

Decreased relatedness between male prickly forest skinks (*Gnypetoscincus queenslandiae*) in habitat fragments

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Abstract

In species with low levels of dispersal the chance of closely related individuals breeding may be a potential problem; sex-biased dispersal is a mechanism that may decrease the possibility of cosanguineous mating. Fragmentation of the habitat in which a species lives may affect mechanisms such as sex-biased dispersal, which may in turn exacerbate more direct effects of fragmentation such as decreasing population size that may lead to inbreeding depression. Relatedness statistics calculated using microsatellite DNA data showed that rainforest fragmentation has had an effect on the patterns of dispersal in the prickly forest skink (*Gnypetoscincus queenslandiae*), a rainforest endemic of the Wet Tropics of north eastern Australia. A lower level of relatedness was found in fragments compared to continuous forest sites due to a significantly lower level of pairwise relatedness between males in rainforest fragments. The pattern of genetic relatedness between sexes indicates the presence of male-biased dispersal in this species, with a stronger pattern detected in populations in rainforest fragments. Male prickly forest skinks may have to move further in fragmented habitat in order to find mates or suitable habitat logs.

Introduction

Habitat fragmentation is an unfortunate reality of modern ecology. Understanding the effects of fragmentation may help us to better manage remaining tracts of forest and to increase the likelihood of a population's survival in the short- and long-term. The likely effects of fragmentation are often difficult to predict, with the most cohesive factor among different studies being the diversity of changes recorded (Debinski and Holt 2000). Habitat fragmentation has been found to disrupt patterns of habitat use (Sarre 1998), mating systems (Peacock and Smith 1997; Ims and Andreassen 1999; Walters et al. 1999) and dispersal (Wolff et al. 1997; Stow et al. 2001), leading to decreased juvenile recruitment (Wolff et al. 1997) and reproduc-

tive success (Breininger 1999; Walters et al. 1999). Short-term effects of fragmentation may include increased genetic diversity in habitat fragments due to emigration of individuals from the large surrounding area at the time of habitat clearance (Porter 1999). Over a longer term, however, habitat fragmentation may lead to a decrease in genetic diversity due to the combined effects of reduced population size and increased isolation (Frankel and Soule 1981; Young and Clarke 2000) as well as an increased risk of extinction due to an accumulation of deleterious alleles (Higgins and Lynch 2001). The ecology of a species, such as its dispersal ability, can determine the extent to which it is affected by drift and inbreeding as a result of fragmentation, as can the degree to which population size and migration are reduced, and the time since

isolation; (Crow and Aoki 1984; Slatkin 1987). For example, ecological changes resulting from habitat fragmentation could lead to a disruption of inbreeding avoidance mechanisms. This might, in turn, exacerbate the effects of fragmentation on a species by increasing mating between closely related individuals in small populations already affected by decreasing population size and reduced dispersal. Such a pattern of ecological change in a fragmented habitat has been documented in Cunningham's skink (*Egernia cunninghami*), in which dispersal patterns and relatedness changed in response to habitat clearing due to decreased movement by females in disturbed areas (Stow et al. 2001).

The prickly forest skink (*Gnypetoscincus queenslandiae*) is a rainforest endemic skink from the Wet Tropics of north-eastern Australia. It is common inside and under rotting logs on which it relies for cover and prey (Cogger 2000). The prickly forest skink has been subject to substantial habitat loss due to large scale clearing of rainforest at the beginning of last century (Winter et al. 1987). This species is likely to be vulnerable to the effects of fragmentation as it is a rainforest obligate, it is rare in corridors of regrowth, and exhibits very limited dispersal (Cunningham and Moritz 1998; Sumner et al. 2001). It is expected that clearing would result in isolation of populations within rainforest fragments, rendering prickly forest skinks more prone to the effects of inbreeding and increasing relatedness within habitat isolates (Frankel and Soule 1981; Mills and Smouse 1994). Log density has been found to decrease with decreasing fragment size (Sumner et al. 1999) and this may further impact the structure of lizard populations in rainforest fragments. Observed changes in genetic diversity within and among populations of prickly forest skinks in fragmented forest on the Atherton Tableland were found to be small, but in the direction predicted (Sumner et al. 2004). If rainforest fragmentation has led to decreased population size and decreased migration of prickly forest skinks into fragments, then it is expected that average within-fragment relatedness levels would be higher than average within-continuous forest relatedness levels.

