EVIDENCE FOR MALE-BIASED DISPERSAL IN A REINTRODUCED POPULATION OF BURROWING BETTONGS BETTONGIA LESUEUR AT HEIRISSON PRONG, WESTERN AUSTRALIA

BLAIR C. PARSONS, JEFF C. SHORT AND MICHAEL C. CALVER


The pattern of dispersal of burrowing bettongs (Bettongia lesueur) was studied in a population reintroduced to a peninsula protected from exotic predators at Heirisson Prong in Shark Bay, Western Australia. The reintroduced population was growing strongly in numbers and expanding in area during the study. Young were first marked in the pouch and subsequently monitored by trapping and radio-telemetry after independence to establish their movements relative to those of their mothers. B. lesueur on Heirisson Prong dispersed between the ages of 170 and 250 days, coinciding with the period from weaning to sexual maturity. Dispersal was male-biased. Young males dispersed significantly further than young females with mean dispersal distances of 4600 m and 1100 m respectively. Male B. lesueur also frequented significantly more warrens than females, being located at a mean of 0.37 warrens per daily radio-tracking fix compared with a mean of 0.24 per fix for females. Scarring from intra-specific aggression occurred in male bettongs only. Males may disperse to the periphery of the population to escape aggressive interactions with established adult males and visit more warrens to increase mating opportunities. Dispersal in females may be related to resource quality or inbreeding avoidance.

Key words: dispersal, bettong, potoroid, warren, reintroduction, Bettongia lesueur.

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THE burrowing bettong (Bettongia lesueur) is a small to medium sized rat-kangaroo, unique within the marsupials for its habit of living in communal warrens (Burbidge 1995). It was once widespread in arid and semi-arid regions of Australia but became extinct on the mainland after European settlement; with the only surviving populations on islands off the Western Australian coast (Burbidge 1995). It was reintroduced successfully to Heirisson Prong near Shark Bay, Western Australia in 1992 (Short and Turner 2000). This followed the isolation of a section of the peninsula with a predator-proof fence and removal of foxes (Vulpes vulpes) and feral cats (Felis catus) in the protected zone. The population of B. lesueur at Heirisson Prong was young and expanding, and contained within a limited area (Short and Turner 2000). Lidicker (1975) recommended focussing on such enclosed populations to study the nature and influence of the important population process of dispersal. Furthermore, although there are studies based on the dasyurids and wombats (e.g. Cockburn et al. 1985; Johnson and Crossman 1991; Soderquist and Serena 2000), there is little information on the dispersal of macropods and only limited or anecdotal accounts of the dispersal of potoroids (Sampson 1971; Christensen 1980; Pope et al. 2000). There is increasing interest in translocating and reintroducing potoroids, so an understanding of their dispersal patterns would be helpful.

Howard (1960) classified dispersal according to whether the stimulus causing the animal to move was innate or environmental. Innate dispersal is where an animal moves spontaneously because of some intrinsic reason and environmental dispersal occurs where an animal moves because of unfavourable environmental conditions (Howard 1960). Lidicker’s (1975) classification differs from Howard’s in that it was based on density. Saturation dispersal occurs when density is at a level that is causing an individual hardship and movement is a direct response to density. Pre-saturation dispersal occurs when an
animal disperses regardless of density. Within these broad dispersal categories are finer classifications concerned with which particular groups of a population move and when. Is one sex more likely to disperse than the other? Is one age group more likely to disperse than others? Over what distance do individuals disperse?

An animal exhibiting environmental dispersal is likely to settle as soon as it experiences adequate conditions. This may be a movement of a single home range diameter until it no longer experiences parental aggression, a movement to the periphery of a population to obtain adequate food resources, or a movement to the periphery until it avoids all types of intra-specific aggression. Conversely, individuals exhibiting innate dispersal are just as likely to enter a population as they are to exit it and the direction and distance of movement may be highly variable (Caughley 1977). These predictions may be modified by social organization. Greenwood (1983) considered species where males exclude competitors from access to females – a pattern evident in B. lesueur (Sander et al. 1997). He argued that in such species the distribution of females is governed by resource availability, whereas male distribution is governed by the availability of females. In reality, it is likely that several factors interact to produce differences in dispersal between the sexes.

The aim of this study was to investigate the process of dispersal for B. lesueur at Heirisson Prong by radio tracking mother-young pairs and determining the distances between the locations of the offspring and their mothers. The following questions were posed:

- Do male B. lesueur disperse further than females?
- At what age do male and female B. lesueur disperse?
- Do young male B. lesueur visit a greater number of warrens than do young female B. lesueur?
- Do sex ratios and densities of B. lesueur differ between core (long-established) areas of their range and adjacent peripheral (newly colonised) areas? If so, is this consistent with the early and predominant arrival of males in newly colonised areas?

