Inbreeding in Littledale’s Whistling Rat

*Parotomys littledalei*

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**ABSTRACT** Despite its rarity in nature, inbreeding is sometimes evident in species occupying ephemeral, unpredictable habitats, and which occur at low densities. One such species is Littledale’s whistling rat, *Parotomys littledalei*, a murid rodent endemic to the south-west arid region of South Africa. Using a captive population of *P. littledalei*, I studied mate choice for kin and nonkin, and the reproductive performance of inbred and outbred pairs. In choice tests, estrous females presented with either odors or actual males showed a preference for siblings or half-siblings to unrelated males. Males did not discriminate between the odor of estrous kin and nonkin. In breeding studies, inbred (mother-son; brother-sister) and outbred (proven female and an unrelated young male and nonsiblings) pairs had a similar reproductive output, although the sex ratio favored males in inbred litters. The development of inbred young was indistinguishable from outbred young. The results indicate that female *P. littledalei* prefer to inbreed, but there are no apparent advantages to inbreeding over outbreeding. *J. Exp. Zool. 293:171–178, 2002*. © 2002 Wiley-Liss, Inc.

Inbreeding is generally regarded as being disadvantageous, particularly when mating occurs between close relatives, such as between parents and offspring and siblings (Clutton-Brock and Harvey, '76). The detrimental effects of inbreeding are well known, and they are assumed to be the result of increased homozygosity of deleterious recessive alleles (Charlesworth and Charlesworth, '87), affecting, for example, the pre- and postzygotic viability of inbred offspring (Lacy et al., '96) and the reproductive success of inbred adults (Margulis, '98). Many have argued and shown that the detrimental effects of inbreeding lead to outbreeding mechanisms through behavioral and physiological adaptations.

Despite the wide acceptance of inbreeding avoidance, it is known that close inbreeding may occur when alternative mates are not available. For example, mating occurs in sibling groups in some insects upon emergence but females will later outbreed (Hamilton, '93; Chapman and Stewart, '96). Inbreeding may also occur when the costs of avoiding inbreeding outweigh the benefits (Partridge, '83; Pugh and Tamarin, '88; Shields, '93). For example, the costs of dispersing or delaying reproduction may be higher than those of mating with close relatives (Rowley et al., '86). In addition, inbreeding may maintain adaptations to local conditions (Partridge, '83), and prevent disruption of gene complexes (Partridge, '83; Shields, '93).

Ecologically, inbreeding is apparently more common in populations occupying ephemeral, patchy, or unpredictable microhabitats than in those occupying habitats that are permanent and predictable (Batzli et al., '77; Anderson, '89). In ephemeral-patchy microhabitats, the costs of dispersal may favor philopatry and mating with kin (Smith and Ivins, '83; Bollinger et al., '91), particularly at low population densities. For example, the high level of inbreeding in the meadow vole *Microtus pennsylvanicus* may be explained by the high costs of dispersal between widely spaced grassland patches (Pugh and Tamarin, '88).

Littledale’s whistling rat *Parotomys littledalei* is a medium-sized (adult mass range 107–120 g) murid rodent endemic to the south-west arid biome of southern Africa. The known distribution pattern of *P. littledalei* includes the Nama Karoo,
succulent Karoo, the southern Kalahari regions in the South Africa-Namibia border, and along the Namib and Kunene rivers (Coetzee and Jackson, '99). This distribution covers some of the most arid regions of southern Africa where rainfall may be less than 200 mm per annum.

The presence of *P. littledalei* in an area is usually indicated by a complex warren system under bushes (Coetzee and Jackson, '99; Jackson, 2000). Apart from providing protective cover against predators and extreme environmental conditions, bushes serve as a source of food; *P. littledalei* is strictly herbivorous, feeding on the leaves of a limited number of succulent and nonsucculent vegetation (Coetzee and Jackson, '99). Field studies indicate that the taxon apparently does not readily venture beyond the warren to feed or forage (Coetzee and Jackson, '99), and Jackson (2000) maintains that such burrowing and foraging habits of *P. littledalei* effectively restrict its distribution within its geographical range.