Inbreeding depression (a reduction in fitness resulting from mating between close relatives) has been demonstrated to be a potential problem in a number of natural populations (Jiminez et al. 1994; Keller et al. 1994; Madsen et al. 1996; Olsson et al. 1996). Suggested mechanisms that may have

evolved to avoid cosanguineous mating in lizards include: (1) sex-biased dispersal, where one sex is more likely to disperse than the other, or to disperse further (Doughty et al. 1994), (2) multiple mating by females (Olsson et al. 1994a; b), and (3) females mating with the potential mate least related to her (Bull and Cooper 1999; Gardner et al. 2001). Dispersal in *G. queenslandiae* is extremely restricted, evidence for which is seen in the occurrence of an isolation by distance pattern in an area of just 3 ha (Sumner et al. 2001). A mechanism such as sex-biased dispersal may therefore be in place to avoid breeding between closely related individuals, and as this is relatively straight forward to assess, I aim to examine sex-biased dispersal as a mechanism for avoiding inbreeding depression first.

Molecular methods utilising highly variable loci, such as microsatellite DNA, are ideal for calculating relatedness between individuals with unknown ancestors and hence for assessing the occurrence of mechanisms such as sex-biased dispersal (Queller et al. 1993; Luikart and England 1999; Sunnucks 2000). Molecular methods also allow one to gain information on dispersal that may not be possible with field based mark recapture methods, especially in species like the prickly forest skink with low dispersal and that is not easily seen or captured without disturbing its log habitat (Sumner et al. 2001). Dispersal patterns can be inferred by examining pair-wise relatedness coefficients between individuals. If sex-biased dispersal occurs, then individuals of the philopatric sex in close proximity to one another will have higher pairwise relatedness relative to members of the dispersing sex (Taylor et al. 1997; Stow et al. 2001).

The aims of this study are first to determine whether relatedness patterns in populations in fragmented forest sites differ from those in continuous forest sites. Second, I wish to determine whether relatedness patterns within, and between, all males and all females at each site indicate the presence of sex-biased dispersal, and to ascertain whether there is any change in these patterns in fragmented versus continuous forest sites.

Materials and methods

Study species

Prickly forest skinks are a rainforest obligate species that live under and inside rotting logs on the forest

floor (Naylor 1980; Cogger 2000). They mature at approximately 65 mm snout to vent length (SVL), with females giving birth to one to five live young between January and April (Cunningham 1993; Sumner et al. 2001). They are moderately long-lived, with an estimated generation time of 6.5 years and a maximum age of approximately 10 years (Cunningham 1993; Sumner et al. 2001). Dispersal distance, or the average distance between an individual's birthplace and that of its offspring, has been estimated as occurring at a rate of 843 m²/generation (assuming a generation time of 6.5 years) using mark recapture data, or 404 m²/generation using a genetic method based on microsatellite DNA genotypes (Sumner et al. 2001).

Field work

Large scale clearing occurred on the Atherton Tableland in the Wet Tropics of Australia between 1920 and 1940 due to logging and clearing for dairy farming. A substantial number of rainforest fragments remain, surrounded by pastureland (Winter et al. 1987). Large tracts (> 3000 ha) of continuous forest survive only on steeper hillsides encircling the Tableland, the majority of which has been selectively logged (Laurance 1990). Skinks were captured from seven rainforest fragments and four continuous forest sites on the Atherton Tableland during a single field trip in January 2000, with samples at an additional continuous forest site (Massey Creek) collected in November 1998 (Figure 1). The fragments were spread over a similar, but slightly longer and narrower, geographical area relative to the sites in the continuous forest. Fragments were isolated at approximately similar times (Pahl et al. 1988; Sumner et al. 2004), between 1920 and 1940 (Winter et al. 1987). All fragments were at least 200 m from neighbouring forest, more than twice the greatest movement distance recorded for an individual in a 3 year mark-recapture study (Sumner et al. 2001). From this information, and from knowledge of this species specific habitat requirements, I assume that immigration into fragments is negligible and that most emigrants perish. Sites were searched until approximately 30 individuals were captured, during which time approximately 2–5 ha were covered, depending on the size of the fragments and the density of individuals at the site. At Massey Creek 3 ha, exactly,

