

Maternal influence on philopatry and space use by juvenile brushtail possums (*Trichosurus vulpecula*)

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Summary

1. The causes of juvenile sex-biased philopatry and space use in mammals remain poorly understood, and results of previous research have been conflicting. Experimental interventions and manipulations on wild populations are rare, but can play an important role in establishing the factors governing offspring space use.

2. We experimentally removed mothers of independent juvenile brushtail possums from the maternal home range and examined changes in offspring space use with global positioning system collars. We examined the influence of mother absence on philopatric behaviour, and determined whether or not maternal presence affected offspring space use.

3. We fitted a longitudinal linear mixed effects model to demonstrate a change over time in the home range size of juveniles following experimental treatment by the removal of their mothers. When mothers were removed from the natal range, juveniles occupied significantly larger home range areas, with average increases of 175% in 95% kernel density estimates and 289% in minimum convex polygon estimates. This increase occurred within the first month following mother absence and was independent of juvenile sex. Home ranges of control juveniles did not change during the same time period.

4. Changes in the spatial structure of mammalian populations in response to removal of individuals have important implications for pest management. The impacts of management strategies which target particular individuals in a population may counteract conservation benefits through their effect on the space use of survivors. Studies involving experimental removals provide important information on consequences of control and also yield insights into the causes of mammalian space use, philopatric behaviours and ultimately dispersal.

Key-words: global positioning system collars, home range, offspring, parental absence, population control, sex-bias, space use, spatial organisation

Introduction

Female philopatry and male-biased natal dispersal are prevalent among both solitary and gregarious mammalian species (Greenwood 1980; Waser & Jones 1983; Wahlstrom 1994; Lawson Handley & Perrin 2007). However, the causes of sex-biased space use and philopatry remain controversial (Pusey 1987; Stenseth & Lidicker 1992; Bowler & Benton 2005). Previous studies have suggested that the behaviour of parents may be a determining factor for offspring space use in some species (Dobson 1982; Boonstra *et al.* 1987; Anderson 1989; Wolff 1993).

Removal of a parent resulting in philopatry of the opposite-sex offspring was demonstrated by Wolff (1992) in a study conducted on white-footed mice (*Peromyscus leucopus*). Similar results have been reported for yellow-bellied marmots, *Marmota flaviventris* (Brody & Armitage 1985); male Californian ground squirrels, *Spermophilus beecheyi* (Dobson 1979); and white-tailed deer, *Odocoileus virginianus* (Holzenbein & Marchinton 1992). In contrast, Priotto *et al.* (2004) established that dispersal of juvenile vesper mice, *Calomys venustus*, was independent of parent removal. Therefore, findings regarding the influence of parental removal on space use and philopatry still appear contradictory. The inferences of previous research have also been limited by the problem of accurately distinguishing parents

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from other adults (Wolff 1993), and through a lack of comprehensive studies involving experimental interventions and manipulations in field conditions.

As well as contributing to our understanding of the causes of sex-biased space use and philopatry, the response of mammals to the selected removal of individuals in a population has important implications for pest control techniques, where the spatial structure of populations relates to the effectiveness of control strategies (Travis & Park 2004). In some mammalian species, management operations involving population culling have been shown to induce substantial changes in the spatial behaviour of remaining individuals (Tuytens *et al.* 2000; Coulson *et al.* 2004). In the UK for example, culling of badger (*Meles meles*) populations has resulted in significant alterations in spatial organisation (Tuytens *et al.* 2000; Woodroffe *et al.* 2006), with profound implications for the control of bovine tuberculosis for which the species is a known vector (Krebs *et al.* 1997). However, this effect does not appear to be consistent in all species, as Giuliano *et al.* (1999) demonstrated that orphaned white-tailed deer fawns occupied small home ranges than their unorphaned counterparts. Experimental manipulations involving the removal of known animals provide an important opportunity to improve our understanding of the social disruptions which may occur following population management, thereby increasing our ability to predict the consequences of control operations and assisting in the development of optimal strategies.

