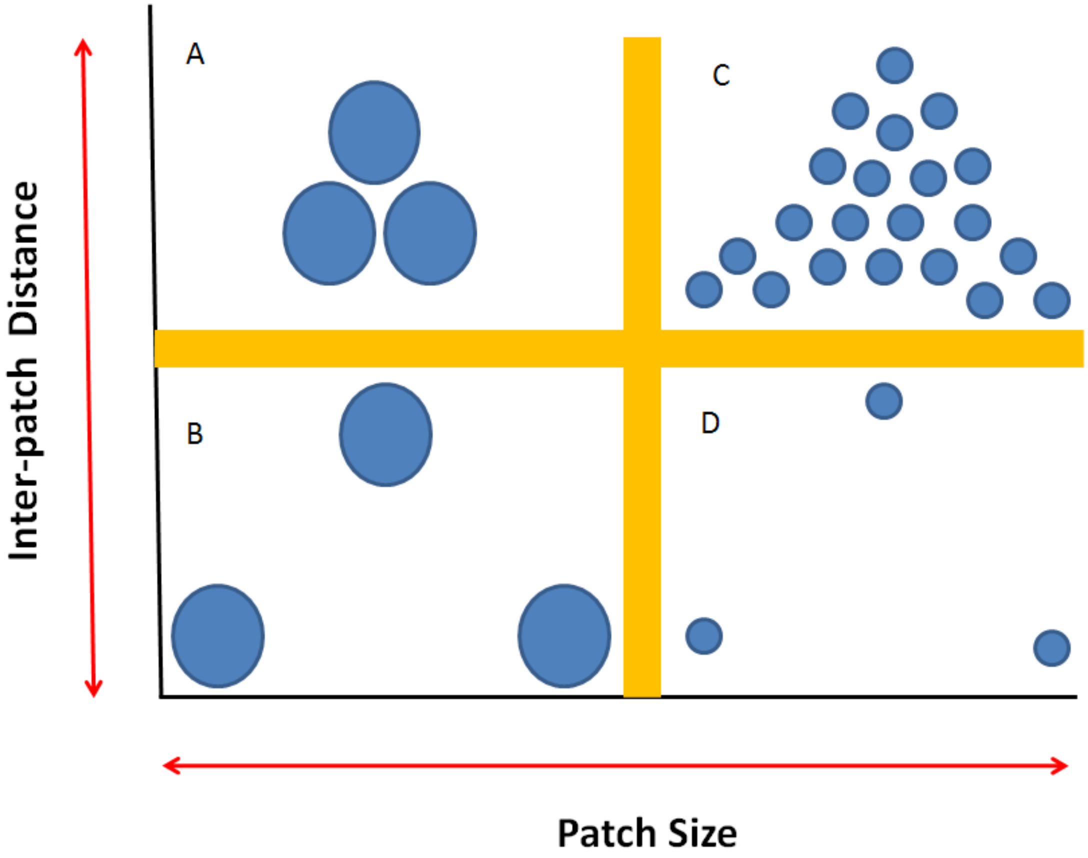
Species	method	estimated home range size	reference
Common Toad (*Bufo bufo spinosus)*	95% Kernel Density	570 m^2	Indemaur (2009)
Green Toad (*Bufo viridis)*	95% Kernel Density	2,456 m^2	Indemaur (2009)
Oregon Spotted Frogs (*Rana pretiosa)*	Fixed Kernels	22,000 m^2	Watson et al. (2003)
Oregon Spotted Frogs (*Rana pretiosa)*	100% Minimum Convex Polygons	26,000m^2	Watson et al. (2003)
Northern Leopard Frogs (*Lithobates pipiens*)	100% MCP	1,096 m^2 – 8,425m^2.	Blomquist and Hunter (2009)
Gold Spotted Pond Frogs (*Rana chosenica)*	95% Adaptive Kernel	713.8 m^2	Ra et al. (2008)
American Toad	95% Fixed Kernel	717.7 m^2	Forester et al. (2006)
Natterjack Toads (*Bufo calamita*) Breeding season	Minimum Convex Polygon	5,000m^2	Miaud and Sanuy (2005)
Natterjack Toads (*Bufo calamita*) Post breeding season	Minimum Convex Polygon	65,000m^2	Miaud and Sanuy (2005)

FIGURE LEGEND

FIGURE 1

Categories of habitat fragmentation based on axis of interpatch distance and patch size.

FIGURE 1



CHAPTER 2: Selection of Daytime Refuge Sites

CHAPTER TWO LINKING STATEMENT

Habitat loss cannot be understood without an appreciation of the components of a landscape which positively contribute to survival of resident organisms. Within Chapter Two I combine natural history observations of behavior and habitat use with a novel application of the use-availability framework of habitat selection. The results provide insight on habitat use and selection based on the relative contributions of multiple interrelated parameters rather than simple categorical classifications of habitat.

ABSTRACT

Many terrestrial amphibians use terrestrial habitat to take refuge from heat, dryness and predators. During daylight hours Fowler's Toads are almost entirely inactive, taking refuge in shelter sites they may or may not dig themselves. These toads preferentially take refuge in locations which are predictable based on elevation, slope and distance to source of water. Vegetation may play a role in determining refuge site placement as well. The relative importance of hydrological and thermal properties of refuge sites is not clear. Refugia tend to be placed in the hottest sites in the landscape, which may maximize digestion and growth. Refuge placement likely represents a balance of risk and reward.

INTRODUCTION

For many anuran amphibians, day to day survival requires access to terrestrial refuge sites. Use of these sites is important to the animals for thermoregulation (Hoffman and Katz 1989; Cohen and Alford 1996), for maintenance of water balance (Tracy, 1993; Schwarzkopf and Alford 1996; Parris 1998; Oromi et al., 2010) and for avoidance of predators (Roznik and Johnson 2009). Without access to refuge sites an animal's ability to maintain homeostatic equilibrium is compromised (Pinder et al., 1992; Wells, 2007). Availability of these sites will inevitably affect the abundance and distribution of a species (Stewart and Pough 1983).

Choosing where to take refuge is a critical decision which may be influenced by a hierarchy of factors at multiple spatial scales (Wu and Loucks, 1995). Factors at the scale of the refuge site itself should influence the environmental suitability of the location to meet the thermal and hydrological needs of the animal using it. Indeed there is much evidence that refuge site choice by amphibians is influenced by the presence of vegetation (Denton and Beebee, 1993; Schwarzkopf and Alford 1996; Griffin and Case, 2001; Spieler and Linsenmair, 1998; Yu et al., 2010; Sanchez et al., 2010), which may affect both water and thermal relations between animal and environment. As seen in Cane toads (Cohen and Alford 1996) and Green toads (Hoffman and Katz 1989), both local temperature and soil moisture profoundly influence the expression of burrowing and refuge seeking behavior. Site choice may also be driven by the presence of shelter objects or burrows made by other animals, which are opportunistically occupied (Denton and Beebee, 1993; Griffin and Case, 2001; Bossert et al., 2003), freeing the user from the expensive costs of digging (Seymour 1973), which in some substrates is not possible (Miaud and Sanuy, 2005), despite morphological adaptations to that end (Emerson 1976; Hillman et al. 2009).

At broader spatial scales refuge site placement may be seen as an aspect of optimal foraging theory (Charnov, 1976). Refuge sites close to food, or other resources, will confer a benefit to their residents as less time and energy will be spent in transit between resting and foraging habitat. This may be especially important for foragers which return to a central nesting site cyclically (Orians and Pearson, 1979). Gilliam's rule predicts that energy gain should be maximized in relation to mortality risk (Gilliam and Fraser, 1987; Houston et al., 1993) and thus we expect that, independent of the highly localized characteristics of refuge sites, they should be located within a landscape at the point where the ratio of energy gain to mortality risk is highest.

Fowler's toad presents a valuable model for studying anuran terrestrial ecology. Adults are highly terrestrial, relying on sand dunes for the daytime refuge sites and seasonal hibernacula required to complete their life cycle. Within Canada, Fowler's Toads are restricted to dune and beach habitats along the north shore of Lake Erie (Green, 1989). Most observations of these animals take place in the evening when they are active and within a few meters of the Lake Erie shoreline. However, by attaching radio transmitters to toads, they can be tracked effectively in order to investigate their burrowing behavior and choice of refuge sites.

Although we do know that Fowler's Toads dig into the sand during the daytime, we don't know what types of locations are most important to them. These toads forage and hydrate at the edge of the lake during hours of darkness and thus refuge placement near the lake edge may optimize resource acquisition rates. While in a refuge site, however, the lake poses a significant risk of mortality towards toads, as the shallow waters are easily disturbed by winds, generating large forceful waves. Toads may be killed outright by wave impacts or drawn out into the lake where survival probabilities are likely reduced. Mortality risk should drop with increasing distance from the waterline or increasing elevation, both of which can shelter toads from dangerous wave action. Predators may also be driving the choice of refuge sites. Snakes are the main predators of Fowler's Toads at Long Point, chiefly Eastern Hognose Snakes (*Heterodon platirhinos)*. Generally these snakes do not venture out onto the bare sands of the beach, instead remaining in the vegetated areas of the dune. This affords toads at refuge in the open sand of the beach increased protection from predation. If the energetic input/ mortality trade-off drives habitat choice then we expect that refuge sites will not be placed at random throughout the beach and dune complex but rather be influenced, in a predictable fashion, by the relative influence of these two factors.

The presence of vegetation may be a common feature of Fowler's toad refuge sites during summer months since the ability of plant roots to retain moisture in sandy soil may make vegetated sites important for toads attempting to stay hydrated. Vegetation may also be a factor in refuge site selection by the toads because of the shade it provides. If avoiding heat while minimizing energetic expenditure drives refuge site choice then we expect that toads will preferentially seek out vegetated sites which shade them and free them from the cost of digging. Further, we expect that an inverse relationship between the degree of vegetation cover and the expression of burial behavior should exist. Shaded toads should bury themselves less fully than toads in full sun exposure. We explore these hypotheses and provide quantitative natural history observations of refuge behavior which have largely been anecdotal to date.

MATERIALS AND METHODS

Study Site

All field work was conducted during the summers of 2009 and 2010 at Long Point in Ontario, Canada, along the beaches of Long Point Provincial Park and the Canadian Wildlife Service Thoroughfare Beach Unit. This area is located in UTM zone 17 N between 550700 and 553000 (m) Easting and 4713615 and 4714200 (m) Northing (NAD 83 Datum).

Thoroughfare Beach is a 2 km stretch of shoreline oriented almost directly west-east. It is bordered by Long Point Provincial Park, to the west, and private lands owned by the Long Point Company, to the east. The beach varies in size and shape greatly from year to year, and to a lesser degree from day to day, depending on winter storms, summer lake levels and wind action. Immediately north of the beach is a series of sand dunes, followed by a very thin strip of grassland which quickly gives way to a massive wetland, marsh and wet meadow complex. These wetlands are the site of spring and summer breeding for may amphibians including Fowler's Toad. Additionally, some males do call from ephemeral pools on the beach and presumably some mating occurs in these foredune pools.

A gradient of vegetation exists along the north south axis, with the shoreline being completely barren, the dune face lightly vegetated and the dune tops moderately vegetated. Persistent wave action ensures that few plants survive on the lower beach. The wetlands north of the dunes are thick with cattails (*Typha spp.*), the invasive reed *Phragmites austriculus and* numerous other water-loving species. The dunes, foredunes and beach are dominated almost exclusively by American Beach Grass (*Ammophila breviligulata*), with some Riverbank Grape (*Vitis riparia*). A variety of other forbs can be regularly found in limited quantities including Wormwood (*Artemesia spp.*), Evening Primrose (*Oenothera biennis*), Canada Cockleburr (*Xanthium strumarium v. Canadense*), Sea Rocket (*Cakile endentula*), Seaside Spurge (*Euphorbia polygonifolia*), a second grass (*Panicum spp.*) and a legume (Tick Trefoil or Hog Peanut). A handful of far less encountered plants could not be identified but likely play no more than a minor role in the lives of Fowler's Toads given their minimal abundance and distribution. Poison ivy (*Rhus radicans L.)* is widespread in the back dune and dune top areas, as are numerous willow shrubs (*Salix spp.*). Cottonwood (*Populus deltoides*) is the sole large woody species present and plays a role in the stabilization and creation of dunes. From year to year, as dunes are eroded by waves, large living cottonwoods become unstable and fall over. These downed trees, as well as beached driftwood, create structurally complex habitat on the beach.

Initial location of animals and attachment of radio-transmitters

All procedures described below were conducted under McGill Animal use Protocol 4569, issued to D.M. Green in accordance with the Ontario *Endangered Species Act* and the Canadian federal *Species at Risk Act* under permits issued by the Ontario Ministry of Natural Resources, Ontario Parks, the Canadian Wildlife Service and Environment Canada.

Toads were captured opportunistically during evening searches of the beach near the waterline. Once in hand toads were photographed, sexed, measured (snout to vent length) and fitted with a harness belt of surgical tubing through which a filament line was threaded. Radio-transmitters were then tied on to this filament (Figure 1). This mode of transmitter attachment is based on the method published by Bartelt and Peterson (2000).

Transmitters attached in this way regularly caused minor skin abrasions to toads wearing harnesses. Toads were inspected regularly for signs of belt induced abrasions and released from the transmitter harnesses when abrasions were detected. Belts were initially tied at the chest (2009) but were later tied at the waist (2010) as waist belts were less prone to cause abrasion or to be shed. Almost all toads showed signs of belt harness abrasions after extended periods of wear. Because of this, bouts of tracking were limited to periods not in excess of two weeks duration. At the end of each tracking period toads were released from transmitter belts. At the beginning of subsequent tracking sessions previously tracked toads were preferentially sought out for reattachment. Rashes from transmitter belts healed quickly, often within a few days, and this was facilitated by applying vitamin E lotion on irritated skin.

In 2009, Holohil BD-2 radio-transmitters were used, weighing 0.51 g, with a battery life of 21 days. In 2010 Holohil BD-2N radio-transmitters were used, weighing 1.0 g, with a battery life of 75 days. The weight of the remaining apparatus varied with size of toad (as larger toads require more tubing to encircle them) around a mean of 1.0 g. The difference in mass between years was assumed to be of no effect on the behavior of the toads. The 2.0 g total mass of the larger transmitters with tubing is well below the 10% transmitter to body mass limit, closer to 5% of an adult toad's body mass (Rowley and Alford, 2007). The BD-2N radio transmitters used have a functional range, conditional on weather conditions and the location of the transmitter, of approximately 200 meters, more than adequate for a linear beach environment approximately 50 m wide. Toads were radio-tagged and tracked from June 19th to August 16th, 2009 and from June 24th to August 27th, 2010.

Toads often shed their transmitters, especially early in the course of the two years of field work. Locations of shed transmitters were recorded by were not included in any data analyses.

Individual Marking

Toes of captured toads were clipped such that each toad had a unique combination of phalanges removed to allow for individual identification (Green, 1992). Not all individuals were clipped as manual matching of digital photographs (Kenyon et al., 2009) based on unique dorsal spot patterns specific to individuals proved an adequate alternative.

Radio-Tracking and Location Fixes

Toads were radio-tracked and located at least once each evening and once each day during periods of active radio tracking. Tracking was conducted with an H.A.B.I.T. Research HR2600 Osprey Receiver and Yagi 3-element antenna. The locations of toads were recorded using a Magellan Mobile Mapper 6 GPS unit and Mobile Mapper software.

In 2009 radio tracking took place between June 20th and July 2nd, July 8th and July 15th, July 21st and July 27th, July 30th and August 5th, and August 10th through August 16th. In 2010 radio tracking took place between June 24th and July 7th, July 22nd and August 6th, August 11th and August 27th. In 2010, data from opportunistic evening captures during a yearly population survey between May 3rd and June 11th were included in the location data set. Locations of animals were obtained by “homing-in” on radio signals as per White and Garrott (1990). Tracking continued until visual confirmation of either the toad or of its un-shed transmitter. Generally, by using the “homing-in” technique, and moving towards stronger radio signals, toads and/or toad attached transmitters could be located by eye. When radio signals saturated to 100% in close proximity to transmitters, folding the Yagi 3-element antenna allowed for very targeted and precise searches as this focused the radio receiver on small spatial areas directly in front of the now gun shaped antennae. If an exhaustive search for a toad did not reveal the exact location of an individual, this was noted and the strength of the radio signal, as a percentage, was used as an estimate of location confidence. Locations without visual confirmation but with radio signals approaching 99% were included in the location dataset. Data on fine scale habitat qualities for refuge locations could not be collected for these visually negative locations, however larger scale habitat information was recorded. Toads were generally active and mobile in the evening. During daylight hours toads were almost always found at rest in refuge sites.

Refuge Site Characteristics

At each refuge site for which the presence of a toad could be confirmed we recorded:

1) LOCATION AND TIME OF DAY with a handheld Magellan Mapper 6 Global Positioning System (GPS) unit running Mobile Mapper software. GPS coordinates were recorded as two dimensional points (X and Y only) in WGS 84 Datum, Universal Trans Mercator (UTM) zone 17N. Locations were automatically averaged over ten seconds with estimated error less than 1 m.

2) SLOPE – with a handheld adjustable carpenter's level approximately 25 cm in length

3) PERCENT BURIAL – by visual estimation, the degree to which toads were exposed or buried in loose sand or excavated burrows.

4) VEGETATION COVER- by visual estimation, a categorical estimate of percent vegetation cover in the immediate vicinity of refuge sites at three

spatial scales (circles of radius 0.1 m, 1m and 2m, centered on the refuge). At each spatial scale every refuge site was scored as either: Barren, 0 ; At least a single stem, 1; Up to ten percent cover, 2; Up to fifty percent cover, 3; Up to one hundred percent cover, 4; Up to two hundred percent cover, 5. When vegetation was structured into multiple layers (e.g. canopy, understory, low lying forbs and grasses) the sum of these vegetation layers was considered thus allowing for scores beyond one hundred percent cover.

Monitoring Thermal Properties of Refuge Sites

We installed twenty-three (23) iButton data loggers on three different dunes (Dune One: Easting: 551830 Northing: 4713854 ; Dune Two: Easting: 552201 Northing : 4713782; Dune Three: Easting: 552638 Northing: 4713698) to record air and substrate temperature every 3 minutes over a period of eighty four hours between 4:40 pm on August 23rd and 4:04 am on August 27th, 2010. At each of the three dune sites we installed loggers on vegetation free flat sections of beach and on similarly barren sloped fore-dunes. In each of these categories of refuge site we buried data loggers at shallow and deep depths (5 cm and 10 cm respectively). At vegetated sites, at which we did not discriminate slope, we also buried loggers at the same two depths. At each dune we also placed a single logger a hollowed out cave or burrow and left one logger to record air temperature. We did not record air temperature at site 2. These locations and depths were chosen based on two summers of observing toads at rest to serve as categorical representatives of typical refuge sites. No toads occupied these locations concurrent with the presence of the data loggers. On a marginally larger spatial scale, the dunes we chose were well frequented by toads throughout the course of 2010.

Landscape Characteristics: Mapping

We obtained LiDar (Light Detection and Ranging) images showing both bare earth and vegetation of the Thoroughfare Beach dune ecosystem courtesy of the Ontario

Ministry of Natural Resources, Vineland, Ontario. These aerial images of the study site were captured during flyovers made on April 13th and 14th, 2010. We also obtaned ARCMAP raster layers of digital elevation maps (DEM) of the study site for both bare earth and vegetation which had been processed by interpolating raw point data by kriging. As the beach landscape changes drastically with time, these maps were used only for analysis of the 2010 refuge dataset. Due to erosion of dunes and shifts in elevation it would not have been appropriate to use this information with the 2009 refuge data.

We used a Magellan Mobile-mapper to map the terrestrial extent of the beach by walking along the edge of the lake once in 2009 and each day of active field work in 2010. The 2010 waterlines were projected in ARCMAP 10 and manually transformed into a single approximately median waterline.

Landscape Characteristics: Processing

For 2010 we defined the area available for potential use of Fowler's Toads by projecting all day and nighttime captures of toads (n=1219) in ArcMap. A minimum convex polygon (Mohr, 1947) of occupied habitat for the entire group of animals studied was created. This polygon was further altered by matching its southern, lakeside edge, with the waterlines described in the previous section of our method. The western and eastern edges of this polygon where limited in extent to the section of beach for which we had mapped the waterlines and dunes. This required that a very small portion of the complete refuge site data set be removed.

The minimum convex polygon of all occupied habitat was used to delineate the spatial extent of a variety of secondary raster sets required for analysis. A raster containing continuous to the waterline data was created using the Euclidian Distance function in ArcMap 10. A raster containing continuous slope data was created using the elevation raster and the Slope function in ArcMap 10. Lastly a categorical raster of vegetation cover was created using the Raster Calculator function. We subtracted the bare earth elevation raster data from the vegetation raster data and then transformed all values below 0.4 m to category 0 (bare), all values between 0.4 m and 1.5 m to category 1 (low level vegetation) and all values above 1.5 m to category 2 (trees and canopy vegetation).

Maximum Entropy (MaxEnt) Analysis

Maximum Entropy (MaxEnt) analysis was performed using MaxEnt 3.3e, as hosted by http://www.cs.princeton.edu/~schapire/maxent/ as of June 8th, 2011. We transformed each relevant raster layer into ASCII format and used these as our "Environmental Layers". A shapefile of 2010 refuge site locations was used as our "Samples". Our MaxEnt model included three continuous parameters (Elevation; Distance to Waterline; Slope) and one categorical parameter (Vegetation Class). We conducted 1000 replicates each with 10,000 background sampling points using the Bootstrap replicated run option. We trained the model with 65% of our refuge data set (270 of 415 refuge site locations) and tested the model with the remaining one third (35% or 145 locations). We used the logistic output option. Only data from 2010 was included in this analysis.

Maximum entropy modeling produces a Receiver Operator Curve (ROC) as its primary output. Receiver operator curves are a graphical representation of threshold independent measure of a model's ability to discriminate between presences and absences. They plot the relationship between sensitivity (true positives as a proportion of the sum of true positives and false negatives) and 1-specificity (true negatives as a proportion of the sum of true negatives and false positives) across all possible threshold values derived from a confusion matrix of predicted and actual test data (Fielding and Bell, 1997).

Seasonal Shifts in Refuge Site Characteristics

We investigated the possibility that characteristics of refuge sites shift during the season by using t-tests to compare mean elevation and distance from the waterline data for refuge sites based on three categories of season, late spring (June 25th to July 6th), mid-summer (July 23rd to August 5th) and late summer (August 12th to August 26th) for the 2010 refuge site data set.

RESULTS

General Observations of Refuge Site Use

Toads were able to use almost any location within the beach and dune complex as a refuge site. We found toads at refuge in thickly vegetated back dunes areas, more than 50 metres removed from the shoreline. We also found toads making use of flat beaches, totally devoid of vegetation, 2 meters from the lake. A great degree of behavioural plasticity while in refuge sites was also observed, ranging from full burial as deep as 10 cm below the surface to full exposure with little evidence of any digging. In general, however, refuge placement and behaviour were relatively predictable and interrelated.

