

## Inbreeding and promiscuity in the endangered grand skink

Oliver Fleetwood Berry

*School of Animal Biology, University of Western Australia, 35 Stirling Highway, Crawley, Perth, 6009, WA, Australia (\*Corresponding author: Phone: +61-8-6488-2247; Fax: +61-8-6488-1029; E-mail: ofb@cyllene.uwa.edu.au)*

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### Abstract

The inbreeding avoidance hypothesis predicts that organisms that often encounter relatives as potential mates should evolve behaviours to avoid incestuous matings. Avoidance behaviours have practical importance for small populations because deleterious genetic processes may be less imminent than otherwise expected from genetic models that assume random mating. I used genetic techniques to investigate the extent of inbreeding and inbreeding avoidance behaviours in rare lizards from southern New Zealand. Grand skinks, *Oligosoma grande*, live in small patchily distributed groups, and have low rates of inter-group dispersal (ca. 3–20% disperse). I used data from 15 microsatellite loci to test the hypothesis that adults are likely to encounter kin as potential mates and will inbreed. These data showed that adult skinks usually inhabited rock outcrops with adult relatives of the opposite sex – up to 35% of potential mates were of equivalent relatedness as half-sibs and 17% were equivalent to full sibs. However, skinks did not preferentially breed with less related mates, and 18.2% of matings were between individuals of equivalent relatedness as full-sibs. Instead, skinks mated with partners of all levels of relatedness, and were promiscuous – almost half of adult females and nearly three quarters of adult males reproduced with multiple partners. In addition, inbreeding had no effect on survival of offspring in their first year. Two other putative mechanisms of inbreeding avoidance, sex-biased and natal dispersal, were not pronounced in this species. This study adds to a growing list of species that inbreed despite the risks.

### Introduction

Addressing the dual threats of inbreeding depression and loss of genetic variation is central to many conservation programs, particularly those focussed on small or captive populations (Caughley 1994). These concerns stem mainly from theoretical, laboratory and captive animal studies suggesting that inbreeding can reduce individual fitness (Frankham 1995; Lynch et al. 1995), and that populations with low genetic variation may be unable to respond adaptively to environmental change (Fisher 1930; Lande and Shannon 1996; Franklin and Frankham 1998).

The extent of inbreeding depression in the wild is less well documented and remains controversial (Elgar and Clode 2001; Frankham 2001). In part this is because of the inherent difficulty of demonstrating inbreeding effects in the wild (Frankham and Ralls 1998), but it may also reflect a genuine pattern because wild animals may have mechanisms to avoid mating with close relatives (the inbreeding avoidance hypothesis, Harvey and Ralls 1986; Ralls et al. 1986; Waldman McKinnon 1993; Pusey and Wolf 1996). Two putative examples of such mechanisms are kin recognition and avoidance (Waldman et al. 1992), and natal or sex-biased dispersal (Johnson and Gaines 1990).

These behaviours have practical implications for the management of small populations, such as those affected by habitat fragmentation, because inbreeding depression and loss of genetic variation will occur more slowly than predicted from population genetic models that assume random mating (Falconer 1989; Frankham 1995; Earnhardt et al. 2004; Stow and Sunnucks 2004).

Empirical evidence for inbreeding avoidance in animals has been mixed and comes mostly from mammals and birds (e.g. Cockburn et al. 1985; Keller and Arcese 1998; Wheelwright and Mauck 1998; Duarte et al. 2003), and its prevalence in the wild has been debated (Ralls et al. 1986; Shields 1993; Komdeur and Deerenberg 1997). Some of the contention stems from the difficulty of obtaining accurate data on dispersal and mating systems by observation (Koenig et al. 1996; Parker and Waite 1997); a problem which has now been largely overcome with the development and application of highly variable co-dominant DNA markers, which permit detailed analyses of mating systems, kinship (Queller et al. 1993), and natal and sex-biased dispersal (Favre et al. 1997). These approaches provide an opportunity to clarify the extent of inbreeding, inbreeding depression, and inbreeding avoidance in wild populations. Further, this understanding will be strengthened by a focus on non-mammalian and non-avian animal groups, which have been underrepresented in studies to date (Waldman and McKinnon 1993; but see Olsson et al. 1996b; Stow and Sunnucks 2004).