The Australian brushtail possum (*Trichosurus vulpecula* Kerr) is a nocturnal phalangerid marsupial (2–4 kg). It is an introduced pest species in New Zealand, where it damages native forests and wildlife (Cowan & Moeed 1987; Payton 2000; Innes *et al.* 2004) and acts as the main wildlife vector for bovine tuberculosis (Morris & Pfeiffer 1995; O'Neil & Pharo 1995; Coleman & Caley 2000). Whilst there is no strong evidence to suggest possums in New Zealand exhibit territorial behaviour, limited core areas of the home range (such as preferred den sites) may be defended (Green 1984), especially in low-density populations (Winter 1976). Generally, older and heavier possums are dominant over their younger, smaller counterparts (Jolly 1976; Biggins & Overstreet 1978; Day, O'Connor & Matthews 2000), and females are usually dominant over males (Winter 1976; Jolly & Spurr 1996). Subordinate possums have been shown in both captive and wild populations to remain temporally or spatially separate from dominant individuals (Jolly 1973; Winter 1976).

Adult females give birth to a single young in a well-defined autumn breeding season and are the exclusive parental caregivers (Green 1984; Fletcher & Selwood 2000; Cowan 2005). Offspring cease to forage in spatial association with their mothers from approx. 8 months of age, but nevertheless remain within the maternal home range (Winter 1976). Approximately 20–25% of the juvenile population undertake long-distance dispersal (Clout & Efford 1984; Cowan & Rhodes 1993; Cowan *et al.* 1996; Efford 1998; Cowan 2000), with a sex biased of roughly 4 : 1 towards male dispersers

(Efford 1991; Cowan 2000). Dispersal commences between 9 and 12 months of age (Cowan *et al.* 1996; Efford 1998) with settlement in new locations generally occurring within a month (Blackie 2010). Dispersal frequency is independent of population density (Cowan *et al.* 1997).

In contrast to male offspring who gradually shift away from the natal range (Cowan *et al.* 1996; Isaac 2005), daughters generally establish overlapping home ranges with their mothers (Crawley 1973; Clout & Efford 1984; Ward 1985; Ji *et al.* 2001; Stow *et al.* 2006). Aggressive behaviour by mothers (including threatening, striking or biting) was suggested by Winter (1976) as a factor influencing the movements of juvenile brushtail possums out of natal areas. Dunnet (1964) also speculated that young, subordinate males are driven out of their natal ranges by the behaviour of resident, dominant males. However, no experimental manipulations of field populations have yet occurred.

This study had two main objectives, first to examine whether brushtail possum offspring continued to retain close spatial association to the maternal home range if their mothers were absent, and secondly to address Winter's (1976) the suggestion that mother behaviour instigates dispersal of offspring out of natal ranges. To examine these hypotheses, we conducted an experiment whereby the mothers of known, independent juveniles were euthanised and the movements of their offspring were recorded through global positioning system (GPS) collars prior and subsequent to mother euthanasia, during the key developmental phase of independent space use from age 8–12 months. If space use of juvenile possums during the phase of independency is motivated by the presence of mothers only, changes in space use will not occur if mothers are absent. For philopatric offspring, removal of mothers with overlapping home range areas may diminish competition for shared resources and consequently result in a decreased home range size. Alternatively, when mothers are absent offspring may expand their ranges to avoid interactions with neighbouring conspecifics moving into the vacated area. Juvenile home range size was compared before and after mother removal, and the rate of any changes in home range area evaluated. A greater knowledge regarding the role of adults in determining juvenile space use and philopatry provides important contributions to mammalian demography and population management.

Materials and methods

STUDY SITE

The study was conducted from November 2007 – May 2009 within a remnant fragment of native forest in the Waikato region of New Zealand (38°01'S, 175°43'E). The study area encompassed a 15-ha forest patch dominated by tawa (*Beilschmiedia tawa*), totara (*Podocarpus totara*), rimu (*Dacrydium cupressinum*), rewarewa (*Knightsia excelsa*) kahikatea (*Dacrydium dacrydioides*) and pukatea (*Laurelia novae-zelandiae*). No possum control had occurred at the site for 7 years, and the population density was high (*c.* 14 possums/ha) and stable. Population density was calculated by obtaining a total count of the number of possums

present when an intensive ground control operation to eradicate all possums from the area was conducted at the end of the study.