Coetzee and Jackson ('99) suggest that locating a suitable bush, a limiting resource in the arid environments, will influence dispersal in *P. littledalei*, and cohabitation has been observed in large bushes in parts of its distributional range. Whether such a situation leads to inbreeding in nature is unknown, but I observed inbreeding during an earlier breeding study of captive *P. littledalei* (Pillay, 2002). Similarly, I showed in two mesic relatives of *P. littledalei* that inbreeding is common in the species (*Otomys angoniensis*) occupying patchy ephemeral habitats and absent in the species (*O. irroratus*) inhabiting dense habitats—the latter displaying behavioral inbreeding avoidance (Pillay, '98).

The objectives of the present study were to establish whether male and female *P. littledalei* discriminate between kin and nonkin in mate choice tests and to ascertain the reproductive performance of inbred and outbred pairs.

**MATERIALS AND METHODS**

Study animals were live-trapped at Springbok (29°40'S, 17°53'E) in the Northern Cape Province, South Africa. Thirty adults were collected from several sites within the Springbok area. The minimum distance between sites was 400 m, and although dispersal distances of *P. littledalei* are unknown, they are unlikely to exceed 100 m (Jackson, personal communication). In captivity, pairings were established between individuals of different sites that were unlikely to be closely related. The F1 offspring were outbred and their offspring (F2) were used in experiments.

Animals were singly maintained in Lab-o-tec cages (400 × 250 × 120 mm) or as pairs in glass aquaria (900 × 300 × 400 mm). Environmental conditions were partially controlled (22–25°C; 30–70% rH; light regime of 15L:9D, lights on at 0500 hr). Coarse wood shavings were provided as litter and hay was provided as nesting material. Cages were washed and the shavings were replaced weekly. Food was comprised of ad libitum spinach, vegetable tops (e.g., carrot and beetroot), and Epol rabbit pellets. Water was provided at all times.

**Mate preference**

The preference by individual females and males for the odor of related and unrelated opposite sex individuals was tested in two combinations: (i) littermate sibling vs. unrelated individual; and (ii) half-sibling (same father) vs. unrelated individual. For each combination, I tested the responses of 15 estrous females and 14 males; males were tested with the bedding of estrous females. The estrous state of all females (test or stimuli) was determined using vaginal smears.

Tests were conducted in a neutral arena, consisting of a square perspex apparatus (400 × 400 × 200 mm) connected to three clear, plastic choice chambers (150 × 150 × 150 mm) by PVC pipes (60 mm internal diameter) at the middle of each side. Each choice chamber contained a petri dish (55 mm diameter) with soiled bedding from donor individuals or clean bedding (control). The entrance to each choice chamber was guarded with a removable, opaque partition. Prior to each test, soiled bedding was randomly assigned to one of the three nest boxes. A test individual was placed in the middle of the test arena. After an acclimation period of 10 min, partitions to the choice chambers were removed and the time spent within each of the three chambers by test subjects was video-recorded for 15 min under fluorescent lights during the light phase of the light-dark cycle—*P. littledalei* is a diurnal rodent. After tests, the choice apparatus was thoroughly cleaned with warm soapy water and alcohol, dried, and the floor was covered with a thin layer of wood shavings.

Soiled bedding used in choice tests was collected from estrous stimuli females, sealed in air-tight bags, and stored at −15°C until use (after Heth et al., '98). It was necessary to freeze samples since...
female *P. littledalei* do not display synchronous oestrus, making it unlikely that all the appropriate stimuli were available on one day. For consistency, bedding from donor males and clean bedding were also frozen. Frozen samples were thawed out at room temperature just prior to tests. No bedding was frozen for more than a week.

All test subjects were sexually mature (i.e., > 100 days old; Pillay, 2002) virgins that were used once in experiments. None made contact with half-siblings or unrelated individuals prior to tests, and they were separated from siblings for at least two months (i.e., they were housed in different rooms).

The effect of relatedness upon female preference for males, as opposed to odors, was examined in a separate experiment by comparing individual preferences of estrous females for a brother and an unrelated male, and for a half-brother and an unrelated male; 12 replicates were conducted per combination. The protocol of these tests was identical to that of the odor preference tests except that instead of containing soiled bedding, the nest boxes were divided in two using a wire-mesh partition. In two of these nest boxes, males were placed behind the partition, and the third nest box contained clean bedding behind the partition. When making a choice, test females entered a nest box but could not make physical contact with males or wood shavings. Again, the time that a test female spent within each of the three chambers was recorded. In addition to recording the duration of visits, I also recorded the number of aggressive-retreat and sexual acts that females displayed toward males across the wire mesh barrier. Typical aggressive-retreat (hereafter referred to as aggressive) behaviour included biting wire mesh, pilo-erection, and upright sparring. Sexual behaviour included presenting and/or lordotic behaviour.