Toad were typically found at refuge in the eroding face of the fore dune. The animals readily made use of the loose sand that characterizes these areas and tended to be fully buried. Vegetation and woody debris were often incorporated into refuge sites. Toads hid under broad leaved plants, amidst clumps of grass, and inside or under logs. We occasionally found toads in burrows they had presumably carved out themselves in vertical cliff faces, hidden behind a veil of beachgrass roots. On two occasions we found animals sharing burrows.

Daytime Refuge Behavior

On 668 occasions we tracked toads to refuge sites: 223 in 2009 and 445 in 2010. Almost half of these (321) did not result in a visual confirmation of either toad or transmitter. In 31 cases toads were active, but in all but one of these cases the toads had been disturbed by the presence of researchers. Thus, of 668 daytime observations, an adult Fowler's Toads was found active during daylight hours only once.

Burial Behavior

We recorded data on burial behavior on 232 occasions (Figure 2). More than half the time (127 of 232 observations) toads were 100% buried. Most of the time this was in loose sand but we also scored toads in hollowed out burrows or caves (20 observations) as 100% buried. On 146 occasions toads were found 91% or more buried. The inadequacy of our burial measurement system became apparent towards the end of the field work when we found toads 100% buried in loose sand in the floor of a hollowed out burrow or cave. On only 12 occasions did we find toads with their dorsal surfaces entirely exposed, typically resting in a hollowed out depression (as described by Hadfield, 1966).

We found some relationship between the percentage of burial and the time of day (Figure 3). Toads which fully exposed were never found between 12:00 pm and 16:00 (minutes 720 and 960). A marginal trend towards full burial at midday was found by quadratic regression. ($y = 0.000264x^2 + 0.4414x + 88.453$; Multiple $R^2 = 0.1238$; $F_{2,206} = 14.56$; $p < 0.001$).

Slope at Refuge Sites

We recorded slope data at 213 refuge sites (Figure 4). The most commonly observed slope was 30 ° (43 of 214 observations; 20%). Sites with a wide variety of slopes were used by toads seeking refuge. A roughly bimodal distribution of refuge sites slopes was observed, with peaks at 10° and 30°. In some cases measuring slope was not possible or meaningful. Often toads burrowed into the vertical faces of small (roughly 50 cm high) sand cliffs, carving out small, flat burrows. In one sense the slope at the refuge site in these cases is zero, as the inside of the burrow is flat, in another sense the slope at these sites is 90°. We did not record slope values in these cases.

Vegetation and Woody Debris at Refuge Sites

We made observations of vegetation cover at 249 refuge sites (Table 1). At the smallest spatial scale, a circle of 10 cm in radius (a roughly toad sized measure), approximately a third of the time (72/249; 28.9%) these areas were completely void of living vegetation or woody debris. The remaining 71.1 % of the time vegetation or woody debris was an immediately proximal component of the refuge site. At the intermediate scale, a circle 1m in radius, the most commonly observed category of vegetation cover was Up To 50% cover, occurring half of the time (123 of 246; 50.0%). Only 18 of 246 refuge sites were completely barren of vegetation or cover objects at this spatial scale. At the broadest spatial scale, a circle of 2m in radius, Up to 50% cover was again the most commonly observed degree of vegetation cover, comprising 58.1 % of records (141 of 247).

Burial and Vegetation Cover

Toads in vegetated areas tended to bury themselves less completely than those at open sites (Figure 5). We found a negative linear relationship between percentage of dorsal surface buried and the percentage of vegetation cover at the smallest spatial scale. ($r^2 = 0.174$; $y = -0.3473x + 92.643$; $F_{1,230} = 49.63$, $p \ll 0.0001$).

Since we had already detected an effect of time on burial behavior, we performed a multiple regression which included time (expressed as minutes past midnight), time^2 and vegetation cover at all three spatial scales as predictors. Vegetation cover at 2m was not of predictive value and we report here a reduced model including vegetation cover at only 0.1m and 1m. All predictors (time, time^2, and both vegetation cover measures) were and significant and useful in predicting burial behavior (Table 2). This model predicted 22.4% of the variation in percent burial, performing better than models which considered time of day or vegetation cover alone.

Thermal Properties of Dunes and Putative Refuge Sites

Air temperature varied between 12.5° C and 36.5 ° C over a period of eighty four hours between 4:40 pm on August 23rd, 2010 and 4:04 am on August 27th. Dune and beach temperatures varied between 13°C and 48.5° C over the same period of time. The hottest temperatures (48.5 ° C) were recorded by probes buried at shallow depths (~5 cm) on dune slopes free of vegetation between 1:34 and 1:37 pm on August 26th just after air temperature at the same dune peaked at 34.5 ° C.

Temperatures in shallow putative refuge sites free from vegetation on dune slopes and on the flat beach both met or exceeded the critical thermal maxima (CTM) of 36.5°C previously determined for heat acclimated Fowler's Toads (Brattstrom and Lawrence, 1962).

Considering only daylight hours (7 am to 9 pm), when toads were most likely to be found at rest in refuge sites, median temperatures (Figure 6) were coolest in deeply buried (~ 10 cm) vegetated sites (median temperature = 24.67°C) and in hollowed out burrows (median temperature =24.83°C). Across this same time period deeply buried vegetated locations were the least thermally variable, ranging across 6°C (21.33 – 27.33 °C). Shallow barren sites on slopes were most variable (range = 26.33°C; 19.00 – 45.33 ° C). We found relatively little difference in thermal properties between each of the three dunes, separated by a few hundred meters, (median temperatures: 27.5°C; 26 °C; 27 ° C) indicating that thermal variation is due largely to differences habitat qualities at relative small spatial scales and not to broader spatial scale variation in habitat characteristics (Figure 7).

Maximum Entropy Model

Maximum Entropy analysis (Elith et al., 2011; Philips et al., 2006) of GIS layers representing toad refuge locations, dune elevation, dune slope, distance from waterline and vegetation cover indicated that refuge sites are not placed at random, with elevation was the most important factor in predicting refuge site locations while vegetation cover was of almost no predictive value. Contrarily, field observations of toads in refuge sites almost never were made without vegetation less than a meter away.

The receiver operator curve produced by 1000 bootstrapped replicates of our MaxEnt model (Figure 8) incorporating elevation, distance to the waterline and slope as continuous variables and vegetation cover as a categorical variable a mean area under curve (AUC) of 0.851 and a standard deviation of 0.009. The expected AUC for a random null model is 0.5.

Elevation was the most important parameter, with a weight of 53.4% according to permutation importance. The distance from the waterline was the second most important, weighted at 35.7%. Slope was responsible for 8.1% of the model's predictive capacity while vegetation was of limited value, weighted at 2.8%. Permutation importance quantifies the predictive value of a parameter by exchanging the data values for this parameter with random numbers and standardizes the loss in predictive power of the entire model, as a relative reduction in the area under the receiver operator curve.

Probability of presence of a toad at refuge was highest between elevations of 176 and 177 m, waterline distances of roughly 29 m and slopes 30° or greater (Figures 9 through 11). The terrestrial area used by toads during the period of study, as delineated by a minimum convex polygon of all locations for all individuals, ranged in elevation from 173.63m (roughly Lake Erie water level) to 183.63 m, in distance to the waterline from 0m to 72.16m and in slope from 0° to 62.30°.

Removal of variables through jackknifing illustrated that the best single parameter model was constructed using elevation only. Removing the waterline distance parameter had the greatest effect on reducing AUC values for multi-parameter models, indicating the least redundancy due to correlation with other parameters (Figure 12). Models created lacking solely slope or vegetation performed almost as well as the complete four parameter models.

Seasonal Shifts in Refuge Site Characteristics

Mean refuge site distance to the waterline increased between the late spring (mean = 27.27 m) and late summer (mean=31.20 m; *t*-test: p=0.0003) indicating that refuge site characteristics may shift with seasonality especially in preparation for hibernation which is believed to preferentially occur in back dune locations (Figure 13). The same tests performed on elevation data detected no significant difference between mean elevation at refuge sites between late spring and late summer.

DISCUSSION

Refuge behavior of toads

Our results support previous evidence (Clarke, 1974; Green, 1989) that adult Fowler's Toads are active almost exclusively at night and spend daylight hours at rest. These toads are generally, but not necessarily, buried during these periods. We found some evidence that the degree of burial depends both on the time of day and on the degree of vegetation cover immediately surrounding refuge sites. Daytime dune temperatures in excess of the critical thermal maximum for toads imply that full exposure or shallow burial during the hottest part of the day is not a physiologically viable strategy. Toads can thus avoid sub-optimal by expending energy to dig deeper into the dune sand or by expending energy to move to cooler locations.

Since overland motion is less energetically costly than digging (Seymour 1973; Walton, 1988; Walton and Anderson, 1988) it seems counterintuitive that toads tend to be found fully buried more often than hiding on the surface within the shadows of vegetation. This, of course, considers only thermoregulation and not hydro-regulation or predator evasion, both of which may also be driving refuge site choice and behaviour at refuge sites. Burial is almost certainly favorable both in maintaining water balance and evading predators. Thus the benefits of burial may be threefold. Even so, energetic conservatism might only play a role when food is limiting. This does not seem to be the case, however, at Long Point, where the population is very small relative to historic abundance and invertebrate prey are available in vast quantities.

Maximum Entropy Model of Habitat Use

Our radio tracking data show that refuge sites of Fowler's Toads are not randomly distributed in space throughout the dune ecosystem at Thoroughfare Beach. The most likely location for toad refuge sites, based on our MaxEnt model, is at moderate elevation, between 176 and 177 m above sea level, and at a moderate distance from the waterline, close to 30 m. The same model predicts terrain with a slope of roughly 30° or greater as most likely to serve as refuge habitat.

Our MaxEnt model matches the field measurements of refuge site slope. Agreement between these two methods is promising given the differences in scale of measurement. Field measurements were done on a very finely grained scale, using a 20x3 cm hand level. The slope values used in the MaxEnt model derived from elevation values taken from raster cells of 50 cm x 50 cm, a much broader spatial grain.

In contrast to our field observations, vegetation is not important or informative in our MaxEnt model. This may be an artifact of our method; our categorization of vegetation cover was crude at best. Comparing elevation values from Bare Earth LiDar to Vegetation LiDar derived rasters often resulted in negative values. This implies that the vegetation at these sites is less elevated than the bare ground, which is clearly not possible. There are numerous possible causes for this. LiDar relies on extremely high point sampling rates to generate reliable landscape scale data. It is not likely, however, that the bare earth measurement on the spatial scale of a single herbaceous plant and the vegetation elevation would be derived from the exact same location. Once the data were collected, the interpolation of points into rasters generated some error due to spatial averaging. This could also explain this discrepancy. Transforming the negative values to zeros and including a broad range of positive values (up to +0.3m) in our bare vegetation class (category 0) almost certainly compromised our analysis in this regard.

Regrettably we did not collect data on random, toad-less sites in order to statistically compare vegetation cover between occupied and unoccupied locations. Alternatively our method for categorizing vegetation cover may have over-estimated the amount of vegetation which was functionally relevant to a toad at rest. Vegetation analysis at larger spatial scales (1m and 2m radii circles) inevitably included heavily vegetated dune tops when refugia were located on the fore dune face. Thus in many cases our estimates of vegetation cover are arguably inflated and obscure the true vegetation structure at refuge sites as well as the distinct dune top to shoreline vegetation gradient. At the smallest spatial scale (0.1 m radius circle) this should not be an issue, but we still may be assuming that vegetation not immediately associated with toads plays some role in determining microhabitat suitability. For many other species vegetation is an important component of refuge habitat site selection (Denton and Beebee, 1993; Schwarzkopf and Alford, 1996; Spieler and Linsenmair, 1998; Griffin and Case, 2001; Sanchez et al., 2010; Yu et al., 2010).

Physiological Consequences of Preferred Refuge Sites

Most of previous literature suggests that refuge sites serve to protect amphibians from extremes of heat and dryness (Hoffman and Katz, 1989; Cohen and Alford, 1996;Schwarzkopf and Alford 1996; Parris 1998). It is therefore intriguing that our MaxEnt model indicates that Fowler's Toads preferentially select refuge sites in locations which are the hottest and most thermally variable (Fig. 6). There are two possible interpretations of this. The first is that temperature regulation is less important that locating refuge sites which guarantee safety from wave action. Dune slopes are typically well removed from the shoreline and would afford a very safe location for resting.

The second is that Fowler's toads are actively seeking warm temperatures which will maximize growth rates. Temperature interacts with growth and development of amphibians (Hutchison and Dupré, 1992) and in some cases only exposure to high temperatures results in measurable growth (Browne and Edwards, 2003). Fat depostition and growth for Fowler's Toads is maximal close to 21°C (Bush, 1963), though a more rigorous test on Western Toads cites 27°C (Lillywhite et al., 1973). Terrestrial juveniles emerge from natal ponds no earlier than July 1st and will certainly be in winter refugia by October 1st. At most ninety days are available for growth and development before entering winter refuge sites. Toadlets which are able to reach reproductive size in a single season have a huge fitness advantage over those animals that require two seasons to become reproductively functional. Seeking out hot sites may be a strategy employed by northern amphibians to maximize growth rates given an incredibly short growing season. In some cases northern populations of amphibians have faster growth rates than southern populations when seasonal growth rates are corrected for number of days (Hemelaar 1988) though the mechanism behind this phenomenom is as yet undescribed. Elevated body temperatures linked to elevated substrate temperatures may help optimize digestion (Hadfield, 1966) and growth. In addittion fed toads do prefer warmer substrates than starving toads (Witters and Sievert, 2001). Thermophily by inacitve toads is supported by a few studies illustrating that active toads operate at lower body temperatures than inactive toads (Hadfield, 1966; Moore and Moore, 1980).

Implications for Conservation

Our results immediately provide conservation planners with valuable information needed to delineate and protect refuge habitat at Long Point and elsewhere within the Canadian distribution range of Fowler's Toads. It is not clear, however, exactly how broadly applicable our findings are. The two other Canadian populations are genetically distinct from the toads at Long Point (Smith and Green, 2004) and exist within potentially radically different landscapes (COSEWIC, 2010). It is because of this that we cannot argue, with any real certainty, that the behavior of Fowler's toads at other locations will be the same. This could be resolved by comparing field observations of toads at refuge from other locations with our Thoroughfare beach data set. More sophisticatedly we could train a MaxEnt model on our current dataset and test the model against an entirely new digitized landscape and sample of refuge locations.

Should digital elevation models of habitat elsewhere in the range become available this option would be viable and almost certainly fruitful. Complimentary to our concerns of the spatial limits to the applicability of our model of habitat use is a similar temporal concern. We studied Fowler's Toads for two years and within year coverage was patchy at best. For the most closely monitored toads, we approached between one third and one half of the refuge locations used during the post breeding season.

In conclusion, we suggest that, as very specific components of the beach dune ecosystem are used preferentially by Fowler's Toads, conservation efforts should be focused on these elements, even when the integrity of the beach dune system at large may be compromised.

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TABLES

TABLE 1. Comparison of vegetation cover at *A. fowleri* refuge sites at three different spatial scales. Roots or debris were only scored when found incorporated in refuge sites and appear only at the smallest spatial scale, a circle of roughly toad size radius, 10 cm. n=249, 246 and 247 respectively.

Vegetation Cover	Spatial scale		
	0.1 m	1 m	2 m
Barren	0.289	0.073	0.057
Single Stem (~1%)	0.108	0.069	0.036
Up to 10% Cover	0.112	0.297	0.279
Up to 50% Cover	0.145	0.500	0.571
Up to 100% Cover	0.149	0.057	0.053
Up to 200% Cover	0.008	0.004	0.004
Roots or Debris	0.189	NA	NA
sample size (*n*)	249	246	247

TABLE 2. Coefficients and significance levels for multiple regression of predictors of burial percentage. Multiple r2: 0.2374. Adjusted r2: 0.224. F-statistic: 17.67 on 4 and 337 degrees of freedom. *P*=1.1216e-12.

Parameter	Coefficient	Standard Error	t value	P(r>|t|)
Intercept	-2.186	38.098	-0.057	0.954
time	0.252	0.090	2.803	0.006
time2	-0.0002	<0.0001	-2.944	0.004
Vegetation Cover (0.1m)	-0.258	0.0547	-4.730	<<.0001
Vegetation Cover (1.0m)	-0.195	0.0827	-2.355	0.01937

TABLE 3:

Analysis of variable contributions derived from Maximum Entropy evaluation of habitat use. Percent contribution indicates the effect of the variable on training gain averaged over each iteration. Permutation importance shows the relative loss of area under curve (AUC) of the receiver operator curve when data for each variable is randomized rather than drawn from the existing data set, averaged over each iteration.

Variable	Percent Contribution	Permutation Importance
Elevation	48.5	53.4
Distance to Waterline	26.4	35.7
Slope	17.3	8.1
Vegetation	7.7	2.8

FIGURE LEGENDS

Figure 1:

Anaxyrus fowlei with a radio transmitter attached by surgical tubing harness as per Bartelt and Peterson (2000). Beige surgical tubing is threaded with filament to which the transmitter is attached. Photo by Jessica Middleton.

Figure 2:

Burial frequency distribution of *A. fowleri* while in refuge sites. Observations of toads were made in both 2009 and 2010. Percentage burial bins along the x axis are for 10%. n=232.

Figure 3:

Quadratic regression of time of day when observation of toads at refuge were made against percent burial. n=232. (y = -520.21x2 + 601.42x – 79.307. r2 =0.11. p=1.218e-06)

Figure 4:

Frequency distribution of slope at refuge site for *A. fowleri*. Slope bins along x axis are by 5°. n=214.

Figure 5:

Linear regression of percent burial at refuge sites by *A. fowleri* as predicted by vegetation cover. Cover values are transformed from categorical estimates to percentages. (r^2 = 0.1775; y = -0.3473x + 92.643; F-statistic: 49.63 on 1 and 230 DF, p-value: 2.136e-11; n=232).

Figure 6:

Boxplots of mean temperature (n=3 for each refuge site category) at putative refuge sites during daylight hours (7am to 9 pm) over three July days in 2010. The horizontal red line indicates the critical thermal maximum of 36.5°C (CTM) for *A. fowleri* as determined by Brattstrom and Lawrence (1962).

Figure 7:

Boxplots of mean temperature of all categories of putative refuge sites (n=7) at three distantly separated (~500m) dunes during daylight hours (7am to 9 pm) over three July days in 2010.

Figure 8:

Mean receiver operator curve from 1000 replicates of a maximum entropy analysis of habitat use for four parameter model incorporating: elevation (continuous), distance from waterline (continuous), slope (continuous) and vegetation (categorical). Area under curve=0.851; +/- 1 standard deviation in blue; null prediction of 0.50 in black.

Figure 9:

Maximum entropy response curve (red line) of solely elevation. Elevation (m) along x axis and logistic probability of refuge site occurrence on y axis. Variation across 1000 replicates appears in blue. Peak probability of occurrence is at approximately 176.75m.

Figure 10:

Maximum entropy response curve (red line) of solely distance to waterline. Distance to waterline (m) along x axis and logistic probability of refuge site occurrence on y axis. Variation across 1000 replicates appears in blue. Peak probability of occurrence is at approximately 29m.

Figure 11:

Maximum entropy response curve (red line) of solely slopE. Slope (°) along x axis and logistic probability of refuge site occurrence on y axis. Variation across 1000 replicates appears in blue. Peak probability of occurrence is at approximately 31° with much variation at greater slopes.

Figure 12:

Jackknife plot of area under curve (AUC) values for refuge site occurrence models based on all variables (red bar, bottom), each variable in isolation (dark blue bars, upper half of each variable) and without each variable (light blue bars, lower half of each variable). Area under receiver operator curve values (AUC) appear along the x axis with variable along y axis.

Figure 13:

Boxplots of distance to the waterline for refuge sites by season. Distance to the waterline (m) on Y axis. n=133; 258; 145 respectively.