were sampled during a more detailed mark-recapture study (see Sumner et al. 2001 for more details). Skinks were hand captured, a measurement of the snout to vent length (SVL) was made, and the sex was recorded. Individuals of less than 65 mm SVL could not be sexed accurately, so they were recorded as sub-adults. A tail tip was taken from each individual and fresh frozen on dry-ice for later extraction of DNA. Skinks were released at the site of capture.

Genetic data

DNA was extracted using a standard phenol-chloroform extraction procedure (Sambrook et al. 1989) on the fresh frozen lizard tails. Nine microsatellite loci were amplified according to the PCR conditions given in Sumner et al. (2001). The primer pairs used were: GQ10/11F GQ16/17F2, GQ18/19F, GQ20/21F, GQ24F/25, GQ36/37F, GQ38B/39F, GQ42B/43F, and EA1F/2B. PCR products were resolved on a model 373 DNA sequencer and analysed using standard software (Applied Biosystems).

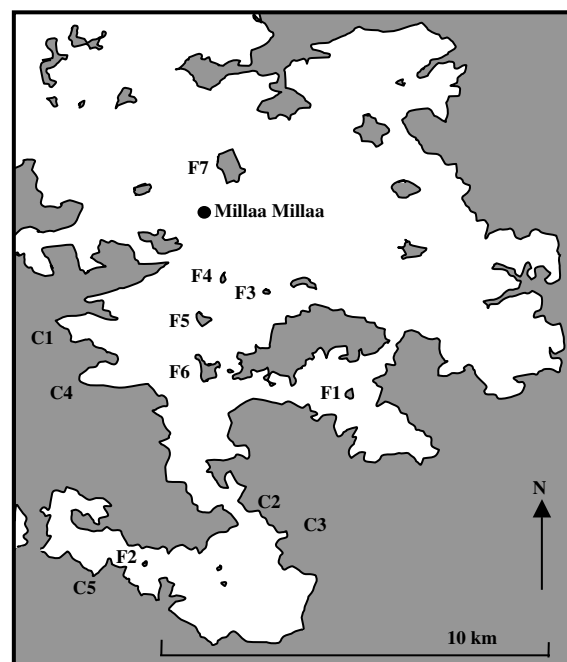


Figure 1. Location of sites sampled on the Atherton Tableland in the Wet Tropics of south-eastern Australia. F1–F7 are fragments and C1–C5 are continuous forest sites. Grey areas indicate primary forest and white areas indicate cleared land.

Measuring relatedness

The average relatedness among individuals was estimated using the programme Relatedness 5.07 (Goodnight and Queller 1998). This method has been found to perform similarly well to other marker-based relatedness programmes (Van de Casteele et al. 2001). The programme calculates the Queller and Goodnight (1989) index of relatedness (R) between individuals or demographically defined groups, using a regression-based measure of relatedness calibrated by the frequency of alleles and number of individuals in the population. An unbiased estimate of relatedness within subsamples of a population requires a large reference population that includes many unrelated individuals. The reference individuals must be genetically different due to being unrelated only, not due to being sampled from a different isolated population, or deme, that has diverged over time. The Queller and Goodnight (1989) R may vary between -1 and $+1$, but with the proper reference population it would be expected to vary between 0 and 1 . The value for pairs of individuals is expected to vary greatly due to stochasticity, in particular, when either of the individuals possesses a rare allele, a negative R value may be expected for a pair (De Ruiter and Geffen 1998). In this study each site was analysed as a separate deme as significant differences in allele frequencies occur between sites (Sumner et al. 2004). Sub-adults were excluded from the allele frequency database for each site for all analyses to avoid biasing the estimates with a high proportion of related animals. Standard errors of R estimates were obtained by jack-knifing over the nine loci and also over the twelve sites (Queller and Goodnight 1989). Values were jack-knifed over loci, preferentially, as the relationship between animals in the samples is not known, but the loci appear to be independent and not sex-linked (Sumner et al. 2001; Sumner et al. 2004). Only the results of jack-knifing over loci are reported, unless the results differ considerably when jack-knifing over sites.

