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The role of local spatial heterogeneity in the maintenance of parapatric boundaries: agent based models of competition between two parasitic ticks

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The role of local spatial heterogeneity in the maintenance of parapatric boundaries: agent based models of competition between two parasitic ticks

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Abstract: Recent models of ecological parapatry, where the geographical distributions of two similar species abut without overlapping, have shown that spatial gradients in intrinsic growth rates can lead to sharp boundaries when dispersal is density dependent. However, a well documented parapatric boundary in southern Australia between two tick species that parasitise a large lizard lacks one or both of these features; dispersal of ticks is random and there may not be a gradient of population growth rates for one of the species. There is local variation in population growth rates arising from variation in the number of host lizards with overlapping host ranges. When more hosts are available there is a shorter waiting time for a host to arrive, and consequently higher survival rates. We construct a spatially explicit agent based model of the interaction between the two ticks and their lizard host and explore the role that this fine scale spatial heterogeneity plays in maintaining the parapatric boundary between the two tick species geographic distributions.

Keywords: Ecological parapatry; Tiliqua rugosa; Aponomma hydrosauri; Amblyomma limbatum

1. INTRODUCTION

Parapatric boundaries occur where the biogeographic distribution of two species abut but do not overlap [Bull 1991]. When there is no hybridization between the two species, the situation is described as ecological parapatry. A number of processes have been proposed to explain the maintenance of ecological parapatry including interspecific competition [MacArthur 1972], reproductive interference [Ribeiro and Speilman 1986], and habitat patchiness [Bull and Possingham 1995].

A recent 1-dimensional diffusion model found that density dependent dispersal could sharpen a boundary by narrowing the overlap zone [García-Ramos *et al*. 2000]; density independent dispersal lead to complete overlap. However, the biology of a well documented boundary between two species of reptile tick in Australia [Bull and Burzacott 2001] seems unlikely to have density dependent dispersal by the two participants. Ticks only move

when attached to hosts, and hosts reduce movement in response to tick infestation [Main and Bull 2000]. If anything, this would lead to inverse density dependent dispersal by ticks. Host abundance also varies across the boundary [Bull 1995], and when more hosts are available there is a shorter waiting time for a host to arrive, and consequently higher survival rates. This variation in tick survival could create habitat patchiness capable of maintaining the boundary [Bull and Possingham 1995]. We used an agent based model of the system to examine the effect of varying host abundance and dispersal rates on the maintenance of the parapatric boundary.

2. THE PARAPATRIC BOUNDARY

The study area is mixed chenopod shrubland and mallee woodland near Mt. Mary in the mid-north of South Australia. The region has an annual rainfall of about 250 mm. *Aponomma hydrosauri*

and *Amblyomma limbatum* are ectoparasites of large reptiles in southern Australia. The predominant host is the sleepy lizard, *Tiliqua rugosa*. The study area straddles a parapatric boundary between the distribution of both species; north of the boundary there are generally no *A. hydrosauri* ticks except for occasional outbreaks

Figure 1. Space-time perspective plots of the incidence of *Ap. hydrosauri* (A) and *Amb. limbatum* (B) along Transect 1 between 1982 and 1997. South is in the direction of decreasing position.

(Figure 1A). South of the boundary there are no *Amb. limbatum* (Figure 1B). The life cycle of both ticks has four stages: egg, larva, nymph and adult [Bull and Burzacott 2001]. They require three hosts to complete their life cycle. Larvae, nymphs and adult females each attach to a host, engorge, and then detach (usually when the host is in an overnight refuge). Engorged larvae and nymphs moult to the next stage. Engorged females lay eggs that hatch into larvae. Unfed larvae, nymphs and adults then wait in the refuge for a new host individual (or the same host) to attach to.