FIGURE 1

FIGURE 2

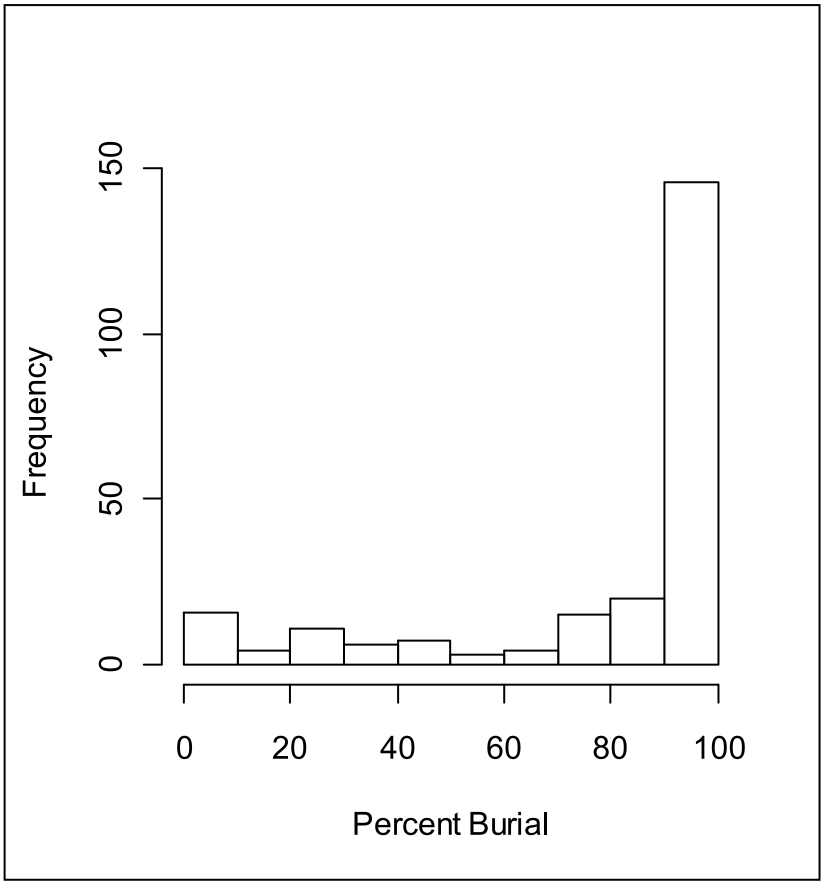


FIGURE 3

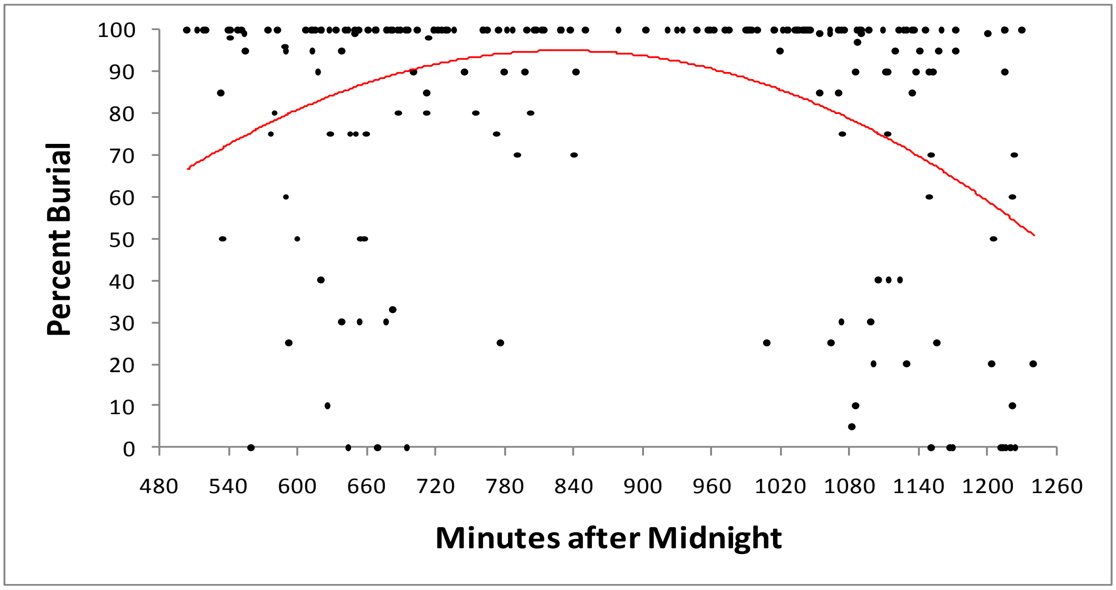

Percent Burial
100
90
80
70
60
50
40
30
20
10
0
480
540
600
660
720
780
840
900
960
1020
1080
1140
1200
1260
Minutes after Midnight

FIGURE 4

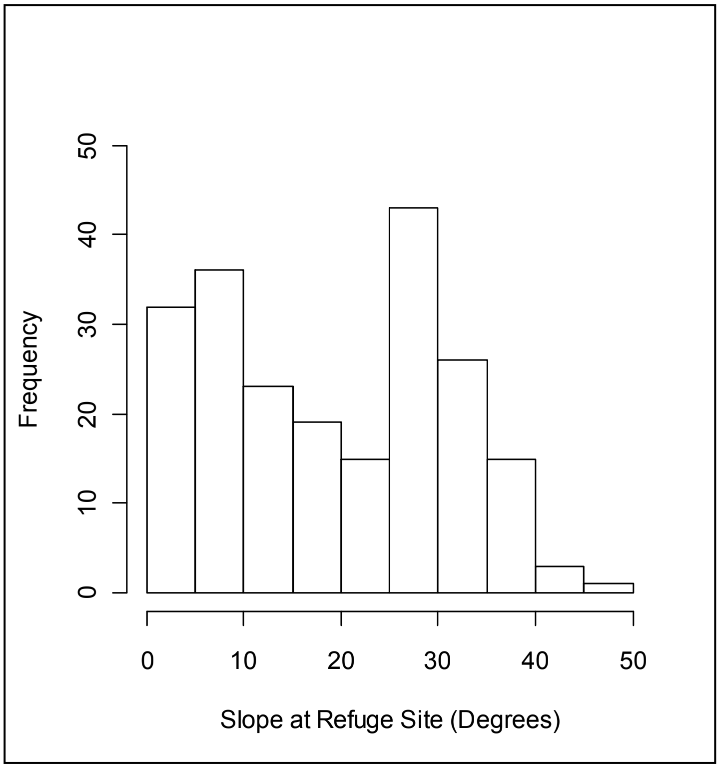

Frequency
0
10
20
30
40
50
0
10
20
30
40
50
Slope at Refuge Site (Degrees)

FIGURE 5

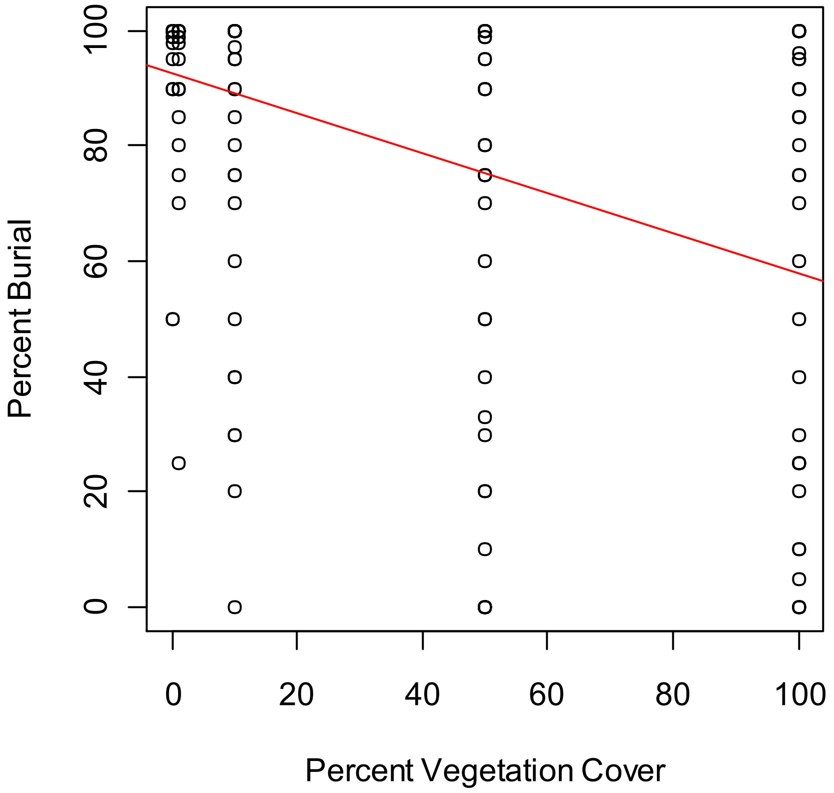

Percent Burial
0
20
40
60
80
100
Percent Vegetation Cover
0
20
40
60
80
100

FIGURE 6

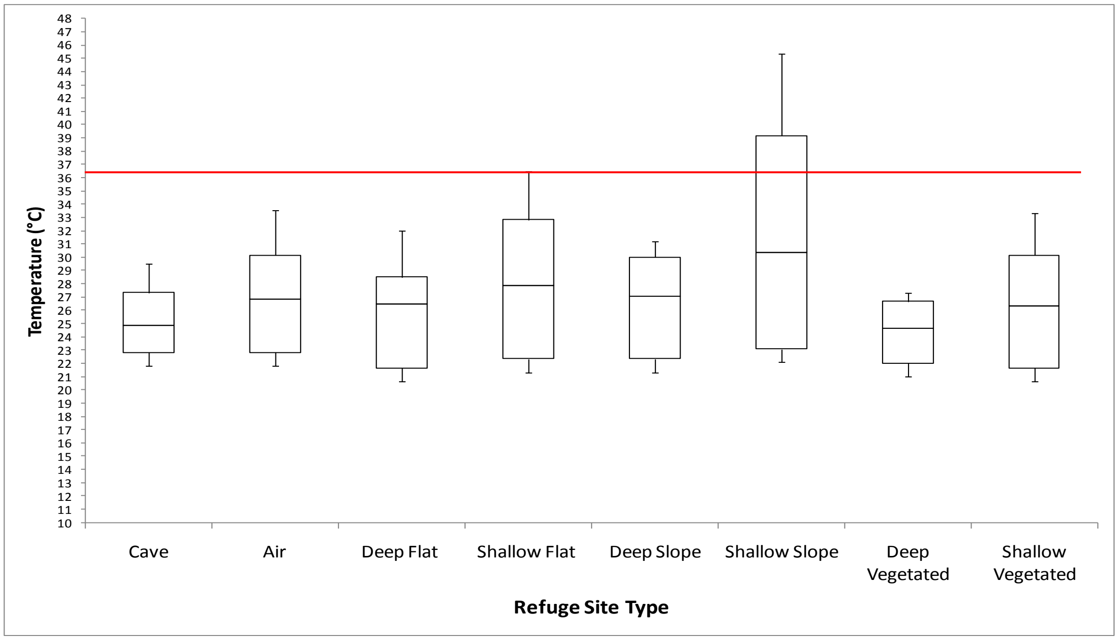

Temperature (°C)
48
47
46
45
44
43
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
Cave
Air
Deep Flat
Shallow Flat
Deep Slope
Shallow Slope
Deep Vegetated
Shallow Vegetated
Refuge Site Type

FIGURE 7

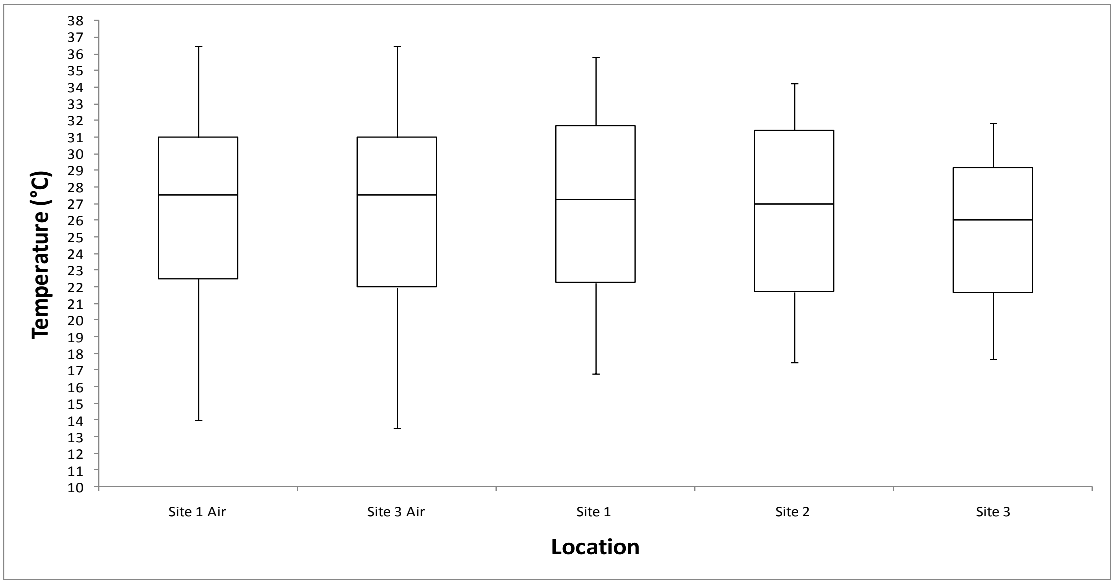

38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
Temperature (°C)
Site 1 Air
Site 3 Air
Site 1
Site 2
Site 3
Location

FIGURE 8

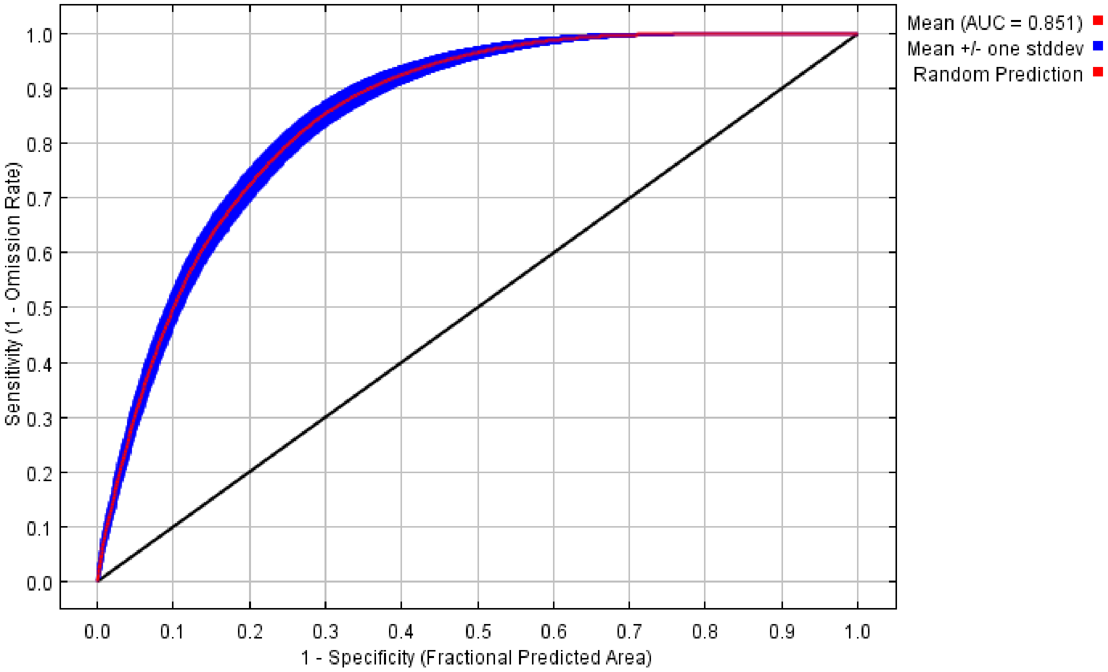

Mean (AUC = 0.851) 🟥
Mean +/- one stddev 🟦
Random Prediction 🟥
Sensitivity (1 - Omission Rate)
1 - Specificity (Fractional Predicted Area)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0

FIGURE 9

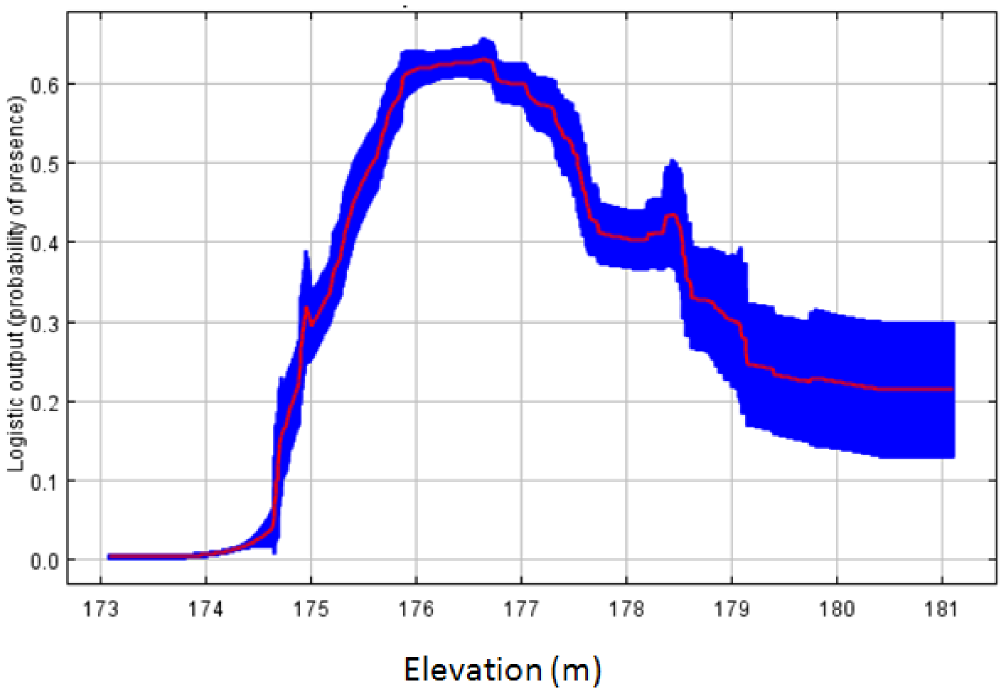

Logistic output (probability of presence)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
173
174
175
176
177
178
179
180
181
Elevation (m)

FIGURE 10

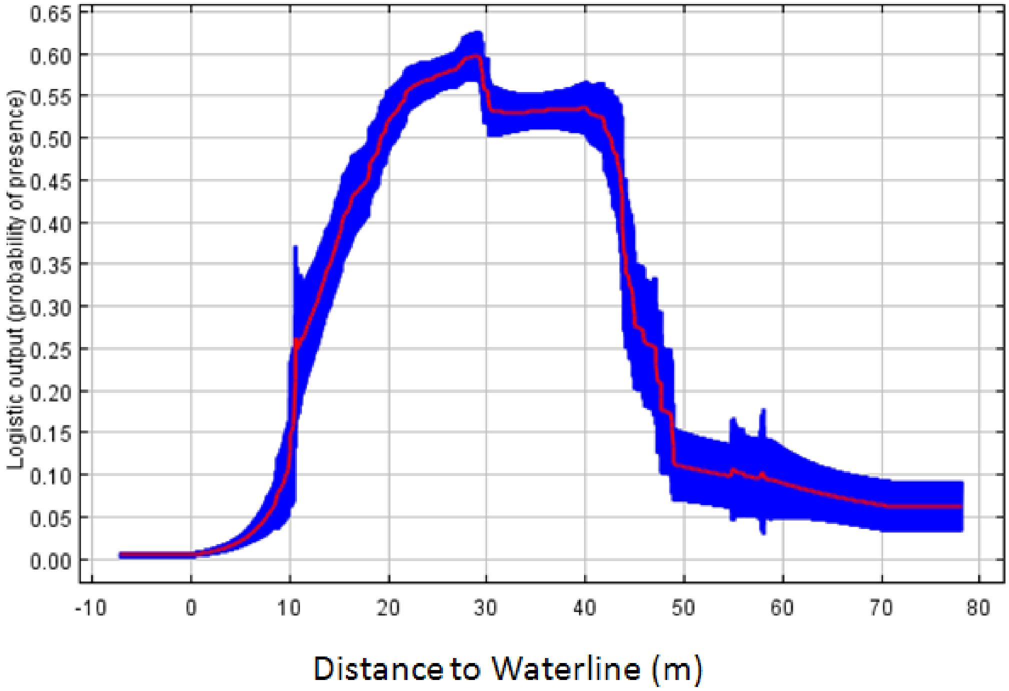

Logistic output (probability of presence)
0.65
0.60
0.55
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
-10
0
10
20
30
40
50
60
70
80
Distance to Waterline (m)

FIGURE 11

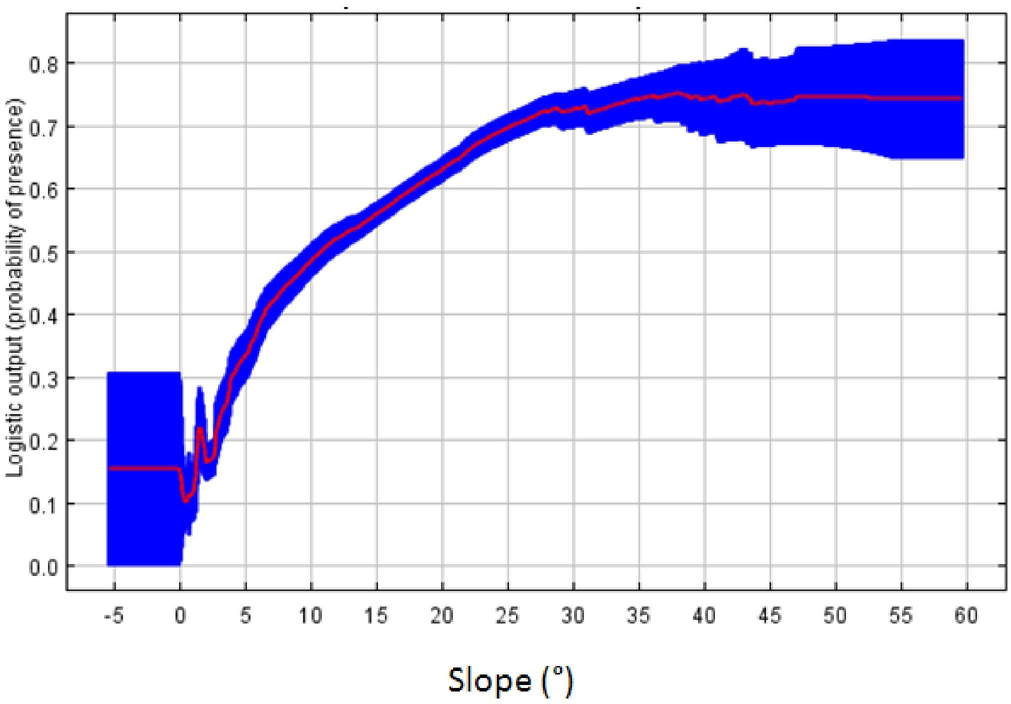

Logistic output (probability of presence)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
-5
0
5
10
15
20
25
30
35
40
45
50
55
60
Slope (°)

FIGURE 12

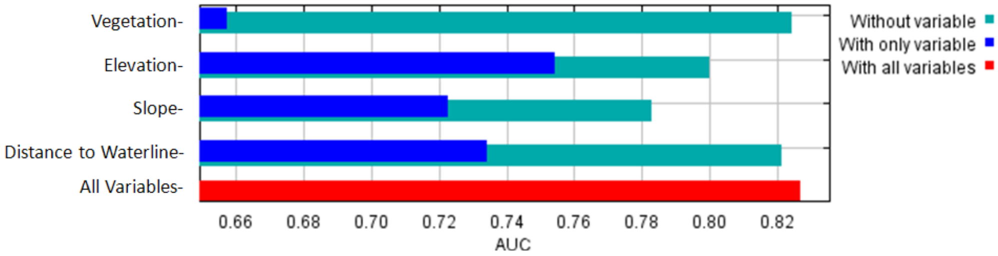
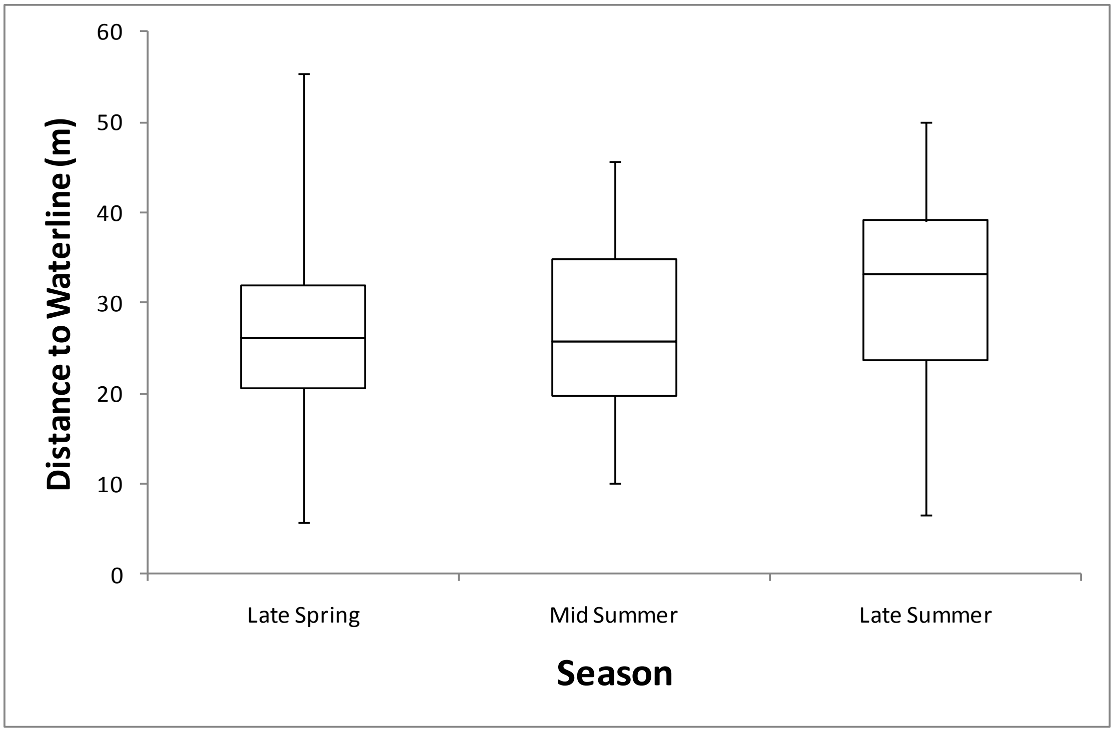

Vegetation-
Elevation-
Slope-
Distance to Waterline-
All Variables-
Without variable
With only variable
With all variables
0.66
0.68
0.70
0.72
0.74
0.76
0.78
0.80
0.82
AUC

FIGURE 13


60
50
40
30
20
10
0
Distance to Waterline (m)
Late Spring
Mid Summer
Late Summer
Season

CHAPTER THREE: Terrestrial Refuge Site Fidelity

CHAPTER THREE LINKING STATEMENT

Philopatry, the tendency for individuals to return to previously occupied locations repeatedly through the course of their lives can profoundly affect an individual's experience of space around them, the use of habitat and the dynamics of populations. . In chapter three I assess the degree to which Fowler's Toads are philopatric towards refuge sites on a daily time scale. Fidelity to breeding sites and terrestrial foraging areas between seasons is well documented in Fowler's Toads. Refuge site fidelity may be the mechanism driving this phenomenon. Site fidelity can influence both the qualities habitats which are selected for use (CHAPTER ONE) and the quantity of space used in a lifetime (CHAPTER THREE).