A prerequisite for the evolution of inbreeding avoidance is the opportunity for incestuous matings (Ralls et al. 1986; Pusey and Wolf 1996). Small and insular populations should therefore be good models for investigation, and here I investigate the mating system, patterns of kinship, dispersal, and juvenile survival in small insular populations of an endangered lizard from southern New Zealand. The grand skink, *Oligosoma grande*, lives in small groups of ca. 20 individuals on house-sized rock outcrops that are separated from similar groups by 50–150 m of inhospitable vegetation matrix (Whitaker 1996). Previous work has shown that dispersal between rock outcrops is limited on small spatial scales (35–350 m, Berry et al. 2004, 2005), which leads to the prediction that adults will share outcrops with kin and potentially inbreed. Further, habitat modification has increased the isolation of some skink popula-

tions (Berry et al. 2005), increasing the likelihood that deleterious genetic processes will occur (Frankham et al. 2002).

I used data from 15 microsatellite loci and kinship analyses to examine four questions related to inbreeding and inbreeding avoidance in the grand skink. First, I investigated whether grand skinks have opportunities to mate with close relatives (equivalent to half- or full-sibs). Second, I tested whether skinks avoid breeding with close relatives. Third, I examined evidence for avoidance of inbreeding by natal or sex-biased dispersal. Finally, I tested whether the offspring of less related parents had higher survivorship in their first year of life than the offspring of more related parents. In sum, I ask whether the deleterious genetic effects of isolation caused by habitat fragmentation of these populations (Berry et al. 2005) will be mitigated by inbreeding avoidance behaviours.

## Methods

### *Field methods*

The study area was located at “Redbank”, near Macraes Flat, southern New Zealand (45°25' S, 170°24' E; Figure 1). Part of this area is a reserve for lizard conservation and consists of a mosaic of tussock grassland and agricultural pasture regularly punctuated by house-sized schist rock outcrops. Nylon fishing line nooses were used to capture skinks from two pasture-dominated (P1 P2) and two tussock-dominated sites (T1 and T2). Skinks were measured, marked with a unique toe-code, and adults were sexed before being released at their point of capture. Nearly all resident skinks on each outcrop were captured by repeatedly visiting rock outcrops over their entire active period (November 2000–May 2001). This was verified by estimation of the population sizes by mark-recapture analyses (Berry et al. 2005). In addition, the skink populations have been monitored intensively since 1995 (Whitaker 1996; M. Tocher, pers. comm.).

### *Laboratory analysis*

Tissue samples from all captured skinks were collected for genetic analysis. Samples consisted of toe-clips or tail-tips (<2 mg tissue), and were

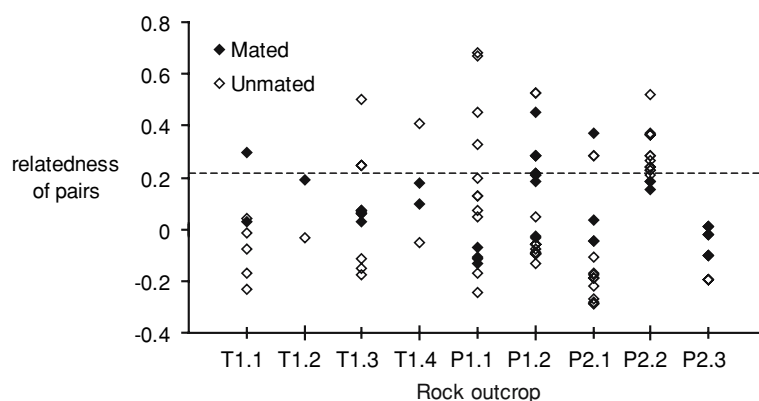


Figure 1. Relatedness values for mated (filled symbols) and potentially mated (open symbols) pairs on each rock outcrop. Potentially mated pairs include each of the known mated individuals and all its potential partners on the same rock outcrop. Dashed line indicates the upper 95% confidence limit of relatedness for unrelated pairs.

placed immediately into liquid nitrogen. DNA was extracted by a salting-out procedure (Sunnucks and Hales 1996). A total of 261 skinks were genotyped for 15 microsatellite DNA loci following the methods described in Berry et al. (2003).