Adult males take in small meals, and wait for long periods on the host where they mate with attaching females. Tick activity and development is confined to the spring and summer months when temperatures are warm and lizards are active [Bull and Burzacott 2001].
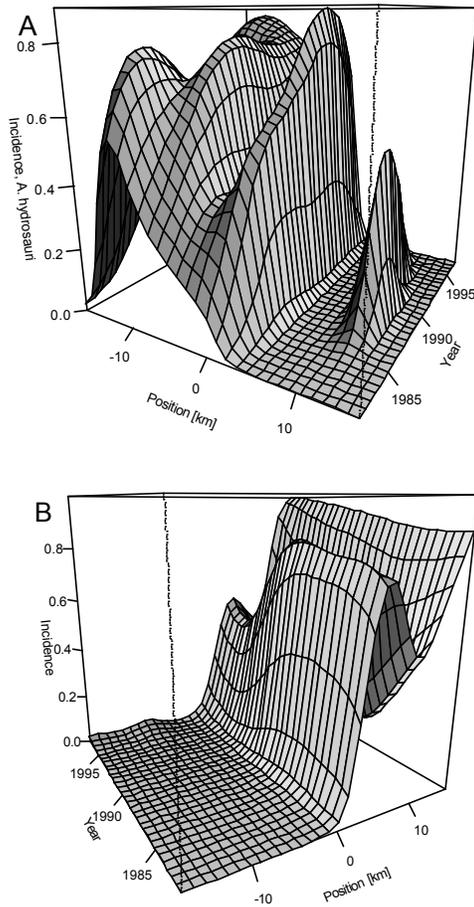
2. AN AGENT BASED MODEL OF TICK POPULATION DYNAMICS

From a tick's point of view, the landscape consists of the lizard hosts and their nocturnal refuge sites. There are R refuges in a 1 km x 20 km rectangle oriented perpendicular to the boundary zone; refuges are distributed with complete spatial randomness. These refuges are used by L lizards whose home ranges are centred on a randomly chosen refuge. All refuges within some distance h of the centre refuge are included in the home range. The landscape "wraps" in the short direction, so the model landscape is a long cylinder; the short boundaries are reflecting. The landscape is initialised with 10,000 ticks of each species. Each species is confined to ½ of the landscape at initialisation.

There are two time scales in the model. On the short time scale, movement of lizards, birth, development, and death of ticks is modelled each day. A series of days is then aggregated into a season, which is 210 days (1st September to 31st March) long. Development is frozen between seasons, under the assumption that autumn/winter temperatures are too low for tick activity. Ticks experience overwintering mortality, and host population dynamics also occurs between seasons.

The choice of a single day as the basic time step is logical given the assumption that all significant movement of ticks on and off lizards occurs only in refuges entered at night. Ticks are adapted to detach in the nocturnal refuges of their hosts, where desiccation risks are lower, and the chances of finding another host are higher [Bull and Burzacott 2001]. Within a single day, the model goes through several steps in the following order: ticks board lizards, lizards move between refuges, engorged ticks disembark from lizards, and ticks develop (Figure 2).

2.1 Tick embarkation, Lizard movement, Tick disembarkation

At the beginning of a model day, all lizards are in the overnight refuges in which they spent the previous night. The model checks all ticks in lizard occupied refuges, and any ticks that are found to be in a suitable state (ie. unfed larvae, nymphs, or adults) are moved onto the lizard. Assuming that all suitable ticks board lizards is almost certainly
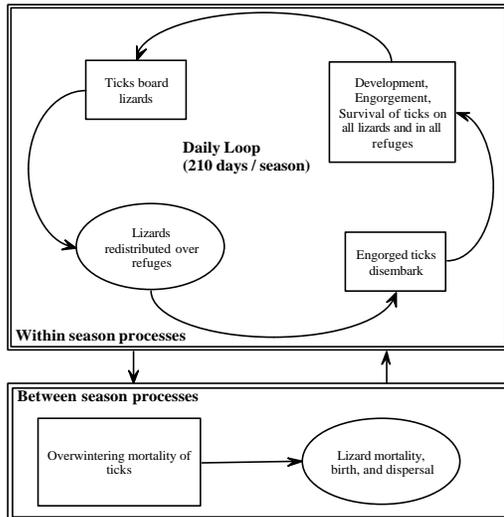

Figure 2 Flowchart of main model processes. Processes that are attributes of lizard population dynamics and behaviour which indirectly affect the ticks are placed in ovals, while processes directly affecting ticks are in rectangles.

an overestimate. If there is more than one lizard in a particular refuge, the number of ticks boarding each lizard is multi-nomially distributed with equal probability of boarding each lizard.