Fragmentation effects

The effect of fragmentation on relatedness was assessed by comparing average relatedness between all individuals sampled in fragments to those in continuous forest. This comparison was

then repeated comparing R between males, females, and sub-adults separately.

Sex-biased dispersal

Relatedness between all male/male pairs was compared to all male/female pairs, then all female/female pairs were compared to all female/male pairs to determine whether the pattern of relatedness suggested sex-biased dispersal. These relatedness estimates were then repeated for all sampled adults in fragments, then all sampled adults in continuous forest, to determine whether there is a change in the relatedness pattern as a result of habitat fragmentation. Bonferroni corrections were applied to adjust the probability level for multiple tests.

Results

A total of 411 prickly forest skinks were captured and genotyped, of which 126 were adult females, 90 were adult males, 190 were sub-adults (Table 1) and five were of unknown age or sex.

Complete genotypes were obtained for 362 individuals, with 2.14% of genotypes missing across the entire data set. The total number of alleles per locus ranged from 5 up to 28, with an average of 19.6 alleles per locus across all sites. Sumner et al. (2001, 2004) found no evidence of sex-linkage or genotypic disequilibrium for these loci, and all loci appeared to be in Hardy–Weinberg equilibrium. There was no strong evidence of null alleles at any locus (Sumner et al. 2001, 2004).

Fragmentation effects

Contrary to the predicted effect, overall relatedness in fragments ($R = -0.0376$; $SE = 0.0004$) was significantly less than in continuous forest sites ($R = -0.0249$; $SE = 0.0005$; $P < 0.0001$; Table 2); after jack-knifing over site the result still differed significantly at the 5% level ($P = 0.0413$), however the considerable decrease in the probability level indicates a substantial site effect (R for each site is shown in Table 1). Males in fragments were found to be significantly less related on average ($R = -0.0836$; $SE = 0.0151$) than were males in continuous forest sites ($R = -0.0345$; $SE = 0.0245$; $P = 0.0002$; Table 2). No significant

Table 1. Sites sampled on the Atherton Tableland, the number of individuals genotyped (No.), the site type, the fragments size in hectares (from Sumner et al. 2004) and the within site relatedness for all sampled prickly forest skinks

Site name	Code ^a	No.	Site type	Fragment size (ha.)	<i>R</i>
Souita Falls	F1	25	Fragment	2.00	0.0035
Maalan Road	F2	42	Fragment	2.46	0.0136
Waltham	F3	27	Fragment	2.64	0.0066
Pat Daley Park	F4	18	Fragment	5.96	0.0065
Nose Ring	F5	29	Fragment	24.19	0.0013
Whiteing Road	F6	30	Fragment	36.31	-0.0009
MillaaMillaa Falls	F7	27	Fragment	65.06	0.0087
Brotherton	C1	28	Continuous	-	0.0015
Cross-eye	C2	30	Continuous	-	0.0056
Mt. Father Clancy	C3	32	Continuous	-	0.0079
Reynolds	C4	28	Continuous	-	0.0091
Massey Creek	C5	94	Continuous	-	0.0367

^aCode refers to sites shown in Figure 1.

difference in relatedness was found between females in fragments ($R = -0.0238$; $SE = 0.0113$) and in continuous forest ($R = -0.0124$; $SE = 0.0187$; $P = 0.1416$; Table 2), nor between sub-adults in fragments ($R = -0.0212$; $SE = 0.0177$) and in continuous forest ($R = -0.0177$; $SE = 0.0121$; $P = 0.6269$; Table 2). Thus the lower overall relatedness in fragments appears to be due to the substantially lower relatedness between males in fragments compared to those in continuous forest.