#### Parentage

The parentage of the two cohorts of skinks born in the late summer of 2000 and of 2001 was determined using a likelihood approach implemented by the program CERVUS 2.0 (Marshall et al. 1998). Almost a year elapses between mating and birth in this species (Cree 1994), and the offspring studied were the result of matings that occurred in Autumn (February–April) 1999 and 2000, respectively. Because detailed capture-recapture history was known for skinks from 1995 on (M. Tocher pers. comm.), I could accurately determine the number of candidate parents for each offspring, and also the number that had not been genotyped (because they were not captured in the 2000/2001 season). Parentage was assigned in a stepwise manner, firstly assigning maternity, then paternity using the prior parentage information where confidence in maternity was  $\geq 0.95$ . If maternity could not be assigned with  $\geq 0.95$  confidence, paternity was assigned without the maternal information. The parameters used for simulations differed between study sites and are listed in Appendix 1. Proportion of candidate parents sampled was determined from the proportion of skinks that were present during tissue-sample collection

(summer 2000–2001), and were also present during the previous mating season (summer 1999–2000). Genotyping error was set at 2.0%. In an empirical test, three individuals were separately genotyped 27 times for the same three loci. They were scored correctly in all cases. However, it was deemed conservative to include an error value in line with those reported in the literature. One relative of  $R=0.25$  was assumed to be present amongst candidate parents in all cases. While it is likely that in some cases closer relatives would have been present amongst candidate parents, documentation accompanying CERVUS indicates that the failure to assume relatives among candidate parents has little effect on parentage assignment in most cases (Marshall et al. 1998).

Grand skinks have four easily recognisable age/size classes based on their snout-vent length:  $\leq 1$  year-old,  $\leq 2$  year-old,  $\leq 3$  year-old, and adults, and are believed to become sexually mature in their fourth year (Cree 1994; Whitaker 1996), and therefore I included all skinks of 4 years or older as candidate parents. While no female skinks in their third year have been recorded as gravid (M. Tocher pers. comm.), I could not discount males of this age being potential fathers. To allow for this possibility I included 3-year-old males as candidates. CERVUS uses simulations of parentage to establish confidence in parental assignments, and requires empirical allele frequencies. I used site-wide allele frequencies for these simulations, and although significant genetic subdivision exists among rock outcrops at each

study site (Berry et al. 2005), the effect of pooling allele frequencies from all rocks at each site had little effect on statistical confidence (analyses not presented).

#### *Kinship on rock outcrops*

I used the program KINSHIP 1.1 (Goodnight and Queller 1999) to estimate pairwise relatedness between all adult skinks ( $R$ ) using the method of Queller and Goodnight (1989). Because inclusion of many related individuals in the population causes downwards bias of relatedness among relatives, I removed all  $\leq 2$  year-old skinks from relatedness calculations.

I used two approaches to determine the proportion of adult opposite sex pairs that were related. First, I used KINSHIP to simulate 1000 unrelated pairs of skinks from allele frequencies at each study site and calculated the 95% confidence limits on  $R$  values between these pairs. Using this information I estimated the chance of a skink mating with kin as the proportion of all opposite sex pairs on each rock outcrop that had  $R$  values greater than the upper 95% confidence limit for unrelated skinks. Second, I tested the hypotheses that each potential pair involved either half- or full-sibs ( $H_a$ ) against the null hypothesis that pairs were either unrelated or half-sibs respectively ( $H_o$ ). KINSHIP was used to calculate the likelihood ratio of  $H_a$  and  $H_o$  based on the allele frequencies at each study site. A test for the significance of  $H_a$  was conducted by simulating 1000 pairs of individuals according to the  $H_a$  and  $H_o$  hypotheses and estimating directly the ratio needed to reject  $H_o$  (Goodnight and Queller 1999). The likelihood ratio tests provide more power to detect pedigree relationships than simply assessing the  $R$  value relative to 95% confidence intervals of unrelated skinks from simulation. Thus, in some cases likelihood ratio tests are able to achieve significance where the observed  $R$  value of a pair was within the simulated 95% confidence limits for unrelated skinks.

#### *Kinship in tussock and pasture*

Grand skink populations occur in both modified (pasture) and unmodified (tussock grassland) landscapes. I used a two-sample randomisation test implemented in POPTOOLS (Hood 2002) to

test whether skinks on rocks in pasture had a higher percentage of close kin (half-sib or greater) as potential mates than skinks on rocks in tussock.