**METHODS**

**Study site**

Heirisson Prong is a peninsula 12 km long and 0.8 to 2.5 km wide, extending into Shark Bay, Western Australia. The topography and climate of Heirisson Prong are described in detail by Short et al. (1994) and Short and Turner (2000). The reintroduction area covers 1200 ha north of a barrier fence designed to exclude mammalian predators. B. lesueur were released initially from a captive colony located 5.5 km north of the barrier fence. Most animals were released to the centre of the peninsula and some to the north of the captive colony. At the time of the study, there were approximately 250 to 300 free-range animals present on the peninsula. The population had expanded both northwards towards the tip of Cape Heirisson and southwards towards the barrier fence.

**Trapping and monitoring of animals**

The B. lesueur population has been monitored quarterly by trapping since first releases in 1992 (Short and Turner 2000). Bettongs were marked individually using either ear tags (in earlier years) or Passive Implant Transponders (PIT tags) (Microchips Australia Pty. Ltd. Keysborough, Victoria), weighed and measured. The sex, PIT number, location and date were recorded for each individual. In later years (from 1995), furred pouch young were marked using PIT tags, allowing life histories to be recorded in more detail. We used capture locations of mother/offspring pairs to identify approximate locations of birth of the offspring. Trapping sessions of between 7 and 12 days each were made in February, March, May and July 2000 to capture and collar mothers and their independent offspring, marked at an earlier date while in the pouch. Mothers and offspring weighing greater than 850 g (collar ≤ 5% body weight) were radio-collared using collars with two-stage transmitters and whip antennae (Titley Electronics, Ballina, NSW). Trapping during the four field trips resulted in 20 animals being collared from nine different mother-young groups. The animals consisted of nine mothers and their six sons and five daughters. Six mother-young groups consisted of mothers and one offspring. The remaining mother-young groups consisted of a mother and two offspring. To overcome problems of data dependence, only one offspring from each of these mother-young groups was used in further analysis. The offspring was chosen at random.

Collared animals were radio-tracked to their warrens during daylight hours. A three element yagi antenna and a receiver were used to locate the animals to particular warrens. These were marked with flagging tape and their position obtained using a Global Positioning System (GPS). Animals were located once every 24 hrs. The radio-tracking points included an error of approximately 20 m or less. Radio-tracking fixes were not obtained if animals had been trapped during the 24 hrs prior to the tracking session as tracking was assumed to have an effect on the position of the animal. Instead, the trap location was used as the animal’s position. Trapping locations were transferred from survey records to a geographic information system (GIS) and combined with radio-tracking positions obtained using a GPS. The
locations of trapping records were accurate to approximately 100 m. A further eleven mothers and their four sons and seven daughters were included in the analysis using trapping data only.

**Determination of dispersal distances**

The dispersal distance of *B. lesueur* was determined by assessing the distance moved by young away from the natal range. The natal range was taken to be the range of the mother, including the locations where both the mother and the offspring were trapped together or tracked to the same warren. The locations of mother and offspring for each pair were plotted and the home range of each was calculated using the minimum convex polygon method with 95% probability limit using the Calhome software package (Kie 1994). The calculation for the offspring always excluded the first location, which was the one where it was trapped with its mother. The centre points of these two home ranges were determined and the distance between these points was taken as the dispersal distance. Female *B. lesueur* have an adult home range of 72 – 104 ha (Robley 1999). Taking the upper figure and assuming a circular home range gives a diameter of 1150 m. Offspring were classed as having dispersed when located or trapped more than 1150 m from the centre of their mother’s home range.

**Age at dispersal**

The age of offspring when first trapped with their mother was estimated using Tyndale-Biscoe’s (1968) description of unique characteristics for different ages of developing *B. lesueur*. Age was taken to be the mid-point of the appropriate age interval. When animals were first classed as dispersed (located or trapped outside the diameter of the maternal home range), their age was estimated by adding the time interval since first capture with the mother to the age estimate at first capture. This was taken to be the dispersal age of the animal.

**Warren use**

On each field trip in 2000, radio-collared individuals were radio-tracked to a warren during the day. Multiple measurements on the same trip were taken but separated by a 24 hr period. A warren use index was defined as the number of warrens used by an animal divided by the number of fixes taken for that individual.

**Sex ratios and densities**

The protected area of Heirisson Prong was divided into three broad regions on the basis of distance from initial releases: a central ‘core’ area of 550 ha surrounding the initial reintroduction site, a northern region of 350 ha where further releases occurred and a southern ‘peripheral’ region of 300 ha where no releases occurred. ‘Known to be alive’ estimates from four census periods (July 1998, February and August 1999, and February 2000) were used to calculate sex ratios and densities for these three regions.