ABSTRACT

The tendency to cyclically return to previously used areas may provide benefits to individuals engaging in such behavior across multiple timescales. Numerous amphibian taxa exhibit a high degree of site fidelity, returning to familiar locations even when experimentally displaced distances well beyond the extent of their usual movements. I tested the hypothesis that Fowler's Toads exhibit no fidelity to daily refuge sites given the ample supply of such locations in the landscape of study and the costs expected with a return to origin rule. Toads were found to exhibit a high degree of site fidelity towards refuge sites, generally returning to within 10 meters of the previous days rest site, despite intervening foraging movements far greater in magnitude. This behavior may be a mechanism for maintaining proximity to breeding and over-wintering habitats used on broader time scales than foraging areas and daily refuge sites.

INTRODUCTION

Refuge sites provide shelter from inhospitable environmental conditions (Wells, 2007), aid in predator avoidance (Roznik and Johnson, 2009) and may have a stabilizing effect on population dynamics (Berryman and Hawkins, 2006). Fidelity to a particular nesting or refuge site can be a key component in an individual animal's behaviour. Animals that periodically return to such sites tend to occupy discrete spatial locations, or home ranges (Burt, 1943), and thus the nest or burrow acts as a central focal attractor from which all its normal movements originate and terminate (Borger et al., 2008).

From the formulation of Switzer (1993), who defines site fidelity as the "return to and reuse of a previously occupied location", site fidelity (or philopatry), depends on an animal's movement capabilities and on the availability of habitat. We propose the term pseudo-philopatry for situations when movement or habitat limitation result in apparent site fidelity. When animals are movement limited they cannot displace themselves from a particular location so they do not return to re-use previously occupied locations (Switzer, 1993), they simply never leave, nor do they have the capacity to do so. When animals are habitat limited there are no other suitable locations to occupy, so the re-use of a particular location is not a matter of choice (Bohnsack, 1989). Thus we consider site fidelity as the return to and reuse of a previously occupied location with that caveat that the opportunity to change locations must exist.

Benefits of site fidelity include increased rates of resource acquisition and decreased rates of predation resulting from familiarity with the landscape (Hestbeck et al., 1991). Returning to a familiar site will incur costs related to movement which should be proportional to distance. The lost opportunity of acquiring a higher quality location than currently occupied can also be considered amongst the costs, though this will depend heavily on the environmental context (Switzer, 1993).

The tendency for amphibians to remain in the same location and return to natal or home areas when displaced is well documented (Wells, 2007). Many amphibian species exhibit high degrees of fidelity to refuge sites, breeding territories, home ranges or foraging sites (Hoffman et al., 2010; Oromi et al., 2010; McVey, 1981; Ringler et al., 2009; Landreth and Ferguson, 1967; Crump, 1986; Watson et al., 2003; Durham and Bennett, 1963; Brattstrom, 1962; Sinsch, 1992). Widespread evidence for amphibian philopatry comes from both observational studies, which often report the presence of individuals in the same location year after year (Clarke, 1974) and from relocation experiments, in which homing abilities are tested after animals are artificially transplanted in foreign sites, sometimes taking years to return home owing to the great distances they have been displaced (Twitty, 1966). In some species nomadic behavior has been described, and its expression is linked to environmental conditions. During the wet season, when water is abundant, wandering movements increase (Schwarzkopf and Alford, 2002). This fits the expectations of theory which predict the expression of site fidelity to vary with the stability, heterogeneity and quality of the environment (Switzer, 1993).

Fowler's Toads (*Anaxyrus fowleri)* are generally nocturnal as adults, occupying terrestrial refuge sites during daylight hours and emerging from them after dark to engage in foraging (Hadfield, 1966; Green, 1989; CHAPTER TWO). Although they are thought to exhibit a high degree of site fidelity to both terrestrial foraging (Smith and Green, 2006) and aquatic breeding areas (Clarke, 1974; Breden, 1988) between seasons, the degree to which these toads return to refuge sites on a daily basis is not known. Refuge behavior may take place in a wide variety of locations but generally involves sites which have ample loose sand to facilitate burial (CHAPTER TWO). During the post breeding season Fowler's Toads occupy beach dune habitats (Green, 1989; COSEWIC, 2010) and prefer the eroding face of sand dunes for refuge seeking behavior (CHAPTER TWO). This component of the dune system is available anywhere there is a dune and thus the number of potential refuge sites is nearly unlimited, relative to the size and spatial needs of the toads.

If nighttime foraging movements result in displacement from the previous day's refuge site, then philopatry will have an energetic cost proportional to the magnitude of the return movements. These costs make it disadvantageous for toads to exhibit site fidelity and thus we expect that fidelity to refuge sites on a daily basis should not be expressed.

We located Fowler's Toads while they were using daytime refuge sites and also while actively foraging and moving during evenings. In order to test the hypothesis that toads do not exhibit fidelity to refuge sites on a daily basis we compare the distances between refuge sites used on sequential days with the distances between active toads in the evening and the refuge sites they had used earlier the same day.

MATERIALS AND METHODS

Radio tracking and location data

Radio-tracking protocols and data collection are described fully in the method of chapter two of this thesis.

Quantification of movements

We used the Animal Movement tool in the Hawth's Tools extension for ARC MAP 9.3 to compute distances between successive locations for Fowlers Toads. From these data we produced estimates of movement capabilities based on refuge site to nighttime foraging site movements for the same day (i.e. DAY to NIGHT) and refuge site to refuge site for subsequent days (i.e. DAY to DAY).

Testing fidelity to refuge sites

To test for fidelity to refuge sites we used a Kolmorgorov-Smirnov test to compare the distribution of single day refuge to refuge displacements (DAY to DAY) with the distribution of displacements between daytime refuge sites and nighttime foraging locations (DAY to NIGHT). We expected that if toads show no fidelity to their refuge sites then these two distributions should be equal. We also tested for possible effects of time since evening emergence (estimated to occur at 9 pm) on foraging displacement from daytime refuge site through linear regression.

RESULTS

Field observations

Toads were very regularly found using the same shelter sites repeatedly for periods as long as a week. In some cases this was more apparent than others, for example, when woody debris or hollowed out burrows and caves on the side of eroding dune faces were used. When these sorts of locations were used it was possible to confirm that that toad had indeed returned to the exact same site. When toads instead took refuge by digging into loose sand it was more difficult to confirm that an animal had in fact returned to precisely the same place as piles of sand are less discrete locations than burrows. In these situations we relied on distances between refuge sites to estimate the degree of site fidelity. Even when toads did not return to exactly the same location they tended to return to the same area or dune site on a daily basis. In many cases larger scale movements away from sites of repeated use were eventually followed by a return to the old refuge area a week or so later on in the season. This is evidence that fidelity to terrestrial refuge sites operates on multiple time scales.

Detection of short distance movements

It is worth noting that our ability to detect short distance movements which are less than 10 m distant from the previous location occupied by a toad is compromised by the use of handheld GPS units with spatial errors typically between 3 and 5 m A selection (n=47) of short (<10m) inter-refuge site distances were measured by hand with a tape measure and were compared to estimates of the same distances made by measuring distances between GPS recorded refuge site locations in ARCMAP (Figure 1).. GPS data tends to overestimate distances measured by hand as almost all points are above the 1:1 line. This clearly affected our ability to reliability detect movements which are very small and thus may influence our tests of site fidelity if very short day to day refuge site relocations are common.

Effects of time elapsed since emergence on distance from refuge sites

We found no effect of time since emergence (assumed to occur at 9 pm) on distance travelled while foraging for the 2010 data (coefficient= 0.018; r2=0.002; p-value=0.4646; $F_{1,332} = 0.5361$) and a marginally significant but very minor effect for 2009 (coefficient= 0.069; r2=0.025; p-value=0.011; $F_{1,251-} = 6.495$) . This allowed us to include all nighttime relocations, regardless of time in the evening, in our null distribution.

Single day refuge to refuge movements

We observed a total of 594 single day refuge to refuge movement events. 409 of these were recorded in 2010 with the remaining 193 taking place in 2009. Average movement length was no different between years (**MEAN STEP LENGTH**: **2009:** 48.39 m ; **2010**: 41.24 m) according to a t test (t = 1.0662, df = 258.137, p-value = 0.2873). Variance in movement step length was far greater in 2009 (variance= 7442.55) than in 2010 (variance =2635.54) according to a variance test ($F_{192,408} = 2.8239$, p-value < 2.2e-16). This difference was driven primarily by the two greatest single day movement events which both took place in 2009 (775.97 and 621.58 m respectively). By contrast the greatest move in 2010 was 293.51m. A Kolmogorov-Smirnov test indicated that the two samples of movement steps (Figures 1 and 2) were not drawn from the same distribution (D = 0.1201, p-value = 0.04557), although qualitatively they are very similar.

Fidelity to refuge sites

A Kolmogrov-Smirnov test indicated that in 2010 the distribution of single day, refuge to refuge site displacements was not equivalent to the distribution of day to night displacements (D = 0.2034, p-value = 4.927e-07). Visual inspection of the two data sets (FIGURE 3) illustrates that refuge to refuge relocations are far more likely to be 10 meters or less than expected by our day to night movement null. This result indicates that toads tend to choose refuge sites closer to their previous daytime refuge site than expected when predicted by their nighttime activity locations.

The same test applied to the 2009 data (FIGURE 4) returned a marginally non-significant p value (D = 0.1232, p-value = 0.07211). In this case the evidence for philopatry is less apparent. This may be due to yearly variation in movement behavior or, more likely, the reduced size of the data set for day to day movements in 2009 (n=193) relative to 2010 (n=409). Given the marginality of failure to reject the null hypothesis in 2009 and the strength of the 2010 data which argues for site fidelity we interpret these results together as good evidence for fidelity to refuge sites on a daily time scale.

DISCUSSION

Site Fidelity

Fowlers Toads clearly exhibit fidelity to terrestrial refuge sites, often returning to the same burrow repeatedly for periods as long as a week. Even when they do not return to precisely the same location, they tend to return to within 10m of the refuge site used on the previous day. This tendency to remain in the same area does not appear to be the result of limitation on movement as toads may often be found hundreds of meters from refuge sites during bouts of evening activity and foraging. Nor can we invoke habitat limitation as an explanation for this behavior. Thus we feel Fowler's Toads exhibit true philopatry to refuge sites, on daily and broader time scales.

Philopatry has many potential advantages. Animals will likely be more familiar with the habitat in an area that they occupy over a longer period of time and this may lead to improved return rates on energy invested in foraging and other resource gathering activities. They may also realize some benefit in predator evasion by maintaining familiarity with one particular locale. Aside from the benefits of spatial familiarity, reusing the same site may confer further benefits when the refuge site is a structurally sound, hollowed out burrow rather than a loose pile of sand which the toad buries itself in. Digging is metabolically expensive (Seymour, 1973) and is likely avoided when not necessary. A burrow can afford this benefit. It is also possible that toads enhance their daytime refuge sites by urinating in them, thus making them more attractive hydric environments to avoid dessication (Cohen and Alford, 1996). This is an intriguing possibility given the important role these sites play in hydroregulation (Oromi et al., 2010)

It may be that the greatest benefits of site fidelity are not realized on short time scales related to foraging and physiology. If the distribution of breeding sites is patchy relative to foraging and refuge habitat then maintaining proximity to breeding sites through fidelity to strategically located refuge sites could be adaptive and subject to natural selection. The same predictions may also be made with respect to overwintering habitat instead of, or in addition to, breeding habitat. If toads behaved like random walkers during the summer months then the probability that they would end their wanderings in locations far removed from suitable breeding or overwintering sites increases with the scarcity of these habitat types. Thus at some point a long distance corrective movement would have to be employed to relocate individuals to overwintering sites, or, following spring emergence, to breeding areas. This would be especially risky following overwintering when energy reserves are drastically reduced. Avoiding this risky behavior by incurring regular low risk energetic costs associated with a return to the previous day’s refuge site is potentially adaptive.

Long Distance Movements

Despite their tendency towards site fidelity and homing individual toads may also cover relatively large distances over short periods of time. The reasons for such long distance movements are not clear. Changes in density of prey, con-specifics or both may also be driving this behavior. We suggest that spatial heterogeneity in prey density is an unlikely driver of refuge site relocations as variation in invertebrate prey during field work was most conspicuous and largely temporal in nature, though this was something we did not systematically measure. If our simple observations of insect availability are accurate, avoiding dense con-specific aggregation likely does not play a role in limiting competition for food. This may, however, play a role in reducing predation. Snakes, arguably the principal predators of Fowler's Toads at Long Point, hunting by olfaction, may be better able to detect clumped toads from a distance. This would make maintaining sufficient space between individuals critical for survival. We have observed a snake resting in a burrow which a toad had repeatedly used up to and including that morning, the toad having relocated its hiding spot to the beach later in the day from the burrow on dune face, presumably inspired to shift location by the arrival of the snake and not before.

The alternative may also be true, that toads relocate refuge sites to maintain proximity to other toads, perhaps even maintaining associations with particular individuals. Preference for the odors of familiar individuals with overlapping home ranges has been demonstrated in Hamilton's frog (*Leioplema hamiltoni*) (Waldman and Bishop, 2004) and the odors of neighbors can either attract or repel con-specifics depending on the sex of both signaler and receiver (Bryne and Keogh, 2007) . Kin recognition has been documented in larval amphibians (Blaustein and O'Hara, 1982) and could also play a role in the behaviour of adults.

Given the tendency for long distance movements to be underestimated (Barrowclough, 1978; Koenig, 1996) and the difficulty associated with observing rare events it is a virtual certainty that the single day movement capabilities of Fowler's Toads are in fact beyond this estimate, especially if we consider the possibility of waterborne movements (Smith, 2003) .

Elucidating how and why animals choose between returning to previously occupied sites and engaging in long distance movements is of critical importance to understanding of ecological process, especially extinction and colonization dynamics (Levins, 1970; Hanski, 1998). Here we have illustrated the somewhat contradictory finding that Fowler's Toads are prone to site fidelity yet also capable of undertaking extremely long distance movements.

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FIGURE LEGENDS

FIGURE 1:

Scatterplot of short distance (<10m) day to day refuge site displacements as measured by comparison of sequential GPS locations (Y axis) and by measuring tape between actual locations (X axis). The one to one line is plotted. n= 47.

FIGURE 2:

Frequency histogram of distance between refuge sites occupied by the same toad on sequential days in the summer of 2009. Bins along X axis are 10 m. n=193.

FIGURE 3:

Frequency histogram of distance between refuge sites occupied by the same toad on sequential days in the summer of 2010. Bins along X axis are 10 m. n=409.

FIGURE 4:

Relative proportion histogram of day to day refuge site displacements (dark bars) and day to night foraging displacements (white bars) for 2010. Bins along X axis are 10m. n= 409 and n= 361 for day to day and day to night respectively.

FIGURE 5:

Relative proportion histogram of day to day refuge site displacements (dark bars) and day to night foraging displacements (white bars) for 2009. Bins along X axis are 10m. n= 193 and n= 253 for day to day and day to night respectively.