In the next step of the daily cycle, lizards move to new refuges. Each day, lizards move from one overnight refuge to another overnight refuge chosen randomly with equal probability from among those in their home range.

The third step within the daily cycle is to drop off successfully engorged ticks into their new refuges. Essentially, ticks which completed engorgement on the previous development step (ie. the previous night), are dropped off in the new refuge chosen by their host lizard.

The final step of the daily cycle handles development and mortality of all ticks, regardless of their current location. During this step, each tick is checked to see whether it ages, survives, or lays eggs, depending on its current stage and whether it is on a lizard or not.

2.2 Growth and Feeding

Stages that are engaged in growth or feeding (eggs, engorged stages in refuges, and unfed stages on lizards) follow a threshold process, where each stage lasts for a fixed number of days for each individual. Each individual is assigned a normally distributed random number as a development or engorgement time on entry to a new life history stage; values less than zero were truncated to zero. Both the mean and the variance are stage specific (Table 1), and refer to the non-truncated distributions. Although there are differences between the two species, at present we assume that all life history rates are equal. During the daily development step, each individual tick has its development or engorgement index decreased by one day. On the day the index reaches 0, the individual moves to the next stage (eg. an egg hatches to an unfed larvae, or a feeding nymph detaches). This means that the duration of all growing and feeding stages are normally distributed. This method is similar to those used for physiologically structured population models [Gurney *et al.* 1986], but includes variability between individuals.

Not all individuals succeed in attaching, engorging and detaching, and this is where density dependence (and hence competition) is known to occur in the system [Tyre *et al.* 2003]. The probability of successfully engorging is

$$p\{successful engorgement\} = \frac{e^b}{1+e^b} \quad . \quad (1)$$
$$b = -0.243 - 0.002(\# of ticks)$$

This depends on the total number of ticks of all stages at the time engorgement is complete. The mechanism underlying the relationship between tick density and engorgement success is presently unknown, and this empirical relationship is the simplest to implement in the model. We currently have no evidence of density dependence in engorgement success for nymphs or adults. We assumed nymphs had a 50% chance of success, and adults 100%, regardless of the number of ticks present on the lizard.

2.3 Survival

Predation on ticks within refuges by other invertebrates does occur [Bull *et al.* 1988], but is both spatially and temporally unpredictable, and

Table 1 Developmental, feeding, and mortality parameters used in the baseline model. All values are estimated from data in [Chilton 1989], assuming temperatures of 21^0C and 50-55% RH. All means have units of days. Feeding times for adult females includes the time required to be mated. Values in italics were extrapolated from estimates for larvae.

Stage	Location	Process	Stage durations Mean [days]	SD
Egg	Refuge	Hatching	53	1.32
Unfed Larvae	Refuge	Mortality	13.8	4.9
Unfed Larvae	Lizard	Feeding	30.6	11.7
Engorged Larvae	Refuge	Moulting	21.9	4.07
Unfed Nymphs	Refuge	Mortality	*37.3*	*5.5*
Unfed Nymphs	Lizard	Feeding	22.7	16.7
Engorged Nymphs	Refuge	Moulting	28	7.34
Unfed Adults	Refuge	Mortality	*100*	*7.3*
Unfed Females	Lizard	Feeding	39	17.6
Engorged Females	Refuge	Pre-oviposition	55.2	8.44
Mature Females	Refuge	egg-laying	40	--

we do not include it in the current model. When a host lizard dies from predation (primarily automobiles near Mt. Mary) or old age all ticks on the lizard also die. We included this mortality in a single, between season event (see below). We assume that the primary source of daily mortality is desiccation. The habitat has low rainfall (150-250 mm annually), and most development occurs during the hot, dry summer. The only moisture source available to ticks is a blood meal, and newly moulted, unfed ticks must wait until another host arrives before they can replenish their moisture supply. Eggs, engorged ticks in refuges, and ticks feeding on lizards are assumed to be unaffected by desiccation. We modelled mortality similarly to development, by providing each individual with a normally distributed time to death. This is the number of days that each individual is expected to survive without feeding. The time is decreased by one day in each developmental step, and individuals that reach zero are killed. Death is presumed to have occurred as a result of higher temperatures during the day, and so mortality in a refuge precedes ticks boarding lizards that enter that refuge on the next day.