#### *Breeding partners*

I tested whether male or female skinks reproduced assortatively by relatedness by comparing  $R$  for the mated pair with the average  $R$  of each of the mated individuals to all non-mated opposite sex candidates on the same rock outcrop. The test was performed by randomisation with the program POPTOOLS (Hood 2002), where the test statistic was a paired  $t$ -value from the observed data, which was compared to the distribution of the same statistic calculated for 9999 randomised datasets. These comparisons assume that all individuals were available to mate. I have no data for males, however on average, 90.3% of females breed each year (Cree 1994).

#### *Offspring survival*

As a test of whether offspring of more inbred matings had lower survival, I compared the relatedness ( $R$ ) of parents of offspring that were captured just after birth with the relatedness of those that were caught approximately a year after birth using a two-tailed  $t$ -test. In addition, because it allowed inclusion of offspring for which I could assign only one parent (and hence provides greater power), I compared the internal relatedness (IR, Amos et al. 2001) of offspring from these two cohorts. Internal relatedness is a modification of the Queller and Goodnight (1989) relatedness estimator, but is calculated for individuals. It is a measure of the genetic correlation between alleles within an individual, weighted by the frequency of those alleles in the population. I also tested for a difference in the variance of IR and  $R$  between newborn and 1-year-old skinks using a two-tailed variance ratio test (Zar 1996).

#### *Sex-biased dispersal*

I tested for sex-biased dispersal in both tussock and pasture and overall by comparing mean relatedness among adult males and adult females on each rock outcrop with two-tailed paired  $t$ -tests.

## Results

### *Genotypic data*

In total, 261 skinks were genotyped. The loci were highly variable, with a mean observed heterozygosity of 0.77 ( $\pm 0.04$  SE) and an average number of alleles per locus per rock outcrop of 7.4 ( $\pm 0.30$  SE). Additional descriptive statistics are provided in Berry et al. (2005). Overall, the loci were in Hardy–Weinberg equilibrium and not in linkage disequilibrium, however two loci, *Oligr2* and *Oligr15* had significant deficits of heterozygotes on some rock outcrops, suggesting the presence of null alleles (Berry et al. 2003). These loci were only included in analyses at study sites where they were in Hardy–Weinberg equilibrium (see Appendix 1).

### *Parentage analysis*

The loci used had very high exclusionary power ( $\geq 0.999$  exclusionary power of the first parent). I examined the parentage of a total of 63 offspring from three study sites (29 in the 1999/2000 cohort and 34 in the 2000/2001 cohort). Study site T2 was not included in parentage analysis because only two offspring were captured. The number of candidate female parents ranged between 13 and 17 at each study site and between 8 and 17 candidate males (Appendix 1).

Overall, 33 offspring had both parents assigned. For the second cohort of young (newborns) the mother of all but one (33/34), and the father of 24 could be assigned with  $\geq 95\%$  confidence. For the first cohort of young (1-year-olds) the mother of 22 (22/29) and the father of 17 could be assigned with  $\geq 95\%$  confidence. A further two offspring from this cohort were assigned mothers with  $\geq 85\%$  confidence, and three were assigned fathers with  $\geq 91\%$  confidence. Three-year-old males, were never assigned paternity.

### *Mating system*

Grand skinks were highly promiscuous as both polyandry and polygyny were common. Of the 15 litters assigned to females where more than one offspring was genotyped, seven (46.7%) were sired by multiple males. A total of 10 male skinks were assigned multiple offspring from the same cohort, and of these, seven (70%) sired their offspring with multiple females.

### *Kinship on rock outcrops*

Kinship simulations and pairwise relatedness calculations showed that adult skinks usually shared rock outcrops with kin, and in some cases more than a third of all possible opposite sex pairs would involve related skinks (Table 1). The proportion of potential pairs that would involve at

Table 1. Summary of the kinship of adult grand skinks on 11 rock outcrops.