### Breeding biology

Two types of inbred and outbred (control) pairings were made: (i) mother and son; (ii) brother and sister—siblings removed from the mother at 30 days old and housed elsewhere; (iii) unrelated female and younger male—a sexually-experienced female and a virgin, 100-day old male; and (iv) nonsiblings—both were approximately 100 days of age at pairing.

In outbred pairs, females displayed extreme aggression to males, necessitating separation of the pair with a wire mesh screen. Following a period of two weeks, the barrier was removed, and the pair had access to each other and the entire cage. Aggression was minimal or absent at this time, with pairs either nesting together or separately. All females were very aggressive toward their mates a week before parturition, so males were removed from the breeding tank at this time and housed elsewhere. Pairs that had not produced a litter after 120 days were separated. This time period allowed for 30-day old individuals to attain sexual maturity (approximately 90 days) and complete gestation (41 days; Pillay, 2002).

I compared the reproductive performance of inbred and unrelated pairs by recording the proportion of pairs that reproduced, the litter size, and sex ratio. In addition, reproductive effort of females was calculated using a modified version of Millar’s (’77) formula: $R_s = N W^{0.75} (m^{0.75}-1)$, where $N$ = litter size, $W$ = mass of litters at weaning (16 days old), and $m$ = mass of postpartum adult female.

The viability of inbred relative to outbred offspring was ascertained by studying their postnatal ontogeny. Young were weighed to the nearest 0.1g every second day from birth to 20 days of age, and weekly thereafter to 98 days of age. Using the growth data from those young that survived to 98 days of age, the increase in body mass of both males and females was fitted with the Gompertz equation (Zullinger et al., ’84): $W = A \exp \left( -K (t-t_i) \right)$, where $W$ = predicted mass at time $t$; $A$ = asymptotic mass; $\exp$ = exponential function; $K$ = growth rate constant; $t_i$ = a parameter indicating the inflection time. The Gompertz model generated the growth rate and inflection point, while the asymptotic value was fixed to the mean body mass at 98 days of age when the last weighing was made and mass gain had leveled off (see Pillay, 2002).

During postnatal development, mass and age data at several developmental stages were of particular biological interest, including litter mass at birth and weaning, and age and mass at sexual maturity for individual males and females. Reproductive maturity in males was indicated by the presence of scrotal testes that were of adult size (i.e., 2 cm) and in females by a perforate vagina and completion of at least one estrous cycle (as determined by vaginal smears).

### Data analysis

Before using parametric tests, I tested data sets for departure from normality and for homogenous variances. If the assumptions of normality were
not met, nonparametric tests were used (Zar, ’96). Data from the choice tests were analyzed using a Friedman ANOVA to compare the time spent with the different types of bedding or males; specific differences were identified using a nonparametric post-hoc test and a Wilcoxon paired ranked test. A G-test was used to analyze the number of aggressive and sexual behaviors displayed by females to stimulus males. In breeding studies, statistical analyses used included $\chi^2$ contingency analyses and one-way ANOVA and Kruskall-Wallis tests. For comparisons of birth mass and weaning mass of litters, I used the ANCOVA test to control for the influences of mother’s mass and litter size. All tests were two-tailed and $\alpha$ was set at 0.05.