FIGURE 1

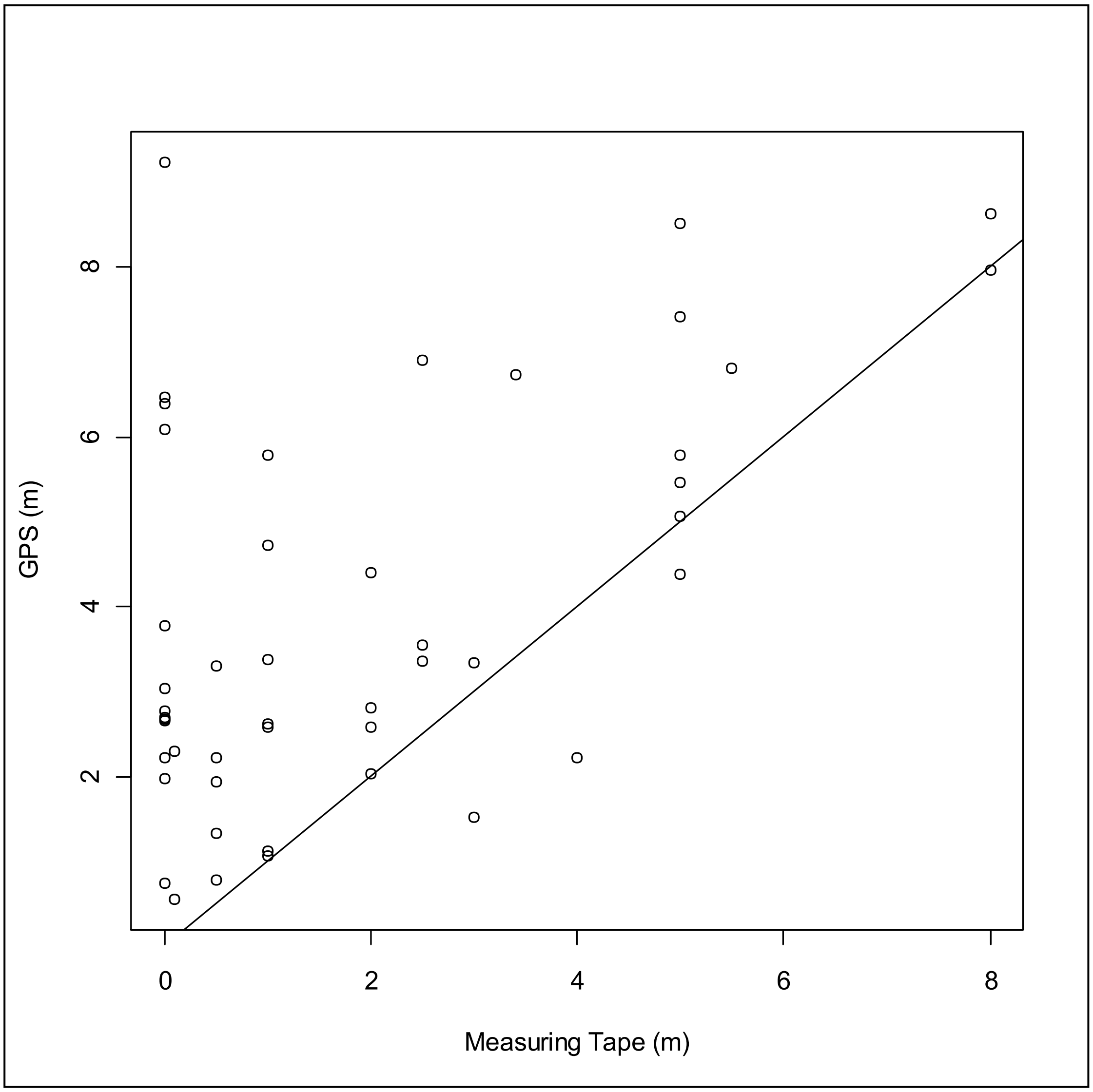


FIGURE 2

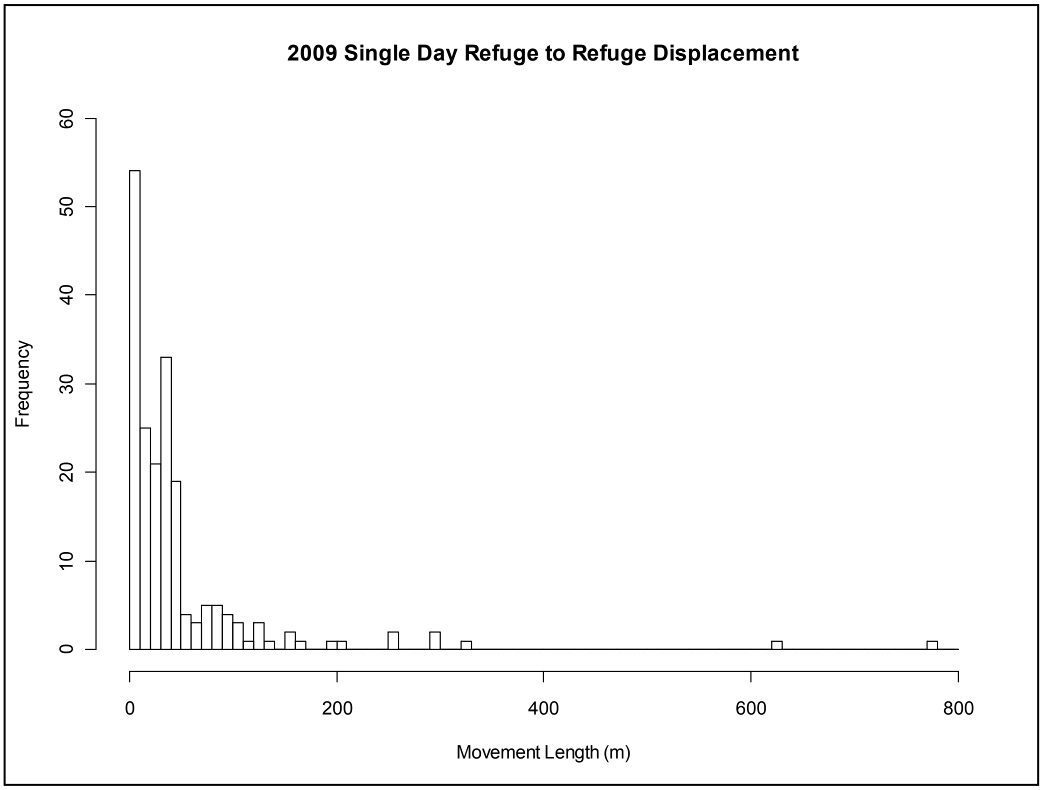

2009 Single Day Refuge to Refuge Displacement
Frequency
0
10
20
30
40
50
60
0
200
400
600
800
Movement Length (m)

FIGURE 3

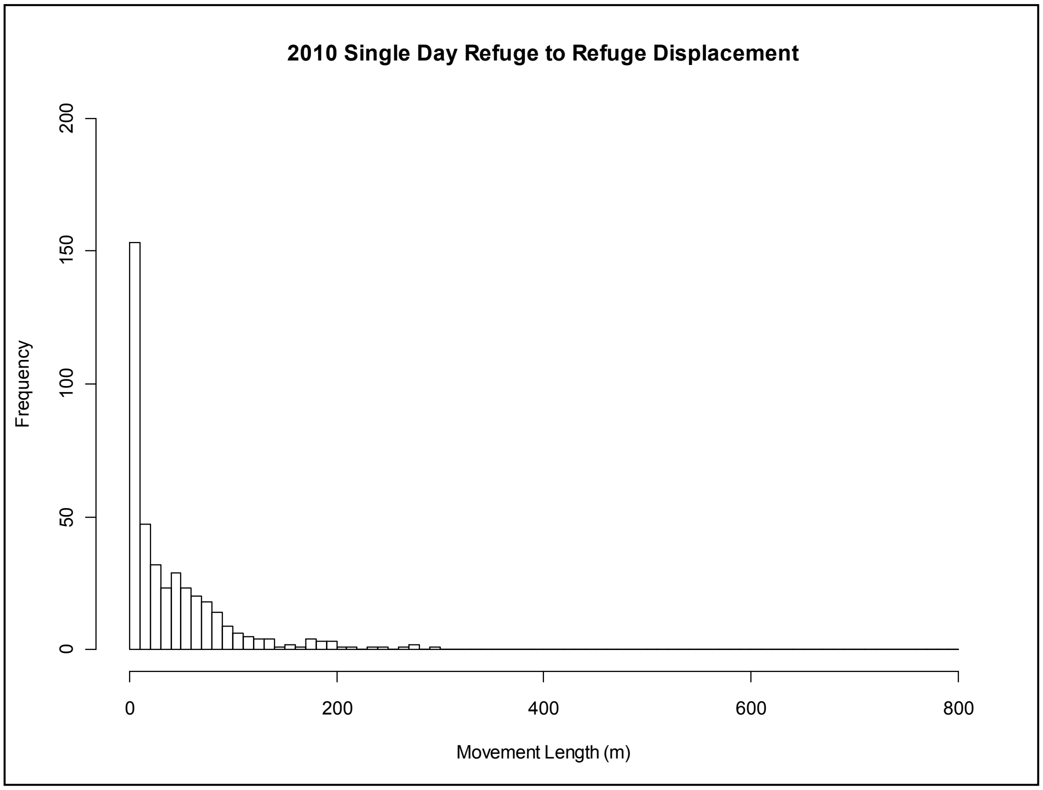

2010 Single Day Refuge to Refuge Displacement
Frequency
0
50
100
150
200
0
200
400
600
800
Movement Length (m)

FIGURE 4

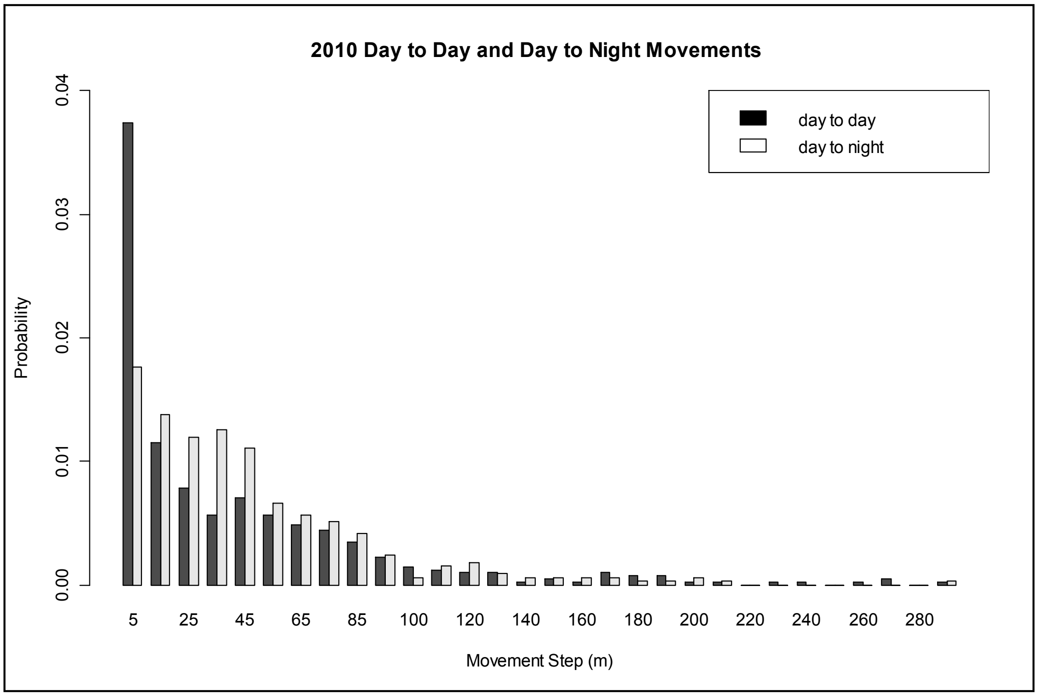
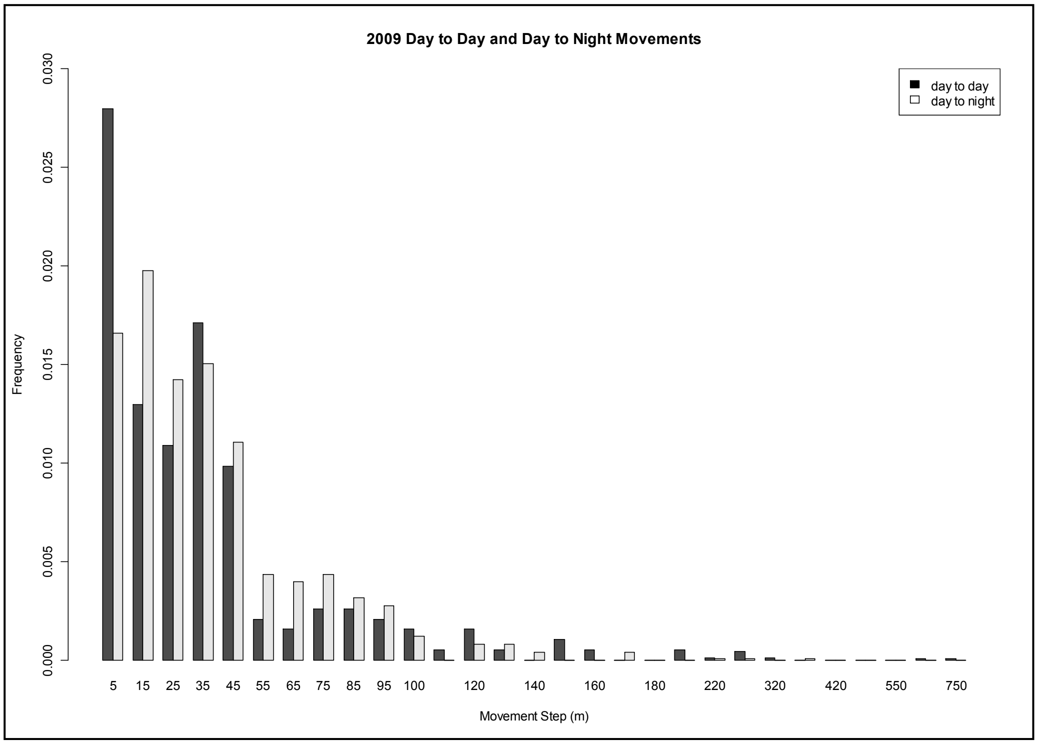

2010 Day to Day and Day to Night Movements
■ day to day
□ day to night
Probability
0.00
0.01
0.02
0.03
0.04
5
25
45
65
85
100
120
140
160
180
200
220
240
260
280
Movement Step (m)

FIGURE 5


2009 Day to Day and Day to Night Movements
day to day
day to night
Frequency
0.000
0.005
0.010
0.015
0.020
0.025
0.030
5
15
25
35
45
55
65
75
85
95
100
120
140
160
180
220
320
420
550
750
Movement Step (m)

CHAPTER FOUR: Home Range and Home Range Area

LINKING STATEMENT TO CHAPTER FOUR

In the fourth chapter I examine patterns of space use by Fowler's Toads within the context of the home range paradigm. I argue that despite ambiguities in the home range concept its application is valuable in illustrating the scale, or more appropriately, the range of scales at which individuals operate within a landscape. Quantifications of spatial utility are provided as calculated by three divergent home range metrics. The effects on home range size, of factors intrinsic to the individual are contrasted with the effects of effort invested in documenting their location. The quantitative estimates of habitat use provided here compliment the qualitative assessment of habitat requirements provided in chapter two.

ABSTRACT

Spatial requirements of animals are a central ecological theme and influence the scale at which individuals interact with their environment. The home range concept provides a framework for evaluating patterns of space use. I quantify the home ranges for 70 Fowler's Toads over two years using variations of three home range metrics, Minimum Convex Polygons, Kernel Density Estimators and Localized Convex Hulls. The considerable variation in home range estimates is explained chiefly by search effort, while body size, a driver of inter-specific home range differences, has little effect. A minimum home range estimate of 3517 m^2 is provided, with the caveat that no stable upper bound may exist.

INTRODUCTION

The Home Range Concept

How much space an animal needs during its lifetime is a fundamental ecological question with broad reaching practical and theoretical implications since the space used or required by an organism influences the scale at which it perceives and interacts with the world around it (Wiens, 1989; Wiens and Milne, 1989). Animals may experience a single location during the course of their lives, if sessile, or as blue whales and seabirds do, may move through great expanses of space. The movement ecology of the great majority of animals falls somewhere in between these divergent behaviors.

Despite the ability to move about the landscape freely, many animals constrain the majority of their movements to a particular home region (Seton, 1909) .This observation is formalized in the "home range" concept, as the area "traversed by an individual in its normal activities of food gathering, mating and caring for young" (Burt, 1943). Defining what normal activities are and when movements outside of a central area of activity should be included or excluded from a home range has led to differences in the application of the home range concept from its inception (Hayne, 1949; Cooper, 1978; White and Garrot, 1990). Presently the term is pervasive in behavior, conservation and ecological literature.

If we assume an animal has a rest site that it returns to cyclically, then it follows that its movements will never take it beyond some limiting radius centered on the rest site. This expectation is supported by random walk models which include a central location that attracts the model animal (Borger et al., 2008) Home range theory predicts that repeated observations of the location of this individual in space through time should delineate this area and provide an estimate of spatial utility (Gaustestad and Mysterud, 1995). If an individual has a true home range, then after some threshold of location observations is crossed, additional observations should provide little new information (Beckhoff and Mech, 1984). In practice, however, even when the number of observations exceeds this theoretical threshold by an order of magnitude the expected asymptotic behaviour of home range estimates is not realized (Gaustestad and

Mysterud, 1995). Thus most organisms do not appear to have strictly defined “home ranges” in the conceptual sense envisioned by Burt (1943). We may, however, still employ the ‘home range’ term in an operational sense (Powell, 2000). This allows us to describe space use patterns without imposing biological function upon them. The value here lies in the elucidation of the scale at which organisms operate.

Drivers of Range Size

When considered through the lens of macro-ecology home range is regularly viewed as a static, idiosyncratic, intrinsic characteristic of a species, chiefly defined by body size (McKnab, 1963; Turner et al., 1969; Bowman et al., 2002; Jetz et al., 2004). On the scale of a single species, however, drivers of range size are much harder to predict and interpret (Kjellander et al., 2004). Intra-specific variation in home range size may depend on sex and reproductive state (Roth, 2005), eco-morph (Sinervo et al., 2000), habit structure (Irwin, 2008; Indermaur et al., 2009), prey density (Indermaur et al., 2009) and individual differences not attributable to sex or age (Borger et al., 2006). The matter is complicated by potential feedbacks and interactions between intrinsic (e.g. body size) and extrinsic (e.g. habitat structure) factors. For example a large bodied individual may compensate for scarcity of resources by expanding its home range to allow more small patches to be exploited, while a small bodied individual might reduce its home range to minimize energetic expenditure in the same environment.

Methods of Home Range Quantification

There exists a multitude of methods for computing home ranges based on point data to discern patterns of spatial occupancy (reviews in: Worton, 1987; Harris et al., 1990; Laver and Kelly, 2008). Two general classes of approach exist, statistical and non-statistical methods. Non statistical methods are simple to apply and generally rely on joining neighboring or outlying location data points (Mohr, 1947). These methods create ranges with hard boundaries, which may be an unrealistic expectation. Statistical methods are computationally intensive and allow utilization distributions to be generated (Van Winkle, 1975). Utilization distributions quantify the probability of locating an animal at any particular location in space and do not have hard limits, instead decaying outwards towards infinitesimally small probabilities (Van Winkle, 1975; Worton, 1989). The most widely applied methods are minimum convex polygon (MCP)(Mohr, 1947; Nilsen et al., 2008), a non statistical method, and Kernel Density Estimators (KDE) (Worton, 1989), a statistical method. New methods are proposed regularly. These include Brownian bridges (Horne et al., 2007), which consider the probable trajectory between two sites occupied in sequence, and localized convex hulls (Getz and Wilmers., 2004), which uses spatial neighbor joining to generate numerous polygons which are subsequently amalgamated. Selection of an appropriate home range metric has significant consequences as patterns of spatial occupancy can expose mathematical biases of some methods of home range calculation (Downs and Horner, 2008). Thus certain metrics may not be appropriate to use for certain taxa depending on their movement behavior (Row and Blouin-Demers, 2006) The impact of these issues may be reduced by not limiting analyses to a single method of home range quantification but instead using a variety of metrics in concert.

Methodological issues beyond the choice of home range metric clearly confound determination of home range size. Ensuring that a suitable number of location fixes has been achieved for each individual is imperative if reliable range estimates are to be generated (Hayne, 1949; Beckoff and Mech, 1984; Seamen et al. 1999; Boyle et al., 2009). A second concern is ensuring a large enough sample of individuals is tracked. This is critical as substantial variation in movement behavior between individuals may exist, leading to great intra-specific variation in home range sizes.

Amphibian Home Ranges

Studies of home range in amphibians may be based on as few as five captures per individual (Wells, 2006). Ra et al. (2008) track many of the gold-spotted pond frogs (*Rana chosenica)*for which they report home ranges for only two days. Limits on the number of tracked animals are also common. Watson et al. (2003), for example, used fewer than 10 Oregon spotted frogs (*Rana pretiosa*) for their analyses.

The only published estimates of home ranges for Fowlers Toads (Clarke, 1974) are based on data from three individuals over less than a month from within a golf course. Given the strong relationship between the number of relocations and mathematical error in home range estimations (Beckoff and Mech, 1984; Seamen et al., 1999) Clarke's (1974) MCP estimate of 3,379 m^2 (range: 1,469 - 5,159m^2) for the home range of Fowler's Toads is a likely a great underestimation of the spatial requirements of these animals.

Fowler's Toads exhibit fidelity to daily refuge sites making them good candidates for investigations of home range as philopatric behavior may lead to bounded patterns of space use (Borger et al., 2008). Thus they may have true "home ranges" in the sense intended by Burt (1943). If search effort, measured by considering both the number of location fixes and the length of time between first and last capture, influences range estimates asymptotically then we may consider these animals to have true "home ranges". If energetic requirements play a role in dictating home range size, then I expect that larger individuals, will on average, require more space to acquire these resources and thereby have larger home ranges. Alternatively, if older individuals are more familiar with the landscape and older individuals then to be larger then I expect that larger individuals will have smaller home ranges. This requires that we control for sex as females tend to be larger than males (Green, 1989).

MATERIALS AND METHODS

Field techniques and details of the study site have been described in the materials and methods of Chapter Two. Therefore I provide here only relevant information not previously explained.

Data Sets

Throughout the analysis we make use of a complete data set (ALL) in which all location data sets (n=73) were included, regardless of search effort, and two truncated data sets (400 EFFORT and 30 FIXES). Within the context of this analysis search effort is the product of the number of days between the first and last location of an animal and the number of location fixes for that animal. Thus a location data set for an animal captured 20 times over 20 days would be assigned a search effort score of 400. The "400 EFFORT" data set includes 45 location data sets for animals with search effort scores of 400 or above. The "30 FIX" data set included 20 location data sets for animals with 30 or more location fixes. Fixes refer to the number of times an animal was observed and its location recorded.

Estimation of home range sizes

I used three approaches to quantify home ranges: Minimum Convex Polygon (MCP) (Mohr, 1947), fixed Kernel Density Estimates (KDE) (Worton, 1989) and Localized Convex Hulls (LoCoH) (Getz and Wilmers, 2004). Minimum convex polygon ranges were calculated using all location data (100%) and by removing a percentage of outliers (95, 96, 97, 98, 99% MCP). Kernel Density Estimates of utilization distributions were computed using bivariate normal kernels and smoothing parameters (h) calculated by least squares cross validation (LSCV). LSCV computation of h was constrained between values of 0.01 and 10 and reached convergence in all cases. Fixed KDE utilization distributions bounded by 90, 91, 92, 93, 94, 95, 96, 97, 98 and 99% isopleths were each calculated and are reported. Localized Convex Hulls were calculated based on both two (k=3) and four (k=5) nearest location neighbors, where k is the number of points included in the formation of each local hull, neighbors and focal data point inclusive. We report solely 100% LoCoH home range estimates for both k=3 and k=5. All home range calculations were made with the adehabitat package (version 1.8.6) for R (version 12.2). In order to best compare 2009 and 2010 range estimates, data from 2009 were standardized to include only a single night location for each evening of monitoring. We arbitrarily choose to keep the data from observations made closest to midnight when multiple captures were made in a single evening. We calculated home ranges for 70 toads over two years, resulting in 73 individual home ranges, 24 in 2009 and 49 in 2010. Three toads were monitored in both 2009 and 2010. Each home range was computed in 18 ways (10 Kernel Density Estimates; 6 Minimum

Convex Polygons; 2 Localized Convex Hulls) for a grand total of 1314 home range estimates.

Visualization of home ranges

We used ARCMAP 9.3 and the Hawth's Tools Extension to prepare Minimum Convex Polygon home range shape files as well as movement paths. MCP home ranges contain all daytime refuge and evening active locations for a given animal, sorted by yea. Movement paths were generated by sorting each animals series of location data points (fixes) in sequence of occurrence.

Drivers of home range size

In order to explore the mechanisms which dictate home range size for individual toads we performed multiple regressions of range size against sex and snout to vent length (svl). Tracking efforts for each toad were not equal. To account for the influence of tracking effort we included two additional variables in our regression, search effort (number of locations fixes * number of days in tracking window) and search intensity (number of location fixes / number of days in tracking window). Home range estimates were log transformed to meet the assumptions of normality implicit in linear regression. If this transformation did not result in normality as per a Shapiro-Wilks test no regressions were attempted for this estimate of home range size. The one exception to this is the MCP100 range estimate for the complete data set (ALL). The Shapiro-Wilks test returned a p value 0f 0.0495, indicating a marginally non normal distribution. Given the marginality of this result we choose to include the data set in the regression analysis. Each of the three continuous variables (snout to vent length, search effort and search intensity) were standardized with the Microsoft Excel "STANDARDIZE" function, based on mean and standard deviation of each variable. We considered the complete data set (n=73) as well as two truncated data sets including either only those animals which had an effort score greater than 400 (n=45) and those toads for which 30 or more location fixes had been recorded (n=20).

RESULTS

Number of Relocations

Toads were located on average 24.74 times each year (range 4-65 locations). The time between first and last location in a year (tracking window) for each toad was on average 40.98 days (range 2-94 days).

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Movements by toads

Toad 548 (Fig. 4) was located 65 times (30 daytime and 35 nighttime) and is the individual for which we have the most data. This individual was first captured on the 31st of May, 2010 and last captured 26th of August, 2010. The final location for the animal was 1045 m east of the previous location, and 700 m beyond the eastern limit of our regular survey area.

Toad 605 (Fig 5) was located 47 times (24 times during the day and 23 times at night), beginning the evening of May 27th, 2010, last seen during the evening of August 26th of the same year. In this case the first location is 888 m east of the second observation made 4 days later on the 1st of June and almost 1000 m east of the first known refuge site used on the 27th of June. In both of these cases locations well east of the activity center are used by the animals either before (Toad 605) or after (Toad 548) the summer season.

Toad 849 was located on 70 occasions, 24 times during the day and 46 times at night, (many removed for regression though) between the 25th of June and the 13th of August, 2009. This individual has the smallest home range of all toads (Fig 6) for which we have a large sample of location data, at 3,543m2. If we consider only daytime relocations the range estimate shrinks considerably, to 712.48 m2. Using only night location data, however, has little consequence on range estimate (3499.82 m2).

Toad 843 (Fig 7) was located 53 times in 2009 (may not match regression table since multi night locations were removed for that analysis), beginning the 22nd of June and ending on the 16th of August. 37 observations were made at night and 16 made during the day while the animal was making use of refuge sites. This individual has the largest home range of all toads, at 47,282.95 m2, a daytime range of 20,195.86 m2, and a nighttime range of 33,566.29m2 (FIGURE SEVEN).

Toad 847 (Fig. 8) was located 61 times between the 4th of May and the 6th of August, 2010, 37 times at night and 24 times during the day. This animal displayed strong site fidelity to three neighborhoods, taking refuge in these 3 locations 22 of 24 times, with 2 exploratory refuge locations. The areas represented by these neighborhoods, when considered in isolation, are 31.94m2, 8.55m2 and 1.91m2, moving from west to east (Fig 8). The individual used these sites at different times over the course of 40 days (Table 4).