Site	Rock	No. males <sup>a</sup>	No. females <sup>a</sup>	Group size <sup>b</sup>	<i>R</i> 95% CI unrelated	% adult M/F pairs kin <sup>c</sup>	% adult M/F pairs half-sibs <sup>d</sup>	% adult M/F pairs full-sibs <sup>e</sup>
T1	T1.1	3	5	32	−0.19 to 0.22	13.3	6.7	0
	T1.2	2	2	22		0	25.0	0
	T1.3	4	4	25		12.5	12.5	6.2
	T1.4	3	2	16		16.7	16.7	16.7
P1	P1.1	5	4	26	−0.18 to 0.22	25.0	35.0	10.0
	P1.2	8	3	38		20.8	25.0	8.3
T2	T2.1	4	2	24	−0.21 to 0.23	12.5	12.5	0
	T2.2	2	2	15		0	0	0
P2	P2.1	4	6	29	−0.19 to 0.22	8.3	8.3	0
	P2.2	5	5	27		36.0	16.0	4.0
	P2.3	4	1	19		0	0	0

<sup>a</sup>Numbers genotyped – repeat visits to rock outcrops and mark-recapture analysis indicate that nearly all skinks on outcrops were genotyped, see Berry et al. (2005).

<sup>b</sup>Minimum group size, see Berry et al. (2005).

<sup>c</sup>Pairs with relatedness greater than the upper 95% confidence limit from simulations of unrelated pairs.

<sup>d</sup>Pairs with significant likelihood ratios in tests of half vs. unrelated.

<sup>e</sup>Pairs with significant likelihood ratios in tests of full-sibs vs. half-sibs.

least half-sibs ranged between 0 and 35% and averaged 14.4%, and the proportion that would involve full-sibs ranged between 0 and 16.7 and averaged 4.1% (Table 1). It should be noted that while the power to distinguish half-sibs from unrelated pairs was reasonably high (range 0.72–0.79), it was considerably lower to distinguish full-sibs from half-sibs. The results presented in Table 1 should therefore be viewed as conservative estimates of the proportion of close relatives present on each rock outcrop.

#### *Kinship in tussock and pasture*

There was no significant difference in the proportion of opposite sex close relatives (half-sibs or greater) on rocks in pasture and tussock as identified by likelihood ratio tests (average percentage close relatives in tussock 12.23%, pasture 16.86%,  $P=0.51$ ).

#### *Breeding partners*

Of the 33 offspring for which both parents were identified, 18.2% were the product of matings between skinks with relatedness equivalent to full-siblings (i.e. including parent–offspring matings), and 21.2% were the product of matings between skinks with relatedness equivalent to or greater than half-siblings (i.e. including grandparent–grandchild matings). On average, neither female nor male skinks mated with partners that were

significantly less related to them than the candidates on the same rock outcrop (mated pairs average  $R=0.11$ ; females to unmated males average  $R=0.06$ ;  $P=0.88$ ; males to unmated females average  $R=0.10$ ;  $P=0.72$ ).

#### *Offspring survival*

Based on the relatedness of parents, offspring that survived their first year were not any less inbred than newborns (Figure 2; mean parental relatedness of newborns =  $0.07 \pm 0.034$  SE, mean parental relatedness of 1-year-olds =  $0.18 \pm 0.043$  SE,  $t=1.95$ ,  $df = 29$ ,  $P=0.06$ ), and neither was the variance in parental  $R$  any different in newborn and 1-year-old skinks ( $F = 1.12$ ,  $df = 17,12$ ,  $P=0.41$ ). Similarly, based on the internal relatedness of offspring, those that survived their first year were not born to less related parents than newborns (mean newborn  $IR=0.003 \pm 0.022$  SE, mean 1-year-old  $IR=0.044 \pm 0.024$  SE,  $t=1.27$ ,  $df = 61$ ,  $P=0.21$ ), and neither was the variance in  $IR$  any different in newborn and 1-year-old skinks ( $F = 1.06$ ,  $df = 33,28$ ,  $P=0.43$ ).

#### *Natal and breeding dispersal*

Parents and their newborn and 1-year-old offspring occurred on the same rock outcrop in almost all cases. One juvenile from the 1-year-old cohort was assigned with 98% confidence to a female on a rock 356 m away at site P2. In addition,