**RESULTS**

**Mate preference**

Figure 1 gives the duration of time that estrous females spent with the soiled bedding of males or the males themselves. In all cases, females spent significantly more time with the stimuli (bedding or males) and showed little interest in unsoiled bedding (Friedman ANOVA and nonparametric post tests). Therefore, comparisons were made between the times spent with stimuli using a Wilcoxon matched pairs test. In tests with odor (soiled bedding), females preferred brothers to unrelated males ($z = 1.95; P < 0.05$) and half-brothers to unrelated males ($z = 2.95; P < 0.01$). Similarly, females tested with actual males spent significantly more time with brothers than unrelated males ($z = 3.06; P < 0.01$) and with half-brothers than unrelated males ($z = 2.90; P < 0.01$). In addition, females displayed significantly higher ($G = 4.82; P < 0.05$) levels of aggression toward unrelated males ($3.55 \pm 0.32$) than toward brothers ($2.08 \pm 0.22$). A similar pattern was observed in tests of half-brothers ($2.53 \pm 0.36$) and unrelated males ($4.30 \pm 0.33; G = 5.96; P < 0.05$). In contrast, females directed significantly more sexual acts toward related than unrelated males: brothers ($3.02 \pm 0.40$) vs. unrelated males ($1.13 \pm 0.12; G = 5.96; P < 0.01$); half-brothers ($2.61 \pm 0.28$) vs. unrelated males ($0.95 \pm 0.16; G = 9.92; P < 0.01$).

Like females, males preferred the bedding of females to unsoiled bedding (Fig. 2). However, males did not discriminate between related and unrelated females, spending equal time with the bedding of sisters and unrelated females ($z = 0.53; P > 0.05$), and with bedding of half-sisters and unrelated females ($z = 0.47; P > 0.05$).

**Breeding biology**

Inbred and outbred pairs had similar high reproductive success and reproductive output in terms of litter size (Table 1). However, the sex ratio of inbred litters significantly favored males while parity was achieved in outbred litters. Post-partum reproductive investment was similar in inbred and outbred litters.

After statistically accounting for litter size and maternal mass, the mass of inbred litters was similar to that of outbred litters at birth and weaning (Table 2). Male *P. littledalei* are significantly heavier than females, but only after weaning (Pillay, 2002), so that the skewed sex ratio of inbred litters did not affect litter masses at birth and weaning. Evidence of male-biased sexual dimorphism was provided statistically using an ANOVA for repeated measures (after Ferron and Ouellet, ’91) with sex as the grouping variable and weekly readings from day 0 to 98 as the dependent variables. From 28 days of age onward, inbred males were significantly heavier than inbred...
females (F_{1.48} = 101.07; P < 0.001), and outbred males were heavier than outbred females (F_{1.46} = 31.69; P < 0.001).

There were no differences between inbred and outbred young in the age and mass at sexual maturity (Table 2). Sex-specific growth rate did not differ between inbred and outbred young. No significant differences were observed in the number of young of all pairs that survived to 100 days of age.

**DISCUSSION**

**Mate preference**

Female *P. littledalei* can distinguish between related and unrelated males. In odor and actual male preference experiments, females preferred brothers and half-brothers to unrelated males. In addition, females displayed less aggression and more sexual behaviour toward brothers and half-brothers than unrelated males. The similarity of responses by estrous females to males or their odors highlights the importance of male odor, and in particular deposited chemosignals, in mate choice in *P. littledalei*.

Females distinguished between half-brothers and unrelated males, despite the fact that they never made contact with these males prior to tests. Therefore, it appears that prior association is not necessary for the establishment of kin recognition and mate preference in *P. littledalei*, as is the case in several other rodents (see Batzli et al., '77; Gavish et al., '84; Boyd and Blaustein, '85; Pillay, '98). Thus, it is possible that *P. littledalei* can use

**TABLE 1. Reproductive data for inbred and outbred *P. littledalei* pairs**

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Mother-son</th>
<th>Brother-sister</th>
<th>Unrelated female-younger male</th>
<th>Non-siblings</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion of pairs reproducing</td>
<td>11/13</td>
<td>12/12</td>
<td>14/16</td>
<td>12/12</td>
<td>$\chi^2=5.27$ NS</td>
</tr>
<tr>
<td>Litter size</td>
<td>2.6 (0.15)</td>
<td>2.3 (0.19)</td>
<td>2.4 (0.13)</td>
<td>2.4 (0.19)</td>
<td>$F_{3.45}=0.64$ NS</td>
</tr>
<tr>
<td>Sex ratio (M:F)</td>
<td>23:8</td>
<td>21:7</td>
<td>14:19</td>
<td>13:16</td>
<td>$\chi^2=11.58; P &lt; 0.01$</td>
</tr>
<tr>
<td>Reproductive effort</td>
<td>2.4 (0.21)</td>
<td>2.3 (0.27)</td>
<td>2.0 (0.18)</td>
<td>1.9 (0.21)</td>
<td>$H_{3.49}=5.60$ NS</td>
</tr>
</tbody>
</table>

1Litter size and reproductive effort values given as mean (±SE).