2.4 Mating and Oviposition

When an unfed adult tick boards a lizard, it is randomly assigned to be a male or female with a sex ratio of 1:1. Adult male ticks remain on lizards for the remainder of their life, assumed to be a fixed 180 days. The only contribution they have beyond this point is to mate with unfed female ticks. After boarding a lizard there is a fixed five day period before an adult male is mature and capable of mating. When an unfed female boards a lizard, if there is one or more mature males aboard she is mated immediately. Otherwise, she waits on that lizard until a mature male appears, or 180 days passes. There is no negative impact of waiting to mate on a females subsequent reproductive output, although a negative impact has been observed in laboratory experiments [Chilton 1989]. Once a female is mated, she begins to engorge as described above for all other stages. This does introduce a slight Allee effect through delaying reproduction by females that board lizards without males.

Adult female ticks that have mated, successfully engorged, and dropped off in a refuge enter a pre-oviposition stage, the duration of which is normally distributed and handled identically to aging, feeding, and moulting. Once the pre-oviposition period is complete, each day for 40 days they add a number of new eggs to that refuge.

2.5 Between season processes

There are two processes that occur between the end of one season and the beginning of the next: overwintering tick mortality and lizard population dynamics. All ticks, regardless of location, have a stage specific chance of mortality over winter. This reflects exposure, desiccation, disease, predation, and fungal infection. We set this to 10% for all stages other than eggs. It is set low

relative to mortality during the active season because the risk of desiccation is reduced in the cooler, wetter climate of winter, and invertebrate predators are less active. However, laboratory observations indicate that no eggs hatch when held at temperatures of less than 15°C. Therefore, egg mortality is 95% over the winter in the model, which allows for a small margin of error in the laboratory estimate of 100%.

Lizard population dynamics is also simplified. A flat 10% of all lizards are chosen at random and killed at the end of each season. Empirical observations place annual adult survival at around 90% [Bull 1995]. Any ticks on the killed lizards are also killed. The killed lizards are replaced from newborns whose mothers are chosen at random from the surviving lizards. These newborn lizards spend one season in their mother's home range, before randomly choosing a home range of their own (natal dispersal). This results in no net change in the number of lizards available, but tends to redistribute 10% of the population to new locations each season after the first two. New home range sites are selected in one of two ways: exponentially distributed dispersal distance with a mean of 500 m (limited dispersal scenario), or effectively unlimited dispersal with a mean of > 6000 m (high dispersal scenario).

3. RESULTS

All results are presented as smooth fits to data sampled along a transect positioned down the centre of the simulated landscape. Simulated samples are collected once per week. Each lizard whose home range overlaps the transect has a 10% probability of being captured and having its current load of ticks enumerated. The incidence is worked out for all captures in a year within a 1 km segment of the transect. This mimics the kind of sampling carried out in reality (Figure 1). In the following, the boundary zone is defined as the area where joint incidence of both species is greater than 1%.

High Dispersal: A representative space-time perspective plot of the "joint" incidence (probability that a host has both species of tick) is shown in Figure 3. Although both species are separated by 4 km at initialisation, their distributions broadly overlap in less than 50 years. In addition, the simulated data show none of the stable spatial heterogeneity evident in Figure 1.