Home range estimates

An enormous amount of variation in our home range estimates exists (min: 23.00 m2; max: 117,425m2; standard deviation: 10,651.03; mean: 6,834.99m2; median: 3,565.99 m2). Home range estimates varied considerably based on method of calculation (Figs 1- 3, Table 1). For the complete data set, localized Convex Hull methods based on 4 neighbors (k=5) produced the smallest range estimates (mean =2261.41 m2; median = 1149.09 m2;standard deviation = 3395.53). Kernel Density Estimates of the 99% isopleths of the utilization distribution produced the largest home range estimates (mean=12,632.21 m2; median = 6,427.23 m2; standard deviation = 17,937.42). Localized Convex Hull methods based on 4 neighbors (k=5) produced the smallest range estimates in both cases, based on mean and median range sizes. MCP 100 range estimates were the largest based on median ranges size in both truncated data sets and for mean range estimates in the 30 FIX data set. Mean KDE 99 estimates were largest in the 400 effort data We excluded one calculated range estimate (TOAD 847, YEAR 2009, KDE99) as its extraordinarily high value is interpreted as an error (343,642.90 m2). The KDE 98 estimate for this toad and year is 6360.69 m2.

Analysis of home range drivers

Results of multiple regression analysis of home range varied greatly depending on home range metric and data set. Hundreds of regression models can be produced considering our eighteen home range metrics, three data sets and four explanatory variables. Thus we interpret marginally significant models and model components with caution. Highly significant relationships, however, are likely robust to our method of analysis and can be more readily accepted as valid. Each data set (ALL DATA; 400 EFFORT; 30 FIXES) is treated separately and a representative from each of three range metrics (MCP 100%; LCH 100% k=3; KDE 90%) is presented for each data set. In general we constructed two sets of models, those based solely on the four main effects (SEX; Snout to Vent Length (Svl); Effort; Intensity), which we refer to as ALL (effects), and those based on main effects and interaction terms, which we refer to as FULL. We explored the model space by removing non-significant components of models based on ALL effects (negative stepwise regression). These are described below categorically by data set (ALL DATA; 400 EFFORT; 30 FIXES).

ALL DATA

Minimum Convex Polygon 100%

The model (ALL) comprised of each of the four explanatory variables was highly significant (p=1.22E-07) and explained 40.19 % of variation in home range size. Within this model Effort and Intensity were both significant, with Effort having the greatest effect on home range size (p=9.7E-08; coefficient = 0.595). Increased search effort was associated with larger range sizes, while increased intensity was associated with smaller ranges (coefficient = -0.1836).

We removed sex from the model as three toads had not been properly sexed and this would allow us to include all 73 MCP100% home range estimates in our analysis. Eliminating the categorical variable Sex produced a similarly significant model (NO SEX; p=2.75E-09) which explained more of the variation in home range size

(r^2=0.4363). In addition to Effort and Intensity, Svl had some explanatory power in this model, with larger toads having smaller home ranges (p=0.0245; coefficient=-0.2239). Given the marginality of this relationship we would expect that accounting for multiple tests would eliminate the significance of this p value.

The FULL model performed no better than either of the other two models and only effort was a significant explanatory variable in this case. In all models the effects of search effort and search intensity far outweighed either of the biological variables (sex and body size).

Localized Convex Hulls 100% with Two Neighbours (k=3)

The same three models (ALL, NO SEX, FULL) derived from Localized Convex Hull estimates of home range sizes were generally less informative than those based Minimum Convex Polygon estimates of home range size but followed a similar pattern.

NO SEX was the most informative model (r2=0.3293; p=9.8E-07) although in this case Svl was not useful in predicting home range size. Both Intensity and Effort were of predictive value (Effort: p=0.000238; Intensity: p=0.00233) with increases in Intensity again correlating to reduced range size and increases in Effort correlating to increased range sizes (coefficients: -0.3962 (Intensity) and 0.5007 (Effort)).

The FULL model was significant (p=0.008294; r2= 0.2397), though far less so than either of the other two models generated from this data set. Intensity was the only parameter of predictive value in this model (coefficient = -1.4688, p=0.0727), though only marginally so.

In this suite of models the effects of biological parameters (sex and body size) were of no predictive value relative to the methodological parameters of search effort and intensity which clearly biased range estimates.

Kernel Density Estimate 90% Isopleths

None of the linear models explored with this home range metric were of predictive value. Estimates of home range produced in this fashion might possibly be free of the biases of search effort and intensity which were clearly driving range estimates made by the other two methods.

TRUNCATED DATA SET I: SEARCH EFFORT GREATER THAN 400

Minimum Convex Polygon 100%

The most informative MCP derived models for this data set performed considerably poorer than those from the complete data set (NO SEX ALL DATA r2=.4363; SIZE AND EFFORT 400 PLUS r2 = 0.3408). In all models save the FULL model, Effort was the only parameter of predictive value excepting the SIZE AND EFFORT model in which body size (SVL) approached significance (p=0.0897; coefficient = -.1787) again with smaller animals having larger ranges. The general reduction in model performance indicates that some of the biasing effects of search effort and search intensity have been eliminated by removing animals for which only a paucity of data exists.

Localized Convex Hulls 100% with Two Neighbors (k=3)

These models performed similarly to those derived from the complete data set. The ALL model was of more predictive value than any of the models generated from the complete data set (r2= 0.3324, p=0.0004905). Search effort and intensity were significant components of each model (ALL; NO SEX: EFFORT AND INTENSITY) excepting the FULL Model. Increasing effort always increased range sizes (coefficients: 0.7531; 0.713; 0.6637) while increasing intensity always reduced range sizes (coefficients: -0.3515; -.3069; -.3388).

Kernel Density Estimate 90% Isopleths

As was the case for the complete data set, none of the linear models explored with this home range metric were of predictive value.

TRUNCATED DATA SET II: MORE THAN 30 LOCATION FIXES

Minimum Convex Polygon 100%

None of the models explored with the smallest and most restrictive data set were significant. A model composed solely of search effort approached significance (p=0.08957) and explained some variation in home range size (r2=0.1046, coefficient = 0.2709). A reduction in probability of model significance, explanatory power and regression coefficient slope argues for a reduced role of search effort in driving home MCP home range size and suggests that for this most restrictive data set we are approaching a saturation point, and thus relatively reliable estimates of home range size.

Localized Convex Hulls 100% with Two Neighbours (k=3)

The LoCoH models derived from the 30 fix or more data set were the most useful as predictors of home range size relative to the other two data sets. A model incorporating Effort and Intensity was the least likely to be an artifact of chance (p=0.005093) and was nearly the best at explaining variance in home range size (r2=0.3995). Intensity was the most important factor in this model (coefficient = -0.5427; p=0.0186), again being negatively correlated with home range size. In one instance the reduced number of home range estimates resulted in a clear case of over-fitting (FULL model: r2=0.7026, p=0.0608).

Kernel Density Estimate 90% Isopleths

As was the case for the two larger data sets, none of the linear models explored with this home range metric were of predictive value

DISCUSSION

We set out to determine if Fowler's Toads have home ranges and, if so, how big those home ranges are. Considering the great variation movement behaviour expressed by the toads we have studied, and the variable estimates of their home range sizes, it is difficult to answer either question. A single quantitative estimate of spatial requirements, which could be treated as a species-specific home ranges estimate, appears to be highly unrealistic. There are many possible reasons for this, both biological and methodological.

Due, in part, to the ill-defined nature of what constitutes a home range, the problems of delimiting home ranges are severe. Following individuals for longer periods of time and relocating them on more occasions expands range estimates in a predictable fashion. This is the expectation of diffusion and random walk models of movement (Borger et al., 2008), although gradually the effects of time should saturate as in a sigmoid function. Although we did not reach this saturation point we seem to have approached it. By restricting the data set to only those individuals for which we have a robust set of locations we were able to remove most of the effects of search effort, though not entirely.

This may indicate that on short time scales toads behave as random walkers but on broader time scales they are attached to very specific spatial locations which anchor their short term wanderings into bounded home ranges. When the timescale of observation becomes greater than the timescale at which movement ceases to be random the pattern of random movement disappears. Field observations and movement quantifications (CHAPTER THREE) corroborate this, suggesting that within the course of an evening toads move more or less randomly with a strong tendency to return to the previous day's refuge site. The home range data presented here are not useful for making interpretations on daily timescales, however. Over the course of a season refuge sites may shift gradually or, for reasons we don't yet understand, toads may make long distances movements and relocate home ranges. We included all location data in our estimates of home range size, rather than trying to arbitrarily decide which movements were normal and which were unusual enough to be excluded. It is certain that we have captured some of these infrequent, dispersal like movements in our range estimates. Thus in some cases our range quantifications will represent the sum area occupied by two or more subsequent home ranges and any intervening territory between them. This makes reporting both mean and maximum range sizes rather dubious. Median range sizes are likely far more reliable estimates of true spatial requirements, though perhaps the most reliable estimate of minimum spatial requirements for Fowlers Toads should be drawn from the animal with the greatest search effort and the smallest resulting home range (TOAD 849, YEAR=2009,fixes=53, KDE90=956.25m2, MCP100=3517.31m2, LCH3=721.35m2). However, since this animal was only tracked between June 26th and August 12th of 2009 we can't confidently say that it did not leave the study area by means of a long, home range relocating movement outside of the monitoring period.

A number of individual toads engaged in intense periods of long range movement at the very beginning or very end of our field seasons. We interpret this as seasonal migratory behavior important for moving toads between overwintering and breeding sites. Whether or not all toads engage in this is unclear. Likely the quality of overwintering sites in the landscape varies in space, with deep dunes being the most favorable locations for evading the penetrating winter frost. Some individuals may have the good fortune of overwintering near breeding sites and others, either due to competition for these high quality low commute sites, or a lack of awareness of their existence, make long distances movements to previously used or distal overwintering sites. At the beginning of the season the location of calling males likely has a very strong effect on movement patterns as acoustic signals can carry for great distances providing many remotely distributed individuals with information about the location of that seasons breeding areas, which may be ephemeral or perennial. We expect that landscape complementation (Dunning, 1992) resulting from the arrangement of breeding and overwintering sites in space (habitat physiognomy) interacts with the experience of individual toads to drive the incidence of these long range movement or migration events.

We found some evidence that larger animals had smaller home ranges. As larger animals are generally older this may indicate that older animals, which would presumably be more familiar with the location of breeding sites and overwintering sites, may be taking advantage of this spatial information to position themselves optimally in the landscape.

Most of our regression models, however, provided no evidence that biological factors (body size and sex) play a role in determining the home range size of Fowler's Toads. Stochastic processes may be more important in determining the space use of these animals. An interesting possibility is that the experience of toads as larvae affects their behavior as adults and thus we may never be able to fully understand space use when not tracking life history through ontogenetic changes. For now, the oft cited body-size home range size relationship(McKnab, 1963; Jetz et al., 2004), is either far more difficult to detect or, more likely, not present when considering a single species in its natural environment on broad timescales. We do not dispute that in some highly contrived situations one may be able to find evidence for this relationship, however.

Fowler's toads may occupy a number of neighborhoods, which we define as areas of densely clustered refuge sites, through the course of an active season. In addition to strong site fidelity on a daily timescale (CHAPTER THREE) these animals appear to exhibit site fidelity on broader sub-seasonal time scales as well, potentially making use of two or three neighborhoods, over the course of a few weeks. It is difficult to say on what spatial scale these neighborhoods exist at from a toad's perspective. We have witnessed a great degree of site fidelity on a daily timescale, with toads returning repeatedly to the same burrow. It may be the case that each toad has two or three such burrows that it moves between as circumstances dictate; reducing local competition, tracking the environment or simply taking advantage of a known rest spot located close to where the nights foraging comes to an end. The toads may also be working on a larger spatial scale, returning to a particular dune or pair of dunes which they have a cognitive map of. More simply the toads may be attracted to their own chemical markings from previous occupied sites and as their wandering foraging movement leads them about, they may simply be attracted to their own familiar scent and wind up repeatedly attracted to a handful of past refuge locations. Anurans are able to recognize self generated odors and are attracted to them (Waldman and Bishop, 2004). If urinating in refuge sites improves their value hydrologically (Cohen and Alford, 1996) then this explains both the proximate mechanism of site fidelity and its adaptive significance.

Important technical questions need to be addressed. Patterns of location data affect metric output (Downs and Horner, 2008) and it follows that each metric may be better applied to specific taxonomic groups depending on their behavior (Row and Blouin-Demers, 2006). The same rationale may apply within a species as well. Certain metrics may be more appropriate for describing the home range of particular individuals within a population depending on how they move. Although many studies of movement are prudent enough to use multiple metrics for estimating home range sizes we do not know of any that report or model ranges based on individual specific application of range metrics. We feel that this matter is worthy of further exploration.

A second issue is the matter of time. The consequence of time between locations on animal home range estimates has been discussed with regard to independence of observations and sub-sampling methods to reduce the influence of spatial autocorrelation (Swihart and Slade, 1985; Fieberg, 2007). The three classes of home range metrics we used within, which include the two most commonly applied methods, do not take advantage of information about behavior available by considering time between locations and order of locations. The same pattern of points, when differential movement trajectory is considered, can result in very different interpretations of space use (FIGURE NINE). In the first case the trajectory implies avoidance of a central area and thus the individual likely has a very linear, rectangular range and avoids the central area. In the second case the central area is clearly used and possibly important. Ignoring the order of locations impairs our ability to interpret location data.

Brownian bridge methods (Horne et al., 2007) of home range estimation compare time between location fixes with organismal movement capabilities to produced probability envelopes between points. The product of the area of these envelopes and the probability of use within these envelopes provides much information regarding the focal individual’s movement ecology. Summing the bridges resulting from all sequential point pairs provides a robust estimate of space use, especially when time between relocations is short relative to movement rates. We envision an extension of the Brownian Bridge method which produces a three dimensional shape, rather than an areal estimate, which would serve as a symbolic representation of an organism's movement ecology. This shape would be constructed by plotting location data in the X and Y plane. The passage of time is represented in the Z axis, with subsequent locations plotted in this 3rd dimension. Location error, due to GPS inaccuracies, for example, increases the size of location points in X and Y space, and dilutes the probability of a location within each areal component of that space. Brownian bridges would link location points between two neighboring temporal "layers" in the third dimension. If the distance in X and Y space between the two temporal neighbors is equal to the maximum movement rate of the animal then a thin line of dense probability connects the points, with circumference equal to GPS location error. If the time between locations is great then the shape of the Brownian bridge will balloon in the center, indicating uncertainty of the location of the animal through time. With appropriate sampling regimes three dimensional shapes could be collected for species of interest and this could be transformed into movement parameters for spatially explicit models of movement. Development of new analytical methods may be critical in developing our understanding of movement and spatial utility.

Estimates of amphibian home range sizes may depend most on how much effort is invested in monitoring their movements. Much as the spatial extent of a study site skews estimates of dispersal (Barrowclough, 1978) the temporal extent and temporal grain of radio tracking distorts home range estimates. Rare, long distance movements result in range sizes orders of magnitude greater for those toads we observed making them. If we consider home range in its initial formulation (Burt, 1943) these movements should clearly be excluded from home range calculations as they are almost certainly evidence of behavior not consistent with the home range concept. If, however, we are simply interested in patterns of animal space use then these data provide valuable information on less regular, but arguably no less important movement phenomenon.

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TABLE ONE

Home range sizes (m2) by dataset and method of quantification.

DATASET	METRIC	Mean	Median	StDev	Max	Min
ALL	KDE90	6876.70	3446.80	10015.85	61814.39	272.07
ALL	KDE91	7134.42	3614.08	10347.19	64594.97	284.58
ALL	KDE92	7422.45	3803.02	10706.53	67375.55	298.67
ALL	KDE93	7766.21	4006.49	11136.77	70797.80	314.54
ALL	KDE94	8316.66	4239.04	11802.22	74433.94	332.65
ALL	KDE95	8735.36	4488.43	12365.50	78925.64	353.44
ALL	KDE96	9707.79	4792.74	13831.59	84272.91	379.37
ALL	KDE97	10350.21	5121.60	14621.39	91117.41	411.79
ALL	KDE98	11180.23	5706.95	15762.84	100742.48	457.17
ALL	KDE99	12632.21	6427.23	17937.42	117425.95	532.95
ALL	MCP95	3993.13	2508.78	4934.40	37278.56	65.95
ALL	MCP96	4151.32	2785.82	4996.57	37278.56	65.95
ALL	MCP97	4367.56	3515.69	5034.44	37278.56	65.95
ALL	MCP98	4580.90	3515.69	5350.75	39005.21	65.95
ALL	MCP99	4653.62	3515.69	5380.33	39005.21	65.95
ALL	MCP100	6427.56	4482.99	7304.46	47283.07	84.18
ALL	LCH3	2551.64	1420.41	2920.84	17742.44	75.82
ALL	LCH5	2261.41	1149.10	3395.53	19451.21	23.00
400 EFFORT	KDE90	5662.96	3444.52	9474.25	61814.39	597.55
400 EFFORT	KDE91	5907.97	3592.28	9893.11	64594.97	626.84
400 EFFORT	KDE92	6183.34	3749.88	10343.72	67375.55	659.49
400 EFFORT	KDE93	6497.72	3926.43	10883.11	70797.80	696.32
400 EFFORT	KDE94	6820.02	4125.70	11421.90	74433.94	738.59
400 EFFORT	KDE95	7220.67	4353.02	12109.99	78925.64	788.50
400 EFFORT	KDE96	7717.51	4623.52	12948.99	84272.91	848.97
400 EFFORT	KDE97	8384.57	5097.04	13980.38	91117.41	926.40
400 EFFORT	KDE98	9187.61	5553.49	15406.19	100742.48	1033.23
400 EFFORT	KDE99	10615.67	6246.66	18078.42	117425.95	1210.37
400 EFFORT	MCP95	5158.87	3652.83	5502.17	37278.56	931.97
400 EFFORT	MCP96	5408.39	4134.65	5539.85	37278.56	931.97
400 EFFORT	MCP97	5759.18	4426.29	5510.12	37278.56	931.97
400 EFFORT	MCP98	6105.26	4426.29	5891.07	39005.21	931.97
400 EFFORT	MCP99	6223.23	4970.70	5903.45	39005.21	931.97
400 EFFORT	MCP100	8453.95	7561.54	8215.70	47283.07	1070.92
400 EFFORT	LCH3	3224.76	2361.11	3358.99	17742.44	75.82
400 EFFORT	LCH5	2638.11	1430.21	3195.78	15722.94	205.72
30 PLUS	KDE90	4399.05	3473.13	3991.94	19798.48	956.25
30 PLUS	KDE91	4597.23	3632.84	4166.21	20659.28	1016.01
30 PLUS	KDE92	4839.75	3803.39	4511.44	22380.89	1075.78
30 PLUS	KDE93	5112.00	4019.24	4860.76	24102.50	1135.54
30 PLUS	KDE94	5353.52	4249.62	5026.39	24963.30	1195.31
30 PLUS	KDE95	5675.36	4494.54	5372.41	26684.91	1255.07
30 PLUS	KDE96	6091.87	4801.72	5889.67	29267.32	1344.72
30 PLUS	KDE97	6550.48	5159.93	6224.43	30988.93	1434.37
30 PLUS	KDE98	7197.58	6033.83	6739.08	33571.34	1553.90
30 PLUS	KDE99	8165.36	6540.23	7455.22	36153.75	1763.08
30 PLUS	MCP95	6886.81	5632.41	7510.69	37278.56	1717.81
30 PLUS	MCP96	7117.33	5821.50	7500.67	37278.56	1717.81
30 PLUS	MCP97	7362.89	5821.50	7405.73	37278.56	2506.69
30 PLUS	MCP98	8141.57	6610.09	7868.89	39005.21	2612.75
30 PLUS	MCP99	8407.01	6610.22	7815.27	39005.21	2612.75
30 PLUS	MCP100	12207.43	8459.78	10809.15	47283.07	2752.95
30 PLUS	LCH3	4361.47	2959.96	4347.67	17742.44	281.59
30 PLUS	LCH5	3864.83	2400.04	4161.42	15722.94	484.39

TABLE TWO: Regression models of home range size sorted by data set, method of analysis and model parameters (SEX; BODY SIZE (SVL); SEARCH EFFORT; SEARCH INTENSITY). Significant p values are marked with an *; p values approaching significance (0.05<p<0.10) are indicated with a +. Adjusted r2 values from significant models appear in **bold text.**

DATA SET	METRIC	Model	F Statistic	df	RSE	r2	P Value
ALL	MCP100	ALL	12.59	4 and 65	0.7597	**0.402**	1.22E-07*
ALL	MCP100	NO SEX	19.57	3 and 69	0.7997	**0.436**	2.75E-09*
ALL	MCP100	FULL	3.47	15 and 54	0.7924	**0.349**	0.000383*
ALL	LCH3	ALL	7.637	4 and 65	1.005	**0.278**	4.16E-05*
ALL	LCH3	NO SEX	12.78	3 and 69	0.9955	**0.329**	9.80E-07*
ALL	LCH3	FULL	2.45	15 and 54	1.031	**0.240**	0.008294*
ALL	KDE90	ALL	0.9437	4 and 65	1.106	-0.003	0.4445
ALL	KDE90	NO SEX	1.888	3 and 69	1.101	0.036	0.1396
ALL	KDE90	FULL	0.7053	15 and 54	1.142	-0.068	0.768
400 EFFORT	MCP100	ALL	5.993	4 and 39	0.6532	**0.317**	0.007378*
400 EFFORT	MCP100	NO SEX	8.066	3 and 41	0.6453	**0.325**	0.000244*
400 EFFORT	MCP100	SIZE + EFFORT	12.38	2 and 42	0.6378	**0.341**	5.95E-05*
400 EFFORT	MCP100	EFFORT	20.76	1 and 43	0.6526	**0.310**	4.26E-05*
400 EFFORT	MCP100	FULL	1.662	15 and 28	0.7125	**0.188**	0.1194
400 EFFORT	LCH3	ALL	6.352	4 and 39	0.9659	**0.332**	0.000491*
400 EFFORT	LCH3	NO SEX	7.821	3 and 41	0.9657	**0.318**	0.000305*
400 EFFORT	LCH3	EFFORT + INTENSITY	10.4	2 and 42	0.9784	**0.299**	0.000214*
400 EFFORT	LCH3	FULL	1.831	15 and 28	1.041	**0.225**	0.081112+
400 EFFORT	KDE90	ALL	1.183	4 and 39	0.9619	0.017	0.3335
400 EFFORT	KDE90	NO SEX	1.342	3 and 41	0.9519	0.023	0.274
400 EFFORT	KDE90	FULL	1.103	15 and 28	0.953	0.035	0.3967
30 FIX	MCP100	ALL	1.767	4 and 15	0.6453	0.139	0.1879
30 FIX	MCP100	NO SEX	2.445	3 and 16	0.6276	0.186	0.1015
30 FIX	MCP100	EFFORT	3.22	1 and 18	0.6581	**0.105**	0.08957+
30 FIX	MCP100	FULL	2.513	14 and 5	0.4783	0.527	0.1578
30 FIX	LCH3	ALL	3.777	4 and 15	0.8609	**0.369**	0.02562*
30 FIX	LCH3	NO SEX	5.286	3 and 16	0.8369	**0.404**	0.01004*
30 FIX	LCH3	EFFORT + INTENSITY	7.319	2 and 17	0.8398	**0.400**	0.005093*
30 FIX	LCH3	FULL	4.206	14 and 5	0.591	**0.703**	0.0608+
30 FIX	KDE90	ALL	0.9702	4 and 15	0.6876	-0.006	0.4525
30 FIX	KDE90	NO SEX	1.307	3 and 16	0.6694	0.046	0.3064
30 FIX	KDE90	INTENSITY	2.374	1 and 18	0.662	0.067	0.1408
30 FIX	KDE90	FULL	1.041	14 and 5 DF	0.6754	0.029	0.5262

TABLE THREE: Regression coefficients and significance levels for individual model parameters. Significant p values are marked with an *; p values approaching significance (0.05<p<0.10) are indicated with a +.