**TABLE 2. Postnatal characteristics of offspring resulting from inbred and outbred *P. littledalei* pairs**

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Mother-son</th>
<th>Brother-sister</th>
<th>Unrelated female-younger male</th>
<th>Non-siblings</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter mass at birth (g)$^2$</td>
<td>30.7 (1.23)</td>
<td>30.5 (1.32)</td>
<td>27.7 (1.75)</td>
<td>27.0 (1.72)</td>
<td>$F_{3.43}=1.31$ NS</td>
</tr>
<tr>
<td>Litter mass at weaning (g)$^2$</td>
<td>111.8 (6.80)</td>
<td>97.4 (5.03)</td>
<td>97.0 (6.04)</td>
<td>89.8 (5.32)</td>
<td>$F_{3.43}=2.20$ NS</td>
</tr>
<tr>
<td>Male age at sexual maturity (weeks)</td>
<td>7.0 (0.16)</td>
<td>6.6 (0.22)</td>
<td>6.5 (0.3)</td>
<td>6.6 (0.33)</td>
<td>$H_{3.17}=2.56$ NS</td>
</tr>
<tr>
<td>Female age at sexual maturity (weeks)</td>
<td>6.3 (0.36)</td>
<td>6.3 (0.49)</td>
<td>6.7 (0.3)</td>
<td>6.5 (0.31)</td>
<td>$H_{3.39}=0.56$ NS</td>
</tr>
<tr>
<td>Male mass at sexual maturity (g)</td>
<td>92.8 (2.38)</td>
<td>95.1 (2.30)</td>
<td>91.4 (3.32)</td>
<td>88.4 (3.44)</td>
<td>$F_{3.55}=0.95$ NS</td>
</tr>
<tr>
<td>Female mass at sexual maturity (g)</td>
<td>74.7 (2.90)</td>
<td>74.3 (4.02)</td>
<td>72.5 (2.71)</td>
<td>72.7 (2.38)</td>
<td>$F_{3.35}=1.32$ NS</td>
</tr>
<tr>
<td>Male growth rate: $K$ (day$^{-1}$)</td>
<td>0.046 (0.01)</td>
<td>0.046 (0.01)</td>
<td>0.046 (0.001)</td>
<td>0.045 (0.001)</td>
<td>$H_{3.59}=0.19$ NS</td>
</tr>
<tr>
<td>Female growth rate: $K$ (day$^{-1}$)</td>
<td>0.051 (0.004)</td>
<td>0.042 (0.003)</td>
<td>0.045 (0.003)</td>
<td>0.045 (0.003)</td>
<td>$H_{3.39}=4.95$ NS</td>
</tr>
<tr>
<td>Proportion surviving to 100 days of age</td>
<td>26/31</td>
<td>28/29</td>
<td>25/33</td>
<td>23/29</td>
<td>$\chi^2=5.27$ NS</td>
</tr>
</tbody>
</table>

1All values except proportion of surviving young given as mean (±SE). Sample size=number of litters (birth and weaning mass and growth rates) and number of individuals (age and mass at sexual maturity).

2$F$ values=ANCOVA test analysis, with maternal mass and litter size as co-variates.
other mechanisms, such as phenotypic matching (Hepper, '91), to distinguish between kin and nonkin.

Unlike females, males failed to distinguish between related and unrelated females. This lack of preference should be interpreted with caution, since such a situation could imply either an inability to discriminate between the scents or an equal interest in all scents. It is unlikely that males require other stimuli in addition to odor for mate preference, since females were able to use odor for mate choice. During breeding studies, males demonstrated equal interest in related and unrelated estrous females (Pillay, personal observation), suggesting that male *P. littledalei* do not discriminate between kin and nonkin.

Sexual asymmetry in mate choice for kin and nonkin has also been demonstrated in house mice, but the patterns of preference are not always predictable. Females preferred nonkin to kin in some laboratory mouse strains (Yanai and McClearn, '72). In other strains, females preferred close kin to unrelated males, while males preferred distantly related females (Barnard and Fitzsimons, '88). Females of wild house mice did not discriminate between kin and nonkin but males preferred unrelated females (Krackow and Matuschak, '91).