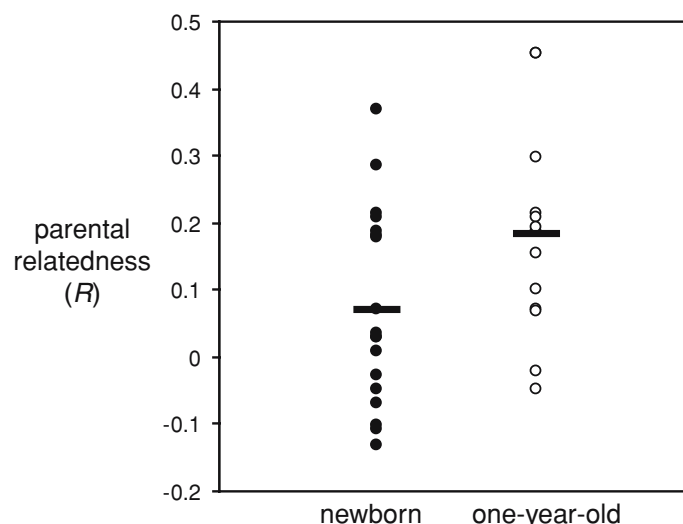


Figure 2. Relatedness of the parents of newborn and 1-year-old offspring. Horizontal lines indicate means.

the newborn offspring of one male occurred on two different rocks at site T1 that were 141 m apart (both assigned with >97% confidence).

#### *Sex-biased dispersal*

There was no difference in relatedness among female and male skinks on outcrops in either pasture (female  $R=0.106\pm 0.027$  SE vs. male  $R=0.108\pm 0.053$  SE,  $t=0.25$ ,  $P=0.61$ ), or tussock (female  $R=0.054\pm 0.023$  SE vs. male  $R=0.077\pm 0.074$  SE,  $t=0.14$ ,  $P=0.15$ ), or overall (female  $R=0.010\pm 0.031$  SE vs. male  $R=0.080\pm 0.043$  SE,  $t=1.22$ ,  $P=0.25$ ).

### **Discussion**

The study of inbreeding avoidance has practical relevance for the grand skink because many populations occur in modified pasture-dominated landscapes where the rate of dispersal between rock outcrops is reduced (Berry et al. 2005). Pasture populations are predicted to face an increased chance of inbreeding and its deleterious effects (Frankham 1995). The magnitude of this effect may depend in part on the mating system of grand skinks and their ability to avoid breeding with kin (Parker and Waite 1997; Amos and Balmford 2001; Stow and Sunnucks 2004), but also their inherent susceptibility to inbreeding effects (Ralls et al. 1988).

#### *Opportunities for inbreeding*

Inbreeding avoidance is most likely to evolve when there are opportunities for inbreeding (Ralls et al. 1986; Waldman and McKinnon 1993). Previous mark-recapture and genetic data indicated that inbreeding is likely in grand skinks because they are sedentary and populations are genetically differentiated at very fine scales ( $= 35$  m, Berry et al. 2004, 2005). Analysis of relatedness confirms this prediction by showing that skinks typically live with many close adult relatives of the opposite sex. Many relationships were equivalent to half-sibs (up to 35% of potential mates), but on some rock outcrops adult skinks were also likely to encounter full-sibs (up to 17% of potential mates). This kinship structure emphasises the sedentary nature of grand skinks because sexual maturity occurs in their fourth year (Cree 1994), providing ample

time for dispersal. In addition, close kinship occurs in both natural (tussock grassland) and modified (pasture) landscapes, meaning that risk of inbreeding is characteristic of the species, and is not just a result of habitat modification.

#### *Inbreeding avoidance by mate choice*

Theoretical reasons for avoiding inbreeding are clear – matings between relatives increase the proportion of loci that are homozygous in offspring compared to unrelated pairs, and higher homozygosity increases the chance of deleterious recessive alleles being expressed (Falconer 1989). Reviews by Ralls et al. (1986) and Keller and Waller (2002) appeared to confirm that these risks apply to wild populations by showing that many mammals and birds avoid inbreeding. Yet, although adult grand skinks usually live with close relatives, they did not avoid breeding with them. This resulted in a high level of close inbreeding (18.2%), not because inbreeding was systematic, but because there were few unrelated mates to choose from on a rock outcrop. Moreover, the level of inbreeding observed is much higher than the  $\leq 6\%$  value reported from the review of mammals and birds by Ralls et al. (1986). The absence of obvious inbreeding avoidance is unlikely to be because lizards lack such discriminatory abilities, as these behaviours have been demonstrated in several lizard species (Léna et al. 2000; Gardner et al. 2001; Stow and Sunnucks 2004). Therefore, unlike outbreeding species (e.g. *Egernia cunninghami* Stow and Sunnucks 2004), grand skinks are not naturally buffered against the potentially deleterious genetic effects of isolation caused by habitat modification. *Oligosoma grande* adds to a growing list of taxa that inbreed despite the theoretical or actual risks (e.g. dwarf mongoose, Keane et al. 1996; song sparrow, Keller and Arcese 1998; white-toothed shrew, Duarte et al. 2003; glanville fritillary butterfly, Haikola et al. 2004).