**Analyses**

Statistical analyses followed verification of basic assumptions of tests. No transformations were required.

**RESULTS**

Dispersal distances estimated by both radio tracking or trapping alone show greater dispersal distances for males than for females (Table 1). The mean dispersal distance of male *B. lesueur* was 4,600 m (radio tracking) and 6,200 m (trapping only) while for females the distances were 1,100 m and 2,500 m respectively. Two-way ANOVA of these data found a significant effect of sex ($F_{1,15} = 9.59$, $P = 0.007$), but no significant difference for the method (radio-tracking or trapping: $F_{1,15} = 1.55$, $P = 0.232$) or the interaction of sex and method ($F_{1,15} = 0.005$, $P = 0.943$). The relative numbers of males and females remaining within the maternal home range (Table 2) was analysed using a two-tailed Fisher-Exact test. Significantly more males than females dispersed beyond the maternal home range ($P = 0.0053$). Males dispersed at a mean age of $220 \pm 14$ days ($\bar{\tau} \pm SE$), females at $276 \pm 27$ days. The difference was not statistically significant ($t_{14} = -1.84$, $P = 0.087$). Warren use, assessed as warrens used divided by the number of fixes, was significantly higher for males in comparison to females (Male = $0.37 \pm 0.05$; Female = $0.24 \pm 0.03$, $t_{18} = 2.57$, $P = 0.019$).

<table>
<thead>
<tr>
<th>Sex</th>
<th>Type</th>
<th>n</th>
<th>Mean distance ± SE (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>Radio-collar</td>
<td>6</td>
<td>4600 ± 700</td>
</tr>
<tr>
<td></td>
<td>Trap</td>
<td>4</td>
<td>6200 ± 1500</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>10</td>
<td>5200 ± 800</td>
</tr>
<tr>
<td>Female</td>
<td>Radio-collar</td>
<td>5</td>
<td>1100 ± 800</td>
</tr>
<tr>
<td></td>
<td>Trap</td>
<td>7</td>
<td>2500 ± 1000</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>12</td>
<td>1900 ± 700</td>
</tr>
</tbody>
</table>

Table 1. Mean dispersal distances for *B. lesueur* on Heirisson Prong, using radio telemetry and trapping locations.

<table>
<thead>
<tr>
<th>Sex</th>
<th>&lt; 1150 m</th>
<th>&gt; 1150 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>Female</td>
<td>7</td>
<td>3</td>
</tr>
</tbody>
</table>

Table 2. A contingency table of dispersal distances for *B. lesueur* on Heirisson Prong. The distance of 1150 m indicates the maximum diameter of the maternal home range.
Sex ratios and densities in the three regions of Heirisson Prong between July 1998 and February 2000 are shown in Table 3. Sex ratios did not appear to differ between the south, centre and north but densities appeared higher in the central and northern regions compared to the more recently colonized southern region. There was no significant association between sex of Bettong and region ($\chi^2 = 0.081, p = 0.96$) and the density in the southern region (14.6 individuals/km$^2$) lay within the 95% confidence limit for the mean of the densities in the central and northern regions (20.6 ± 9.0 individuals/km$^2$).

In the nine year period from 1992 – 2000, 20 of 320 males were noted as having injuries consistent with intra-specific aggression. Scarred animals were largely young males at approximately five to six months from their first capture (i.e. newly independent males). None of the 330 females had such injuries ($\chi^2 = 21.28, p < 0.001$).

**DISCUSSION**

Dispersal of *B. lesueur* at Heirisson Prong was male-biased. Males and females dispersed at similar ages, but males dispersed greater distances and visited a greater number of warrens than females. The age of dispersal coincided with weaning and the onset of sexual maturity. Although we expected that densities and sex ratios should vary in different regions of Heirisson Prong, we could not demonstrate such variations statistically. Possible explanations may include displaced males returning to the core population when they mature, or differential mortality of males and females at the periphery of the population. These observations provide clues to the underlying reasons for dispersal. Any patterns may have been disrupted by a fox incursion into the conservation site in July 1997, which removed approximately 46% of the Bettong population (Short et al. 2002).