**Breeding biology**

Although females preferred brothers and half-brothers in mate preference tests, they bred with unfamiliar males. However, female *P. littledalei* displayed high levels of aggression toward unrelated males in choice tests and initially during breeding experiments. In the latter case, a familiarization period was required before females accepted and mated with unrelated males.

Captive breeding studies of laboratory and free-living rodents have shown that inbreeding can have various negative effects on reproductive success and output. Some studies have shown that inbreeding affects the probability of successful reproduction, but not any other measure of reproductive performance (Blaustein et al., '87; Dewsbury, '88; Krackow and Matuschak, '91). Other studies have shown otherwise, and inbreeding is known to decrease litter size (e.g., Hill, '74; Barnard and Fitzsimons, '89; Margulis, '98; Pillay, '98) or detrimentally affect offspring growth (Laird and Howard, '67; Keane, '90; Pillay, '98) and survival (Keane, '90; Haigh, '83; Pillay, '98). Inbreeding in *P. littledalei* does not appear to affect the probability of producing offspring or the viability of inbred offspring.

In mammal species where there is sexual dimorphism in body size, maternal condition may influence the sex ratio of progeny (Trivers and Willard, '73; Myers, '78). The larger sex is usually more costly to produce and females will produce fewer of this sex when stressed (Fisher, '30). Using this premise, Lacy and Horner ('97) argued that since inbreeding can be stressful (because of inbreeding depression) and is known to cause differential survival between male and female offspring, females may respond by adjusting the sex ratio of offspring in response to inbreeding. Although empirical evidence for this prediction is lacking, a correlation between litter size and sex ratio has been demonstrated in inbred Australian rats *Rattus villosissimus* (Lacy and Horner, '97). These rats have male-biased sexual dimorphism, and inbreeding results in either large litters with more females or small litters with more males. If inbreeding leads to more male young in *P. littledalei*, does this imply that inbreeding is not stressful in this species? An important consideration is that gender differences in body mass only occurred after weaning, such that relative investment in inbred and outbred young (reproductive effort) may not have been affected by the skewed sex ratio.

**Conclusion**

Breeding studies revealed no indication of outbreeding depression, suggesting that outbreeding would be favored. It is intriguing, therefore, that females preferred full and half siblings in choice tests, suggesting that there is some fitness advantage to inbreeding, although such advantages were not observed, since inbred and outbred pairs had similar reproductive performance. There may be other advantages to inbreeding in *P. littledalei*, such as promoting a high degree of adaptation to local conditions (Wilson, '75; Maynard Smith, '78), but the asymmetric preferences in choice tests suggest that there may be sex-specific fitness benefits in mate preferences. Smith ('79) proposed an inclusive fitness argument to explain sex differences in preference for inbreeding in polygynous species. Assuming that females are philopatric and males emigrate from natal demes, incestuous females increase the fitness of a male relative (e.g., father, brother) as well as their own inclusive fitness (Maynard Smith, '78; Smith '79). In contrast, dominant males mate with
relatives within a deme, whereas emigrating males may have to outbreed (Smith, '79). Little is known about the social biology of *P. littledalei*, so it is not possible to fully evaluate Smith’s prediction.

Inbreeding depression occurs because of an increase in homozygosity due to the accumulation of deleterious genes or genetic load (Charlesworth and Charlesworth, '87). Since genetic load is cumulative over generations (Waller, '93), the genetic consequences of inbreeding depend on the history of parental inbreeding (Campbell, '86). If this is the case in *P. littledalei*, the apparent lack of inbreeding depression could have been because the founder population was unrelated and initial matings were outbred. In addition, Charlesworth and Charlesworth ('87) predicted that outcrossing in inbred species could significantly improve fitness. Future studies should therefore consider the genealogical effects of inbreeding.

I predicted that the ecological circumstances of *P. littledalei* would lead to inbreeding as in the meadow vole *Microtus pennsylvanicus* (Pugh and Tamarin, '88). *P. littledalei* did not avoid inbreeding in captivity, and inbreeding did not influence reproductive performance. However, the relationship between dispersal and inbreeding, and the genetic composition of free-living *P. littledalei* populations, should be studied to verify the findings made here.

ACKNOWLEDGMENTS


LITERATURE CITED