DATA SET	METRIC	Model	Parameter	Coefficent	Std. Error	t value	Pr(>|t|)
ALL	MCP100	ALL	Intercept	8.384	0.150	55.997	<2e-16*
ALL	MCP100	ALL	Sex	-0.126	0.213	-0.592	0.556
ALL	MCP100	ALL	Svl	-0.113	0.108	-1.047	0.299
ALL	MCP100	ALL	Intensity	-0.184	0.103	-1.785	0.079+
ALL	MCP100	ALL	Effort	0.595	0.099	6.000	<9.7e-8*
ALL	MCP100	NO SEX	Intercept	8.289	0.094	88.559	< 2e-16*
ALL	MCP100	NO SEX	Svl	-0.224	0.097	-2.300	0.025*
ALL	MCP100	NO SEX	Intensity	-0.245	0.101	-2.433	0.018*
ALL	MCP100	NO SEX	Effort	0.614	0.104	5.919	<1.7e-6*
ALL	MCP100	FULL	Intercept	8.245	0.280	29.464	<2e-16*
ALL	MCP100	FULL	Sex	0.099	0.347	0.286	0.776
ALL	MCP100	FULL	Svl	-0.325	0.671	-0.485	0.630
ALL	MCP100	FULL	Effort	0.667	0.292	2.283	0.026*
ALL	MCP100	FULL	Intensity	-0.653	0.616	-1.059	0.294
ALL	MCP100	FULL	Sex:Svl	0.193	0.699	0.276	0.784
ALL	MCP100	FULL	Sex:Effort	0.002	0.359	0.001	0.996
ALL	MCP100	FULL	Svl:Effort	-0.057	0.700	-0.081	0.936
ALL	MCP100	FULL	Sex:Intensity	0.641	0.680	0.942	0.350
ALL	MCP100	FULL	Svl:Intensity	-0.354	1.099	-0.322	0.749
ALL	MCP100	FULL	Effort:Intensity	-0.824	0.801	-1.028	0.308
ALL	MCP100	FULL	Sex:Svl:Effort	-0.101	0.722	-0.140	0.889
ALL	MCP100	FULL	Sex:Svl:Intensity	0.285	1.131	0.252	0.802
ALL	MCP100	FULL	Sex:Effort:Intensity	0.897	0.898	0.998	0.323
ALL	MCP100	FULL	Svl:Effort:Intensity	-0.952	1.430	-0.666	0.509
ALL	MCP100	FULL	Sex:Svl:Effort:Intensity	0.780	1.473	0.530	0.598
ALL	LCH3	ALL	Intercept	7.147	0.198	36.075	< 2e-16*
ALL	LCH3	ALL	Sex	0.208	0.282	0.739	0.463
ALL	LCH3	ALL	Svl	-0.151	0.142	-1.060	0.293
ALL	LCH3	ALL	Intensity	-0.322	0.136	-2.635	0.021*
ALL	LCH3	ALL	Effort	0.492	0.131	3.749	<3.8e-4*
ALL	LCH3	NO SEX	Intercept	7.248	0.117	62.213	< 2e-16*
ALL	LCH3	NO SEX	Svl	-0.140	0.121	-1.157	0.251
ALL	LCH3	NO SEX	Intensity	-0.396	0.125	-3.162	0.002*
ALL	LCH3	NO SEX	Effort	0.501	0.129	3.878	<4.0e-4*
ALL	LCH3	FULL	Intercept	6.920	0.364	18.997	<2e-16*
ALL	LCH3	FULL	Sex	0.222	0.451	0.492	0.625
ALL	LCH3	FULL	Svl	-0.576	0.873	-0.659	0.625
ALL	LCH3	FULL	Intensity	-1.469	0.802	-1.831	0.073+
ALL	LCH3	FULL	Effort	0.357	0.380	0.939	0.352
ALL	LCH3	FULL	Sex:Svl	0.512	0.910	0.562	0.576
ALL	LCH3	FULL	Sex:Intensity	0.909	0.886	1.027	0.309
ALL	LCH3	FULL	Svl:Intensity	-1.100	1.431	-0.768	0.446
ALL	LCH3	FULL	Sex:Effort	-0.100	0.467	-0.213	0.832
ALL	LCH3	FULL	Svl:Effort	-0.593	0.912	-0.650	0.518
ALL	LCH3	FULL	Intensity:Effort	-1.271	1.043	-1.219	0.228
ALL	LCH3	FULL	Sex:Svl:Intensity	0.970	1.472	0.659	0.513
ALL	LCH3	FULL	Sex:Svl:Effort	0.452	0.940	0.481	0.632
ALL	LCH3	FULL	Sex:Intensity:Effort	0.453	1.169	0.387	0.700
ALL	LCH3	FULL	Svl:Intensity:Effort	-1.165	1.861	-0.626	0.534
ALL	LCH3	FULL	Sex:Svl:Intensity:Effort	1.132	1.917	0.590	0.557
ALL	KDE90	ALL	Intercept	8.309	0.218	38.112	<2e-16 *
ALL	KDE90	ALL	Sex	-0.162	0.310	-0.522	0.603
ALL	KDE90	ALL	Svl	0.071	0.157	0.456	0.650
ALL	KDE90	ALL	Intensity	-0.264	0.150	-1.759	0.082+
ALL	KDE90	ALL	Effort	-0.180	0.144	-1.283	0.204
ALL	KDE90	NO SEX	Intercept	8.184	0.129	63.497	<2e-16*
ALL	KDE90	NO SEX	Svl	-0.013	0.134	-0.095	0.924
ALL	KDE90	NO SEX	Intensity	-0.322	0.139	-2.322	0.0232*

TABLE THREE CONTINUED

DATA SET	METRIC	Model	Parameter	Coefficent	Std. Error	t value	Pr(>|t|)
ALL	KDE90	NO SEX	Effort	-0.169	0.143	-1.186	0.240
ALL	KDE90	FULL	Intercept	7.705	0.403	19.111	<2e-16*
ALL	KDE90	FULL	Sex	0.420	0.499	0.840	0.405
ALL	KDE90	FULL	Svl	-0.825	0.966	-0.854	0.397
ALL	KDE90	FULL	Intensity	-0.993	0.888	-1.118	0.268
ALL	KDE90	FULL	Effort	0.153	0.421	0.362	0.718
ALL	KDE90	FULL	Sex:Svl	1.032	1.007	1.024	0.310
ALL	KDE90	FULL	Sex:Intensity	0.656	0.980	0.669	0.506
ALL	KDE90	FULL	Svl:Intensity	-0.944	1.584	-0.596	0.554
ALL	KDE90	FULL	Sex:Effort	-0.209	0.517	-0.405	0.687
ALL	KDE90	FULL	Svl:Effort	0.805	1.009	0.798	0.428
ALL	KDE90	FULL	Intensity:Effort	-1.594	1.154	-1.381	0.173
ALL	KDE90	FULL	Sex:Svl:Intensity	0.900	1.630	0.552	0.583
ALL	KDE90	FULL	Sex:Svl:Effort	-1.006	1.040	-0.967	0.338
ALL	KDE90	FULL	Sex:Intensity:Effort	1.681	1.294	1.299	0.199
ALL	KDE90	FULL	Svl:Intensity:Effort	-2.113	2.060	-1.026	0.310
ALL	KDE90	FULL	Sex:Svl:Intensity:Effort	1.979	2.122	0.933	0.355
400 EFFORT	MCP100	ALL	Intercept	8.883	0.177	50.251	< 2e-16*
400 EFFORT	MCP100	ALL	Sex	-0.233	0.230	-1.010	0.319
400 EFFORT	MCP100	ALL	Svl	-0.128	0.119	-1.070	0.291
400 EFFORT	MCP100	ALL	Intensity	0.000	0.104	-0.003	0.998
400 EFFORT	MCP100	ALL	Effort	0.506	0.108	4.683	<3.4e-5*
400 EFFORT	MCP100	NO SEX	Intercept	8.735	0.096	90.802	< 2e-16
400 EFFORT	MCP100	NO SEX	Svl	-0.181	0.105	-1.720	0.093
400 EFFORT	MCP100	NO SEX	Intensity	0.015	0.100	0.150	0.881
400 EFFORT	MCP100	NO SEX	Effort	0.510	0.105	4.879	<1.7e-5*
400 EFFORT	MCP100	SIZE + EFFORT	Intercept	8.735	0.095	91.878	<2e-16 *
400 EFFORT	MCP100	SIZE + EFFORT	Svl	-0.179	0.103	-1.737	0.0897+
400 EFFORT	MCP100	SIZE + EFFORT	Effort	0.512	0.103	4.975	<1.2e-5*
400 EFFORT	MCP100	EFFORT	Intercept	8.735	0.097	89.796	<2e-16 *
400 EFFORT	MCP100	EFFORT	Effort	0.448	0.098	4.556	<4.3e-5*
400 EFFORT	MCP100	FULL	Intercept	9.133	0.358	25.522	<2e-16
400 EFFORT	MCP100	FULL	Sex	-0.418	0.388	-1.076	0.291
400 EFFORT	MCP100	FULL	Svl	0.147	0.472	0.311	0.758
400 EFFORT	MCP100	FULL	Intensity	-0.307	0.399	-0.770	0.448
400 EFFORT	MCP100	FULL	Effort	0.885	0.509	1.738	0.093
400 EFFORT	MCP100	FULL	Sex:Svl	-0.227	-0.499	-0.455	0.653
400 EFFORT	MCP100	FULL	Sex:Intensity	0.326	0.432	0.755	0.456
400 EFFORT	MCP100	FULL	Svl:Intensity	-0.103	0.803	-0.129	0.899
400 EFFORT	MCP100	FULL	Sex:Effort	-0.258	0.532	-0.485	0.631
400 EFFORT	MCP100	FULL	Svl:Effort	0.212	0.893	0.237	0.814
400 EFFORT	MCP100	FULL	Intensity:Effort	-0.520	0.508	-1.025	0.314
400 EFFORT	MCP100	FULL	Sex:Svl:Intensity	0.075	0.828	0.091	0.928
400 EFFORT	MCP100	FULL	Sex:Svl:Effort	-0.344	0.900	-0.382	0.705
400 EFFORT	MCP100	FULL	Sex:Intensity:Effort	0.251	0.575	0.436	0.666
400 EFFORT	MCP100	FULL	Svl:Intensity:Effort	-0.645	0.905	-0.713	0.482
400 EFFORT	MCP100	FULL	Sex:Svl:Intensity:Effort	0.632	0.993	0.636	0.530
400 EFFORT	LCH3	ALL	Intercept	7.591	0.261	29.040	< 2e-16*
400 EFFORT	LCH3	ALL	Sex	-0.220	0.176	-1.246	0.220
400 EFFORT	LCH3	ALL	Svl	-0.158	0.180	-0.879	0.385
400 EFFORT	LCH3	ALL	Intensity	-0.352	0.153	-2.296	0.0272*
400 EFFORT	LCH3	ALL	Effort	0.753	0.160	4.716	<3.1e-5*
400 EFFORT	LCH3	NO SEX	Intercept	7.549	0.144	52.436	< 2e-16*
400 EFFORT	LCH3	NO SEX	Svl	-0.229	0.158	-1.453	0.154
400 EFFORT	LCH3	NO SEX	Intensity	-0.307	0.149	-2.060	0.0458*
400 EFFORT	LCH3	NO SEX	Effort	0.713	0.157	4.557	<4.6e-5*
400 EFFORT	LCH3	INTENSITY + EFFORT	Intercept	7.549	0.146	51.756	< 2e-16*
400 EFFORT	LCH3	INTENSITY + EFFORT	Intensity	-0.339	0.149	-2.268	0.029*
400 EFFORT	LCH3	INTENSITY + EFFORT	Effort	0.637	0.149	4.263	<1.1e-4*
400 EFFORT	LCH3	FULL	Intercept	7.741	0.523	14.807	9.0e-15*
400 EFFORT	LCH3	FULL	Sex	-0.182	0.567	-0.320	0.751

TABLE THREE CONTINUED

DATA SET	METRIC	Model	Parameter	Coefficent	Std. Error	t value	Pr(>|t|)
400 EFFORT	LCH3	FULL	Svl	-0.563	0.689	-0.817	0.421
400 EFFORT	LCH3	FULL	Effort	0.974	0.744	1.310	0.201
400 EFFORT	LCH3	FULL	Sex:Svl	0.337	0.729	0.462	0.648
400 EFFORT	LCH3	FULL	Sex:Intensity	0.409	0.631	0.647	0.523
400 EFFORT	LCH3	FULL	Svl:Intensity	-0.336	1.173	-0.286	0.777
400 EFFORT	LCH3	FULL	Sex:Effort	-0.161	0.778	-0.207	0.838
400 EFFORT	LCH3	FULL	Svl:Effort	-0.370	1.304	-0.284	0.779
400 EFFORT	LCH3	FULL	Intensity:Effort	0.257	0.742	0.347	0.731
400 EFFORT	LCH3	FULL	Sex:Svl:Intensity	0.234	1.209	0.194	0.848
400 EFFORT	LCH3	FULL	Sex:Svl:Effort	0.281	1.315	0.214	0.832
400 EFFORT	LCH3	FULL	Sex:Intensity:Effort	-0.694	0.840	-0.827	0.415
400 EFFORT	LCH3	FULL	Svl:Intensity:Effort	1.163	1.322	0.880	0.386
400 EFFORT	LCH3	FULL	Sex:Svl:Intensity:Effort	-1.019	1.451	-0.702	0.488
400 EFFORT	KDE90	ALL	Intercept	8.099	0.260	31.112	<2e-16*
400 EFFORT	KDE90	ALL	Sex	-0.041	0.339	-0.122	0.904
400 EFFORT	KDE90	ALL	Svl	-0.157	0.176	-0.090	0.376
400 EFFORT	KDE90	ALL	Intensity	-0.263	0.152	-1.724	0.093+
400 EFFORT	KDE90	ALL	Effort	0.146	0.165	0.882	0.383
400 EFFORT	KDE90	NO SEX	Intercept	8.097	0.142	57.060	<2e-16 *
400 EFFORT	KDE90	NO SEX	Svl	-0.153	0.155	-0.987	0.330
400 EFFORT	KDE90	NO SEX	Intensity	-0.231	0.147	-1.575	0.123
400 EFFORT	KDE90	NO SEX	Effort	0.116	0.154	0.749	0.458
400 EFFORT	KDE90	FULL	Intercept	8.520	0.479	17.800	<2e-16*
400 EFFORT	KDE90	FULL	Sex	-0.450	0.520	-0.867	0.393
400 EFFORT	KDE90	FULL	Svl	0.870	0.631	1.379	0.179
400 EFFORT	KDE90	FULL	Intensity	-0.621	1.137	-1.163	0.255
400 EFFORT	KDE90	FULL	Effort	1.499	0.681	2.201	0.036
400 EFFORT	KDE90	FULL	Sex:Svl	-0.992	0.667	-1.488	0.148
400 EFFORT	KDE90	FULL	Sex:Intensity	0.511	0.578	0.885	0.384
400 EFFORT	KDE90	FULL	Svl:Intensity	-0.735	1.074	-0.685	0.499
400 EFFORT	KDE90	FULL	Sex:Effort	-1.485	0.712	-2.086	0.046
400 EFFORT	KDE90	FULL	Svl:Effort	2.073	1.194	1.737	0.093
400 EFFORT	KDE90	FULL	Intensity:Effort	-1.132	0.679	-1.668	0.107
400 EFFORT	KDE90	FULL	Sex:Svl:Intensity	0.491	1.107	0.444	0.661
400 EFFORT	KDE90	FULL	Sex:Svl:Effort	-2.091	1.204	-1.737	0.093
400 EFFORT	KDE90	FULL	Sex:Intensity:Effort	1.485	0.769	1.931	0.064+
400 EFFORT	KDE90	FULL	Svl:Intensity:Effort	-2.683	1.210	-2.217	0.035*
400 EFFORT	KDE90	FULL	Sex:Svl:Intensity:Effort	2.957	1.328	2.226	0.034*
30 FIX	MCP100	ALL	Intercept	9.235	0.267	34.593	1.0e-15*
30 FIX	MCP100	ALL	Sex		0.346	-0.363	0.722
30 FIX	MCP100	ALL	Svl	-0.185	0.178	-1.036	0.316
30 FIX	MCP100	ALL	Intensity	-0.255	0.163	-1.565	0.138
30 FIX	MCP100	ALL	Effort	0.252	0.167	1.507	0.153
30 FIX	MCP100	NO SEX	Intercept	9.154	0.140	65.228	<2e-16*
30 FIX	MCP100	NO SEX	Svl	-0.213	0.156	-1.364	0.191
30 FIX	MCP100	NO SEX	Intensity	-0.251	0.158	-1.590	0.131
30 FIX	MCP100	NO SEX	Effort	0.251	0.163	1.546	0.142
30 FIX	MCP100	EFFORT	Intercept	9.135	0.147	62.200	<2e-16*
30 FIX	MCP100	EFFORT	Effort	0.271	0.151	1.794	0.0896+
30 FIX	MCP100	FULL	Intercept	3.618	2.063	1.754	0.140
30 FIX	MCP100	FULL	Sex	5.589	2.070	3.095	0.043
30 FIX	MCP100	FULL	Svl	-8.204	2.884	-2.845	0.036
30 FIX	MCP100	FULL	Intensity	19.764	6.824	2.896	0.034
30 FIX	MCP100	FULL	Effort	-20.503	6.369	-3.219	0.024
30 FIX	MCP100	FULL	Sex:Svl	7.854	2.839	2.715	0.042
30 FIX	MCP100	FULL	Sex:Intensity	-19.913	6.827	-2.917	0.033
30 FIX	MCP100	FULL	Svl:Intensity	18.753	6.624	2.831	0.037
30 FIX	MCP100	FULL	Sex:Effort	20.680	6.371	3.246	0.023
30 FIX	MCP100	FULL	Svl:Effort	-39.581	11.901	-3.326	0.021
30 FIX	MCP100	FULL	Intensity:Effort	32.141	10.078	3.189	0.024
30 FIX	MCP100	FULL	Sex:Svl:Intensity	-18.808	6.626	-2.838	0.036
30 FIX	MCP100	FULL	Sex:Svl:Effort	39.045	11.902	3.280	0.022

TABLE THREE CONTINUED

DATA SET	METRIC	Model	Parameter	Coefficent	Std. Error	t value	Pr(>|t|)
30 FIX	MCP100	FULL	Sex:Intensity:Effort	-32.346	10.079	-3.209	0.024
30 FIX	MCP100	FULL	Svl:Intensity:Effort	-0.744	0.397	-1.876	0.119
30 FIX	MCP100	FULL	Sex:Svl:Intensity:Effort	NA	NA	NA	NA
30 FIX	LCH3	ALL	Intercept	8.009	0.356	22.488	5.7e-15*
30 FIX	LCH3	ALL	Sex	-0.160	0.461	-0.347	0.734
30 FIX	LCH3	ALL	Svl	-0.184	0.238	-0.774	0.451
30 FIX	LCH3	ALL	Intensity	0.583	0.217	-2.687	0.0169*
30 FIX	LCH3	ALL	Effort	0.399	0.223	1.789	0.0938+
30 FIX	LCH3	NO SEX	Intercept	7.905	0.187	42.241	<2e-16*
30 FIX	LCH3	NO SEX	Svl	-0.220	0.208	-1.058	0.306
30 FIX	LCH3	NO SEX	Intensity	-0.578	0.210	-2.747	0.014*
30 FIX	LCH3	NO SEX	Effort	0.398	0.217	1.837	0.085+
30 FIX	LCH3	INTENSITY + EFFORT	Intercept	7.905	0.188	42.095	<2e-16 *
30 FIX	LCH3	INTENSITY + EFFORT	Intensity	-0.543	0.209	-2.603	0.019*
30 FIX	LCH3	INTENSITY + EFFORT	Effort	0.333	0.209	1.597	0.130
30 FIX	LCH3	FULL	Intercept	-0.275	2.549	-1.080	0.918
30 FIX	LCH3	FULL	Sex	8.174	2.558	3.195	0.024*
30 FIX	LCH3	FULL	Svl	-12.511	3.564	-3.511	0.017*
30 FIX	LCH3	FULL	Intensity	27.723	8.433	3.288	0.022*
30 FIX	LCH3	FULL	Effort	-21.172	7.871	-2.690	0.043*
30 FIX	LCH3	FULL	Sex:Svl	12.088	3.575	3.381	0.02*
30 FIX	LCH3	FULL	Sex:Intensity	-28.350	8.436	-3.361	0.02*
30 FIX	LCH3	FULL	Svl:Intensity	27.369	8.186	3.344	0.021*
30 FIX	LCH3	FULL	Sex:Effort	21.327	7.873	2.709	0.042*
30 FIX	LCH3	FULL	Svl:Effort	-44.919	14.706	-3.054	0.028*
30 FIX	LCH3	FULL	Intensity:Effort	42.051	12.453	3.377	0.02*
30 FIX	LCH3	FULL	Sex:Svl:Intensity	-27.545	8.188	-3.364	0.02*
30 FIX	LCH3	FULL	Sex:Svl:Effort	43.990	14.707	2.991	0.03*
30 FIX	LCH3	FULL	Sex:Intensity:Effort	-42.530	12.454	-3.415	0.019*
30 FIX	LCH3	FULL	Svl:Intensity:Effort	-1.182	0.490	-2.412	0.061*
30 FIX	LCH3	FULL	Sex:Svl:Intensity:Effort	NA	NA	NA	NA
30 FIX	KDE90	ALL	Intercept	8.099	0.260	31.112	<2e-16*
30 FIX	KDE90	ALL	Sex	-0.041	0.339	-0.122	0.904
30 FIX	KDE90	ALL	Svl	-0.157	0.176	-0.090	0.376
30 FIX	KDE90	ALL	Intensity	-0.263	0.152	-1.724	0.093+
30 FIX	KDE90	ALL	Effort	0.146	0.165	0.882	0.383
30 FIX	KDE90	NO SEX	Intercept	8.097	0.142	57.060	<2e-16 *
30 FIX	KDE90	NO SEX	Svl	-0.153	0.155	-0.987	0.330
30 FIX	KDE90	NO SEX	Intensity	-0.231	0.147	-1.575	0.123
30 FIX	KDE90	NO SEX	Effort	0.116	0.154	0.749	0.458
30 FIX	KDE90	FULL	Intercept	8.520	0.479	17.800	<2e-16*
30 FIX	KDE90	FULL	Sex	-0.450	0.520	-0.867	0.393
30 FIX	KDE90	FULL	Svl	0.870	0.631	1.379	0.179
30 FIX	KDE90	FULL	Intensity	-0.621	1.137	-1.163	0.255
30 FIX	KDE90	FULL	Effort	1.499	0.681	2.201	0.036
30 FIX	KDE90	FULL	Sex:Svl	-0.992	0.667	-1.488	0.148
30 FIX	KDE90	FULL	Sex:Intensity	0.511	0.578	0.885	0.384
30 FIX	KDE90	FULL	Svl:Intensity	-0.735	1.074	-0.685	0.499
30 FIX	KDE90	FULL	Sex:Effort	-1.485	0.712	-2.086	0.046
30 FIX	KDE90	FULL	Svl:Effort	2.073	1.194	1.737	0.093
30 FIX	KDE90	FULL	Intensity:Effort	-1.132	0.679	-1.668	0.107
30 FIX	KDE90	FULL	Sex:Svl:Intensity	0.491	1.107	0.444	0.661
30 FIX	KDE90	FULL	Sex:Svl:Effort	-2.091	1.204	-1.737	0.093
30 FIX	KDE90	FULL	Sex:Intensity:Effort	1.485	0.769	1.931	0.064+
30 FIX	KDE90	FULL	Svl:Intensity:Effort	-2.683	1.210	-2.217	0.035*
30 FIX	KDE90	FULL	Sex:Svl:Intensity:Effort	2.957	1.328	2.226	0.034*

TABLE FOUR

Refuge site neighborhood timeline for toad 847 in 2010. This table compliments FIGURE EIGHT. Refuge site placement indicated by black when in one of the three identified neighbourhoods, in grey when in one of two exploratory refuge sites, west and east.