Sex-biased dispersal

All 12 sites were analysed to determine whether patterns of relatedness suggested sex-biased dispersal. Males prickly forest skinks were, on aver-

Table 2. Average pairwise relatedness (*R*) and standard error (SE) in fragmented and continuous forest sites

Site type	Comparison	<i>R</i>	SE
Fragment	All	-0.0376	0.0004
	Male	-0.0836	0.0151
	Female	-0.0238	0.0113
	Sub-adult	-0.0212	0.0177
	Male/female	-0.0286	0.0087
	Female/male	-0.0526	0.0199
Continuous	All	-0.0249	0.0005
	Male	-0.0345	0.0245
	Female	-0.0124	0.0187
	Sub-adult	-0.0177	0.0121
	Male/female	-0.0080	0.0171
	Female/male	-0.0009	0.0171

age, significantly less related to other males in the same sites ($R = -0.0614$; $SE = 0.0174$) than to females in the same site ($R = -0.0269$; $SE = 0.0187$; $P < 0.0001$), whilst females were, on average, as related to other females in the same site ($R = -0.0238$; $SE = 0.0113$) as they were to males ($R = -0.0526$; $SE = 0.0199$; $P = 0.2561$). When the later result was jack-knifed over sites, however, the result neared significance ($P = 0.0737$) suggesting substantial differences between sites. This pattern of relatedness does suggest the presence of male biased dispersal in prickly forest skinks.

When fragments were analysed separately, male prickly forest skinks in fragments were, on average, found to be significantly less related to other males in the same sites ($R = -0.0836$; $SE = 0.0151$) than to females in the same site ($R = -0.0286$; $SE = 0.0087$; $P < 0.0001$; Table 2), whilst females in fragmented forest sites were, on average, significantly more related to other females in the same fragment ($R = -0.0238$; $SE = 0.0113$) than to males in the same fragment ($R = -0.0526$; $SE = 0.0199$; $P = 0.0024$; Table 2). This pattern again suggests male-biased dispersal in these populations of prickly forest skinks.

Males in continuous forest were found to be significantly less related to other males at the same site ($R = -0.0345$; $SE = 0.0245$) than to females at the same site ($R = -0.0080$; $SE = 0.0171$; $P = 0.0182$; Table 2). When females were analysed, there was no significant difference in relatedness

between females at the same site ($R = -0.0124$; $SE = 0.0187$) compared to relatedness between females and males ($R = -0.0009$; $SE = 0.0242$; $P = 0.2757$; Table 2) in contrast to the pattern found in rainforest fragments.

Discussion

Fragmentation effects

The results of this study indicate a significant effect of fragmentation on prickly forest skinks, with a decrease in average pairwise relatedness, specifically between males, in fragments compared to those in continuous forest. This result is the opposite of the hypothesised increase in relatedness levels among populations within fragments as a result of decreased population size and decreased migration. Immigration of individuals from the surrounding area at the time of habitat clearance may have artificially increased genetic diversity in fragments in the generations following habitat fragmentation, leading to a decrease in genetic relatedness (Porter 1999). Fifty to 80 years, or approximately 10 generations, have passed since the majority of the fragments in this study were isolated (Pahl et al. 1988; Sumner et al. 2004). From the current study, there is no evidence of genetic erosion in fragments, leading to a decrease in genetic diversity and an increase in relatedness as predicted. However, in a previous study, using the same samples and sites, Sumner et al. (2004) detected a decrease in average allele number in the four smallest fragments compared to large fragments and continuous forest sites and a breakdown in isolation by distance patterns in fragments, both of which conform to the expectations of decreased genetic diversity and increased drift in small, isolated populations (Frankel and Soule 1981; Woodruff 2001).