Young male *B. lesueur* displayed environmental dispersal, seeking to avoid aggression from established males, find mates, and possibly to improve their access to resources such as food and perhaps suitable warrens. If male *B. lesueur* were leaving the natal home range to escape maternal influence, they would only have to travel as far as the edge of the natal home range, but at Heirisson Prong, this was not the case. Males moved far greater distances than was necessary to separate from their mothers. It is possible that males moved to escape aggression from dominant males within the population and possibly to obtain access to undefended females. This interpretation is supported by the observed intra-specific aggression between male *B. lesueur* (Sander et al. 1997), the incidence of fur loss and scarring on male *B. lesueur* reported in this study, and the higher warren visitation rates found in males. It is likely that young males are continually harassed and only stop moving when they reach the edge of the population where fewer established individuals exist. At our study site, this was the southern region of the protected Heirisson Prong site where the density of Bettongs appeared lower. By contrast, inbreeding avoidance is probably significant for females. Seventy five percent of female *B. lesueur* dispersed a distance of less than two kilometres suggesting that the shift was initiated by the need to escape paternal influence. Once this was achieved, no further movement was necessary.

The dispersal pattern of *B. lesueur* contrasts markedly with that of another burrowing marsupial, the northern hairy-nosed wombat (*Lasiorhinus krefftii*). This marsupial, although sharing many characteristics, such as a gregarious lifestyle and the use of multiple burrows, possesses a female-biased dispersal pattern where females disperse after breeding (Johnson and Crossman 1991). Johnson and Crossman (1991) suggest that adult females disperse because the process of establishing a new burrow would be too energetically demanding for juveniles. This explanation is not likely to apply to *B. lesueur* in this habitat as their warrens are considerably smaller than those of wombats and they are often occupied by several individuals. Therefore, the energetic demands associated with warren establishment appear low.

The dispersal pattern of *B. lesueur* is similar to that of several macropod species such as the brush-tailed bettong (*Bettongia penicillata*) and *Macropus*.

<table>
<thead>
<tr>
<th>Sex and site</th>
<th>July 1998</th>
<th>February 1999</th>
<th>July 1999</th>
<th>February 2000</th>
<th>b (slope)</th>
<th>r$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male South</td>
<td>1.94 (6)</td>
<td>4.53 (14)</td>
<td>7.12 (22)</td>
<td>8.74 (27)</td>
<td>4.60</td>
<td>0.99</td>
</tr>
<tr>
<td>Female South</td>
<td>1.94 (6)</td>
<td>3.24 (10)</td>
<td>6.47 (20)</td>
<td>7.77 (24)</td>
<td>4.14</td>
<td>0.97</td>
</tr>
<tr>
<td>Male Centre</td>
<td>3.85 (21)</td>
<td>5.49 (30)</td>
<td>9.16 (50)</td>
<td>11.17 (61)</td>
<td>5.12</td>
<td>0.98</td>
</tr>
<tr>
<td>Female</td>
<td>3.85 (21)</td>
<td>6.04 (33)</td>
<td>9.52 (52)</td>
<td>10.81 (59)</td>
<td>4.88</td>
<td>0.97</td>
</tr>
<tr>
<td>Male North</td>
<td>5.52 (19)</td>
<td>9.01 (31)</td>
<td>11.05 (38)</td>
<td>12.50 (43)</td>
<td>4.60</td>
<td>0.96</td>
</tr>
<tr>
<td>Female North</td>
<td>6.10 (21)</td>
<td>7.85 (27)</td>
<td>10.47 (36)</td>
<td>12.21 (42)</td>
<td>4.18</td>
<td>0.99</td>
</tr>
<tr>
<td>Total Density</td>
<td>7.84 (94)</td>
<td>12.09 (145)</td>
<td>18.18 (218)</td>
<td>21.35 (256)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3. Densities (individuals per km$^2$) and number (in parentheses) of *B. lesueur* within three areas on Heirisson Prong between July 1998 and February 2000. The slope and significance of regressions of density versus time (in years) are given.
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spp. (Johnson 1989). Christensen (1980) believed B. penicillata exhibited male biased natal dispersal because areas disturbed by fire were recolonised predominantly by sub-adult males. This view is supported by evidence that male B. penicillata commonly disappeared from trapping grids suggesting that they are more likely to disperse than females (Sampson 1971). Male B. penicillata experience aggressive intra-sexual interactions whereas females do not (Sampson 1971) and this is likely to be a primary factor driving dispersal. However, this pattern of aggression is uncommon in other macropods suggesting that their dispersal is initiated by some innate factor (Johnson 1989).

This study was limited to a population below carrying capacity over its entire range, free of high predation pressures, and not subject to the protracted, irregular droughts characteristic of the semi-arid and arid zones (Morton 1990). Nevertheless, we predict that males should be the first colonizers from expanding populations. The driving forces are intra-sexual aggression and access to undefended females. Females will ultimately follow, motivated by inbreeding avoidance and resource limitation.

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