	Neighborhood of Refuge			
Day	One	Two	Three	Other
4		■		
5		■		
6		■		
7			■	
8			■	
9			■	
10				WEST
11		■		
12			■	
13	■			
14	■			
15	■			
16-32	NO TRACKING			
33	■			
34	■			
35	NO DATA			
36		■		
37	■			
38	■			
39	■			
40		■		
41				EAST
42		■		
43	■			
44		■		
45	■			

FIGURE LEGENDS

FIGURE ONE:

Boxplots of Home Range area by Home Range Metric for the complete data set. Home range metrics (Kernel Density Estimate; Localized Convex Hulls; Minimum Convex Polygon) arranged along X axis by proportion of data included, with Home Range Area in m2 on Y axis. Outliers are not included to better illustrated differences in median values. 73 home ranges are included in each box (n=73).

FIGURE TWO:

Boxplots of Home Range area by Home Range Metric for the data set including only toads with an effort score of 400 or more. Home range metrics (Kernel Density Estimate; Localized Convex Hulls; Minimum Convex Polygon) arranged along X axis by proportion of data included, with Home Range Area in m2 on Y axis. Outliers are not included to better illustrated differences in median values. 45 home ranges are included in each boxplot (n=45).

FIGURE THREE:

Boxplots of Home Range area by Home Range Metric for the data set including only toads with 30 or more location fixes. Home range metrics (Kernel Density Estimate; Localized Convex Hulls; Minimum Convex Polygon) arranged along X axis by proportion of data included, with Home Range Area in m2 on Y axis. Outliers are not included to better illustrated differences in median values. 20 home ranges are included in each boxplot (n=20).

FIGURE FOUR:

a) Minimum Convex Polygon home range, location fixes and movement trajectory for TOAD 548 in 2010. The eastern most location was the last location made for the toad.
b) Two Minimum Convex Polygon home ranges for TOAD 548 including and excluding a large late season eastward movement

FIGURE FIVE:

Minimum Convex Polygon home range, location fixes and movement trajectory for TOAD 605 in 2010. The eastern most location was the first location of the toad.

FIGURE SIX:

Two Minimum Convex Polygon home ranges for TOAD 849 from 2009; based on exclusively day (white polygon) or night locations (grey polygon). Location fixes appear as white (DAY, n=24) and black (NIGHT, n=46) points.

FIGURE SEVEN:

Two Minimum Convex Polygon home ranges for TOAD 843 from 2009; based on exclusively day (white polygon) or night locations (grey polygon). Location fixes appear as white (DAY, n=16) and black (NIGHT, n=37) points.

FIGURE EIGHT:

Refuge site neighbourhoods for toad 847 in 2010. From west to east, neighbourhood one is composed of 10 refuge locations (grey points, white polygon, area=31.94m2), neighbourhood two is composed of 8 refuge locations (black points, white polygon, area=8.55m2) and neighbourhood three is composed of 4 refuge locations (grey points, white polygon, area=1.91m2). Two exploratory refuge sites appear distinct from the neighbourhoods in offwhite. Movement trajectories appear as lines and indicate regular movement between the three neighbourhoods. TABLE 4 contains supporting information regarding the movements of toad 847.

FIGURE NINE

Alternative movement paths (arrows) for four locations of an animal (dots). Numerals indicate sequence. The individual on the left avoids the central area while the individual on the right makes use of the central area.

FIGURE ONE

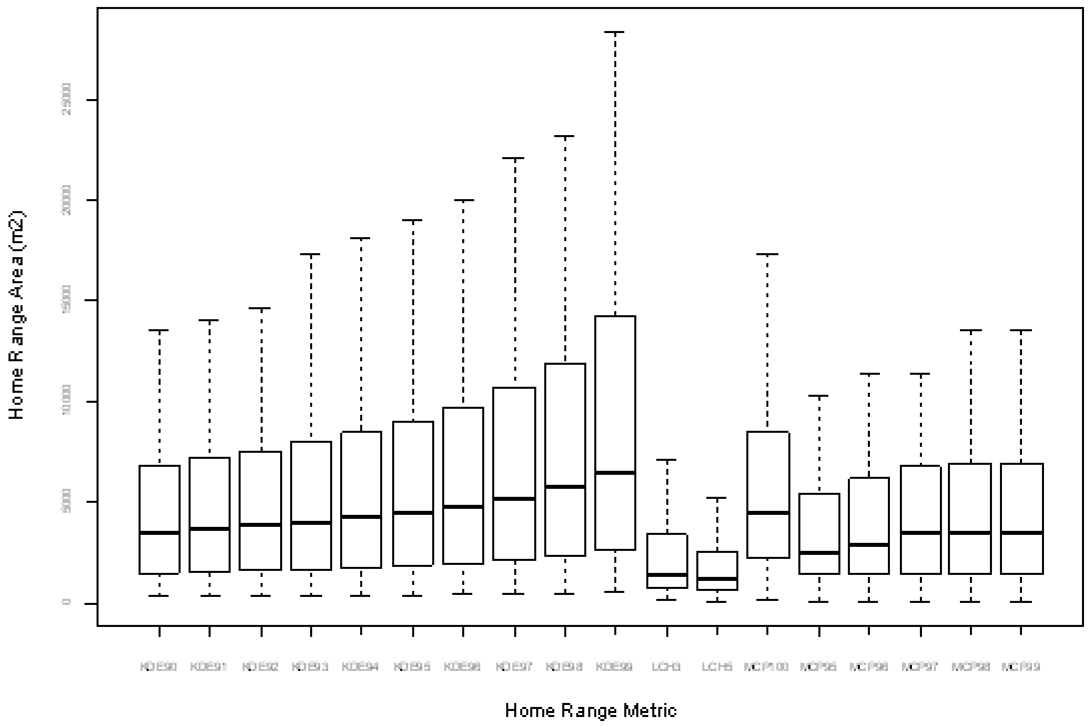
Home Range Area (m2)
0
5000
10000
15000
20000
25000
KDE90
KDE91
KDE92
KDE93
KDE94
KDE95
KDE96
KDE97
KDE98
KDE99
LCH3
LCH5
MCP100
MCP95
MCP96
MCP97
MCP98
MCP99
Home Range Metric

FIGURE TWO

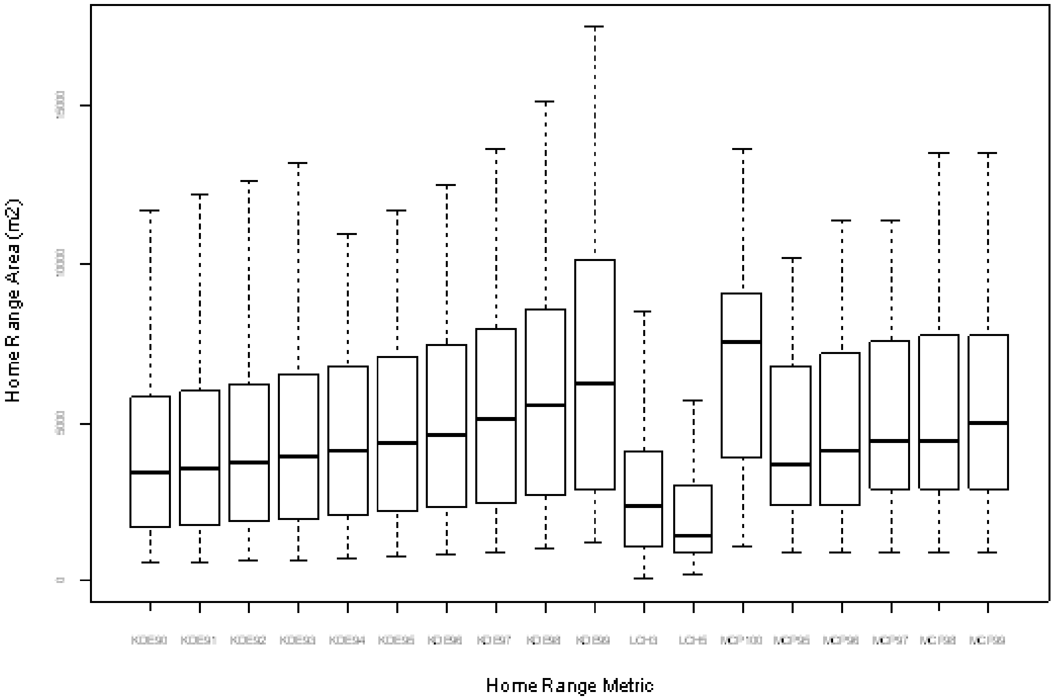
Home Range Area (m2)
0
5000
10000
15000
KDE90
KDE91
KDE92
KDE93
KDE94
KDE95
KDE96
KDE97
KDE98
KDE99
LCH3
LCH5
MCP100
MCP95
MCP96
MCP97
MCP98
MCP99
Home Range Metric

FIGURE THREE

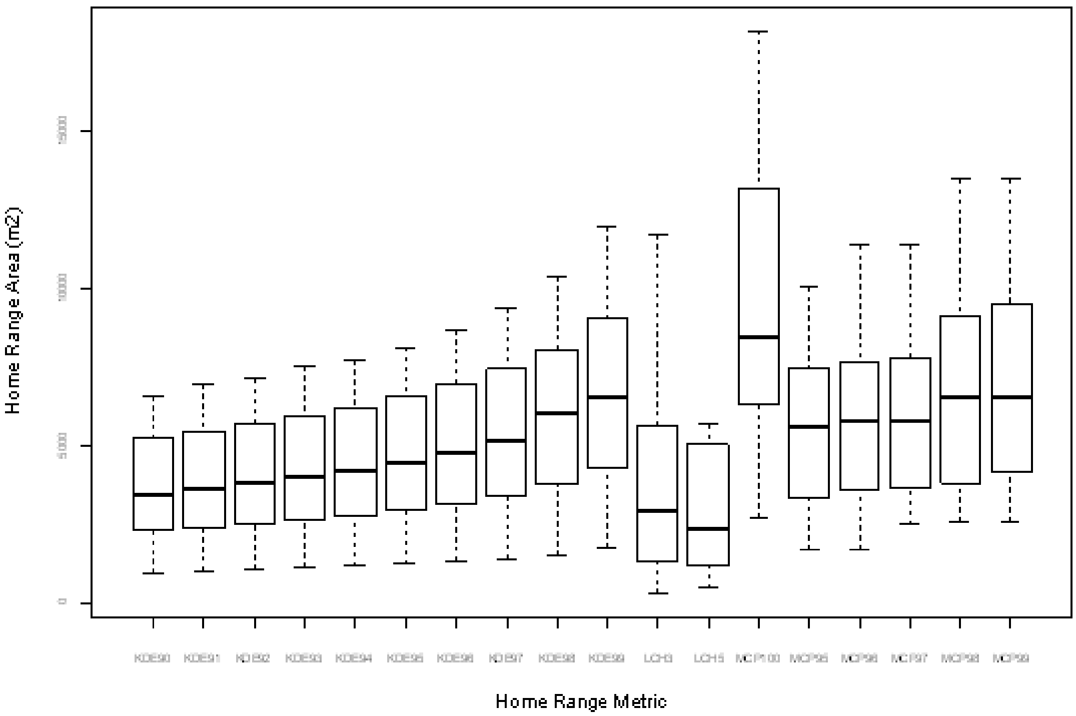

FIGURE FOUR (a)

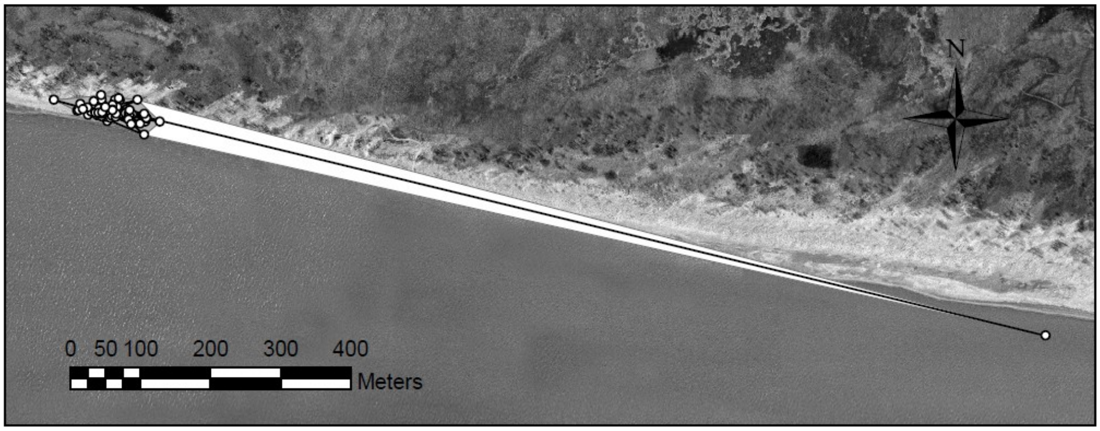

FIGURE FOUR (b)

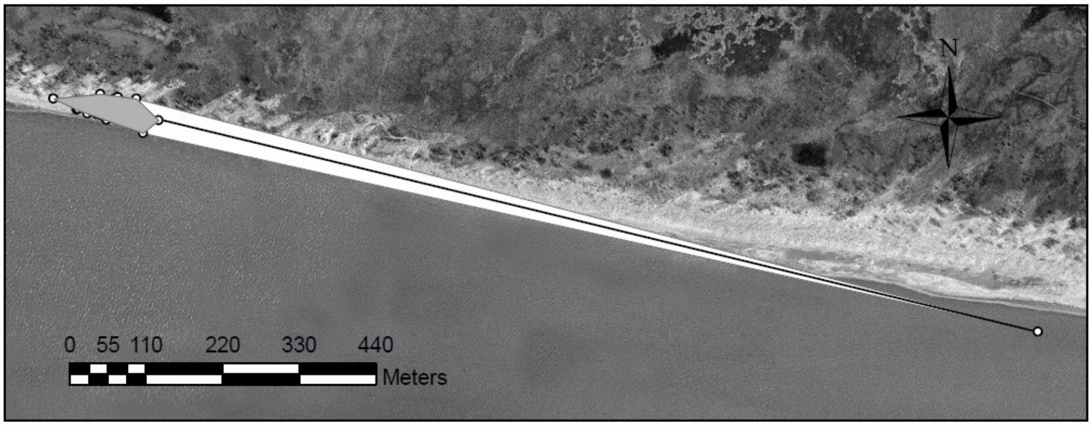

FIGURE FIVE

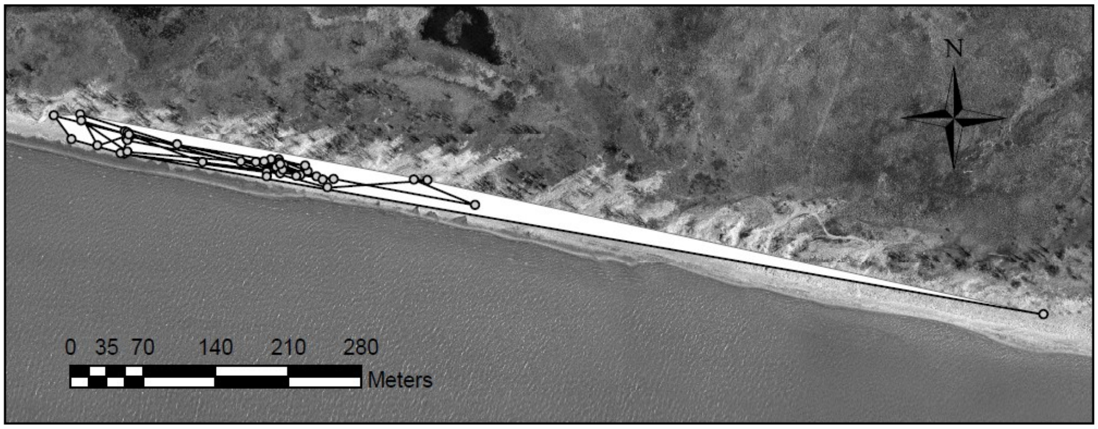

FIGURE SIX

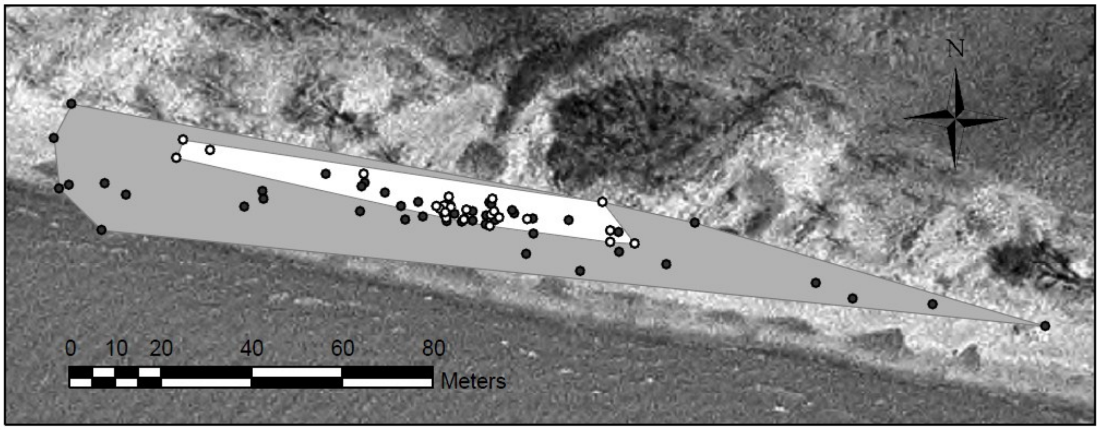

FIGURE SEVEN

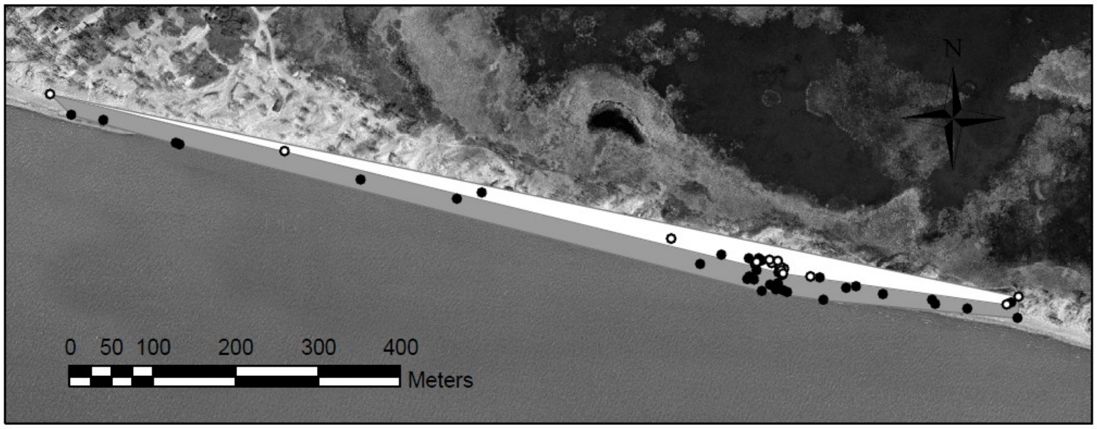

FIGURE EIGHT

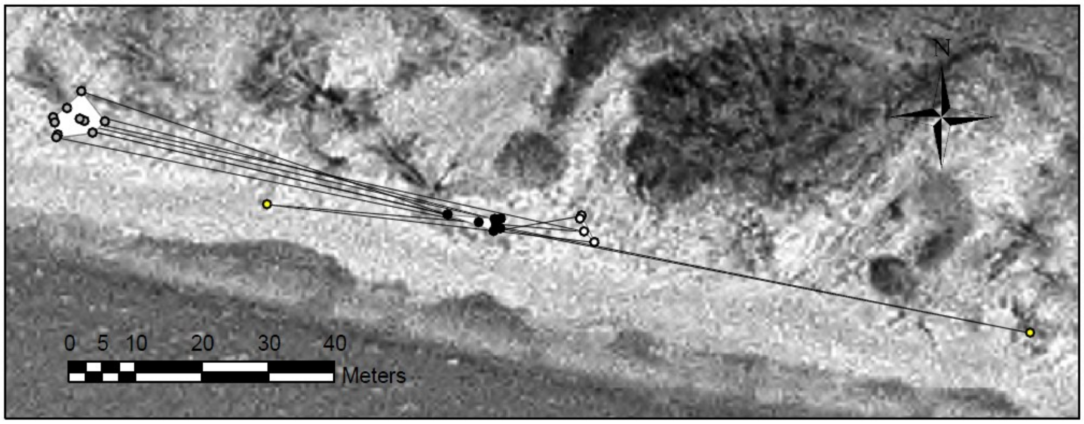

FIGURE NINE