Prickly forest skink abundance was found to be lower in rainforest fragments than in continuous forest sites (Sumner et al. 1999), so it is possible that during sampling individuals were captured from a greater area in fragments, possibly encompassing a greater number of genetic neighbourhoods (Sumner et al. 2001). This may have led to a lower estimate of relatedness between individuals.

Immigration from surrounding areas and sampling design may have had some impact on levels of average pairwise relatedness in fragments,

but neither possibility explains why relatedness among males in fragments is significantly lower than in continuous forest, where as females and juveniles do not differ significantly in relatedness from those found in continuous forest. The decreased pairwise relatedness in male prickly forest skinks may indicate that greater dispersal by males is necessary in order to find mates or suitable habitat within rainforest fragments. Migration into, or among, fragments is unlikely to be common due to the specific rotting log habitat requirements of this species and minimal tolerance for low humidity environments (S. Cook pers comm.; Sumner et al. 2004), so differences in suitability or distribution of microhabitat within fragments (Sumner et al. 1999), forcing increased local movements, appears more likely. Prickly forest skinks were found to have an isolation by distance pattern discernable over just three hectares (Sumner et al. 2001), so in sites such as those in this study, ranging in size from 2 to 65 ha (Sumner et al. 2004) males may not have to increase their dispersal distance by much to have a discernable effect on relatedness patterns. In their work on the skink *Egernia cunninghami*, Stow et al. (2001) found higher within group R -values (mean \pm SD; 0.253 ± 0.274) in cleared forest sites than in a naturally forested reserve site (0.264 ± 0.247). This was a result of significantly higher pairwise relatedness between females in cleared areas compared to those from the forest reserve which they suggested was due to a decrease in dispersal in female *E. cunninghami* in cleared forest. This species had been subjected to habitat disturbance for approximately 100 years, a similar timescale to prickly skinks in this study. In another lizard species, decreased mtDNA diversity in the reticulated velvet gecko (*Oedura reticulata*) was thought to be due to decreased dispersal following habitat fragmentation (Sarre 1995).

Sex-biased dispersal

The results of this study indicate the presence of sex-biased dispersal in prickly forest skinks with males as the dispersing sex. The occurrence of sex-biased dispersal in skinks varies both among and within species in the family Scincidae. No evidence of sex-biased dispersal was found in sleepy lizards (*Tiliqua rugosa*; Bull and Cooper 1999); conversely, some evidence of male-biased dispersal was found in

Egernia stokesii (Gardner et al. 2001). Changes in dispersal patterns as a result of habitat fragmentation have been found in Cunningham's skink (*Egernia cunninghami*), where relatedness estimates indicated that female dispersal decreased as a result of habitat clearing, resulting in male-biased dispersal in the cleared site (Stow et al. 2001). In this study significantly lower pairwise relatedness between males than between male/female pairs was found, indicating male-biased dispersal in populations in both fragments and continuous forest sites. The pattern differed for females however; females were significantly more related to other females in fragments compared to female/male comparisons, whereas this relationship did not differ significantly in continuous forest sites. This suggests a decrease in dispersal in females in fragments, leading to higher pairwise relatedness between females than male/female pairs.

Low movement recorded in adult prickly forest skinks, males especially (Sumner et al. 2001), suggests that once the dispersal phase is over prickly forest skinks remain relatively sedentary, so in order to better understand and explain dispersal patterns in prickly forest skinks it would be important to identify differential dispersal between sub-adult males and sub-adult females. It was not possible to determine the sex of sub-adults in the field; the current attempt to investigate dispersal patterns in prickly forest skinks was somewhat frustrated by this fact. A more detailed ecological study on prickly forest skinks might enable further testing of sex-biased dispersal by identifying breeding adults, determining parentage of offspring, and testing methods for field based, or genetic, sexing of individuals.

Despite prickly forest skinks current decrease in relatedness in fragments, indicating little effect of inbreeding, an overall decrease in allelic diversity has been identified in this species, suggesting that without the creation of forest corridors that allow dispersal into rainforest fragments, there may continue to be genetic erosion over time.

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