#### *Inbreeding avoidance by natal or sex-biased dispersal*

Natal (pre-breeding) or sex-biased dispersal are also mechanisms of inbreeding avoidance (Greenwood 1980). However, parentage and kinship analyses showed that neither natal nor sex-biased dispersal was pronounced in grand skinks, and as

indicated by the high proportion of kin present on rock outcrops, neither effectively removed opportunities for close inbreeding. Only one of the 23 one-year-old skinks, whose mother was identified, was captured on a different rock from her. The only other juvenile captured on a different rock from its parent was probably the result of male breeding dispersal because it was captured on the same rock outcrop as its mother, who had been a long-term resident of that rock. This result tallies with mark-recapture data reported in Berry et al. (2004), which showed that only 3.3% of skinks captured just after birth dispersed in their first year of life. I also did not detect a difference in dispersal between males and females based on comparison of male–male and female–female relatedness. However, a test based on comparison of the assignment index (mAIc) and  $F_{ST}$  statistics between males and females (Favre et al. 1997), has previously shown a statistically significant bias towards female dispersal (Berry et al. 2005), and the relatedness data show the same trend. Nevertheless, the female-bias was not pronounced in either of those tests.

#### *Inbreeding avoidance by promiscuity*

Promiscuity in lizards has been argued to be a mechanism to avoid inbreeding by enabling females to effect post-copulatory mate choice through sperm competition (Olsson et al. 1996b). Despite their small clutch sizes (average 2.4, Cree 1994), I detected a high degree of multiple paternity in grand skinks, and also found that males reproduced with multiple females. Promiscuity is common in reptiles (Olsson and Madsen 1998), and compares with field observations that male grand skinks interact with multiple females during the breeding season (Murphy 1994). Females grand skinks store sperm for about 5 months prior to fertilisation (Cree 1994), which presumably provides opportunities for sperm competition. Because I did not obtain complete offspring arrays nor identify all males that mated, I could not properly test whether post-copulatory mate choice occurs in grand skinks. However, although promiscuity was common, the proportion of offspring produced by closely related parents was still high, and similar to the proportion of close relatives in the populations studied (Table 1, Figure 1). Therefore, it appears that selection for unrelated

mates by either pre- or post-copulatory mate choice is not pronounced in this species.

#### *Costs of inbreeding*

Theoretical models show that inbreeding avoidance will evolve when the cost of inbreeding exceeds the cost of avoiding inbreeding (Waser et al., 1986; Lehmann and Perrin, 2003). The cost of inbreeding is often measured in terms of juvenile survival (e.g. Ralls et al. 1988; Olsson et al. 1996a; Keller and Waller, 2002), but I did not detect a cost of inbreeding to skinks surviving in their first year. Instead, I found that skinks that survived their first year were variously inbred, included full sibs (Figures 1 and 2), and were no less inbred than newborn skinks. In fact there was a near significant trend towards 1-year-old skinks being more inbred. Had there been strong selection against inbred juveniles, I expected both the mean and variance of parental relatedness of 1-year-old skinks to be lower than that for newborn skinks. Although additional components of fitness need to be examined before firm conclusions are drawn (Hedrick and Kalinowski 2000), the costs of inbreeding appear low in this species. Weak inbreeding depression might be explained by a history of inbreeding that has permitted the purging of deleterious alleles (e.g. Gibbs and Grant 1989). This scenario is difficult to verify, and empirical evidence of purging in wild populations is scant (Keller and Waller 2002). However, it is noteworthy that small population size and isolation are conditions conducive to purging, and are also features of grand skink ecology (Whitaker 1996).

#### *Costs of avoiding inbreeding*

The high incidence of close inbreeding in grand skinks may be explained by high costs of avoiding inbreeding, which theory indicates should strongly influence mating behaviour (Waser et al. 1986). Two potential costs are dispersal, and forgone breeding opportunities (Waser et al. 1986; Keller and Arcese 1998), and both are potentially important for grand skinks because of their small demic population structure and the patchy nature of rock outcrops. Skinks would reduce opportunities for close inbreeding by dispersing to neighbouring rock outcrops because neighbouring



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