Low Dispersal: A representative space-time perspective plot of the joint incidence of both tick

species is shown in Figure 4. The distributional boundaries of both species move slowly through time, leading to an increase in the breadth of the zone where both species can be found. Across 4 replicate runs the width of the boundary zone increases at a rate of 20 m / year (SE=4 m / year; Figure 5). Although the rate of increase is small, the boundary zone is clearly not stable.
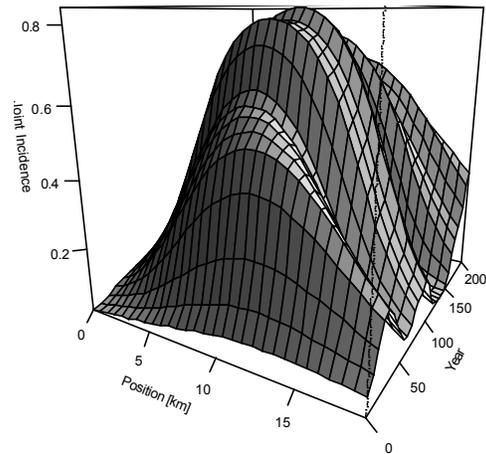

Figure 3 Joint incidence of both ticks in a high dispersal run. Position is in km, with zero the mid-point between the two species initial distributions.
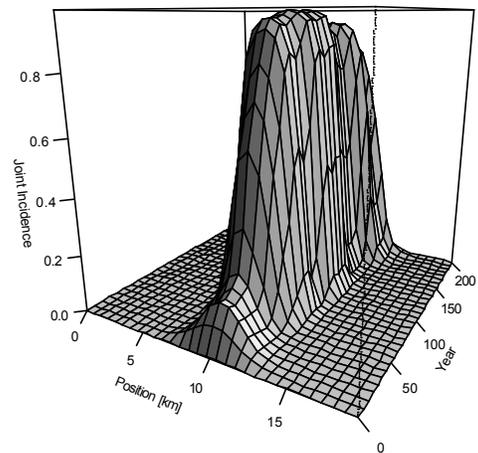

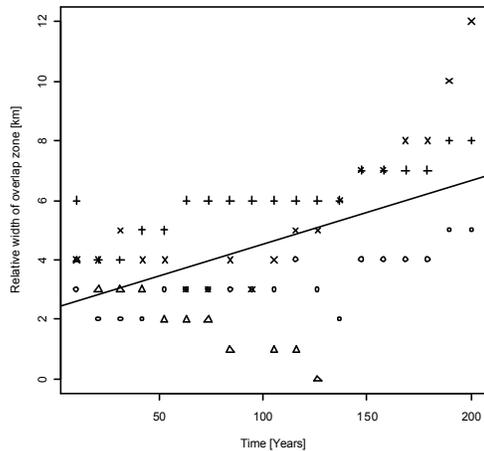**Figure 4** Joint incidence of both ticks in a low dispersal run.

Figure 5 Change in width of the boundary zone with time. Each symbol represents a replicate simulation.

Table 2 Results of GAM fits to incidence of *Ap. hydrosauri* for one replicate south of the initial boundary. s( ) indicates the smooth term, Y is year, P is Position, and L is relative lizard abundance. Lizard effect is the linear coefficient (standard error).

Model	Deviance explained	Lizard Effect
s(Y, P)	77%	-
s(Y,P)+L	78%	0.05 (0.003)
s(Y) + L	33%	0.15 (0.002)

Effect of heterogeneity in host abundance: Table 2 compares three Generalised Additive Model (GAM) fits to incidence of *Ap. hydrosauri* from south of the initial boundary. A model with a smooth term in both space and time explains 77% of the deviance in incidence. Adding a linear effect for the abundance of hosts at each point only increases the explanatory power to 78%. Deleting spatial position from the smooth term dramatically reduces the explanatory power of the model, although the effect of lizard number increases. It appears that heterogeneity in host abundance does influence tick abundance (positive coefficient), but that this effect is largely overridden by spatial autocorrelation in the abundance of ticks themselves.

5.   CONCLUSIONS

Our preliminary results for this model clearly indicate that dispersal of juvenile hosts has a dramatic effect on the rate at which the boundary zone can move. In addition, heterogeneity in host abundance arising simply through random birth, death, and movement of the hosts does influence tick abundance, but does not lead to a stationary boundary. However, despite the absence of a gradient in life history performance or density dependent dispersal the boundary zone remains quite static for relatively long periods of time.

Our future work will concentrate on comparisons of the agent based model outlined here with models based on diffusion approximations to movement, and on comparing the output of the model with the empirical data.

6.   ACKNOWLEDGEMENTS

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