REMOVAL OF MOTHERS

To establish mother–offspring pairs, juvenile possum were ear-tagged as dependent pouch young during live-captures of adult females. Known mothers of independent juveniles were euthanised through overdose of the anaesthetic isoflurane when their offspring were 10–11 months of age. This procedure results in rapid unconsciousness and death in a painless manner, providing a safe and reliable method that minimises animal fear (Flecknell 1996). Mothers chosen for euthanasia were tracked using very high frequency (VHF) radio-telemetry to their den locations, following which treadle-operated cages were set in close vicinity to their den trees for successive nights until capture occurred. They were then placed in a small wooden box with a clear perspex side and sealed end. Gaseous isoflurane was administered with a hand pump until breathing became laboured and then ceased. Euthanised possums were left in the sealed perspex box for a further 10 min to ensure that consciousness was not regained and then checked for a pulse in the femoral artery. Juveniles which had their mothers euthanised are henceforth referred to as the experimental group, whilst juveniles with mothers present formed the control group. Mother–offspring pairings were randomly located across the landscape with respect to treatment and separated by a distance (> 700 m) which made home range overlap with any other studied mother–offspring pairs extremely unlikely.

DATA COLLECTION

GPS collars with in-built VHF transmitters (Sirtrack Ltd, Havelock North, New Zealand) were fitted to 28 juvenile possums from the age of 8 months (treatment: four male, five female; control 12 male, seven female). Juvenile possums were captured in treadle-operated cages and anaesthetised using gaseous isoflurane prior to collar attachment. All collars were fitted with a three-finger gap between the collar belt and the skin, large enough to allow for animal movement and to prevent rubbing, but not large enough to allow collars to slip over the possum's head. GPS collars were deployed for a minimum period of 4 months and configured to obtain two locations each night during the peak period of nocturnal activity. For the experimental group, GPS location data were collected for 2 months prior to mother removal and for the 2 months following their mother's absence. Collars all weighed less than 80 g and had a minimum estimated battery life of 160 days. To ensure that mothers of control juveniles were alive and still occupying the maternal range throughout offspring collar deployments, their locations were also recorded using Sirtrack GPS/VHF collars.

HOME RANGE AREA CALCULATIONS

Estimates of home range size were calculated for four measures: the 95%, 75% and 50% kernel density estimates (KDE); and 100% minimum convex polygons (MCP) using RANGES7 software (South, Kenward & Walls 2005). We compared the estimates for all four home range measures before and after treatment, using Mann–Whitney *U* tests followed by Wilcoxon paired tests. To ensure the accuracy of home range estimates, only juveniles with a minimum of 30 locations per month were included in calculations (Seaman *et al.* 1999). The 100% MCP estimate was chosen to identify possible longer-distance

forays out of the home range (Laver & Kelly 2008), whilst the fixed KDE was selected as it generally provides more accurate estimates of range use (Seaman & Powell 1996; Seaman *et al.* 1999; Börger *et al.* 2006). The MCP estimates were calculated using a harmonic mean peel centre, and kernel estimates using the least-squares cross-validation smoothing parameter (Worton 1989; Seaman *et al.* 1999).

To more precisely investigate home range change over time, we analysed the effect on the experimental group of removal of mothers using longitudinal linear mixed effect models (Fox 2002). For both the control and the experimental groups, we estimated monthly home range size for each of the 2 months prior to removal of mothers in the experimental group, and for 2 months postremoval. Our longitudinal data were the monthly MCP home ranges of all individuals for the 2 months prior to treatment, and 2 months post-treatment (four time periods). We analysed only the MCP home ranges, but noted that results for the KDE home ranges were qualitatively identical. Home range size was log transformed to normalise its distribution and linearise its relationship with the covariates. We modelled the fixed effects of time period and group membership (experimental or control), and specifically looked for a post-treatment interaction in the experimental group, indicating an experimental group-specific change in home range size after the removal of mothers. We corrected for any *a priori* differences in home range size because of individual sex or group membership by including both factors as covariates. Further variation attributable to individuals was modelled as a nested random effect in time. We investigated possible auto-correlation in the monthly home range sizes of individuals by imposing a first-order auto-regressive correlation structure on individual errors. Models were compared using an AIC framework, and the model with highest AIC support was always retained. Nested models were pairwise compared using an AICc framework and likelihood ratio tests.

Results

A total of 19 juveniles formed the control group (12 male, 7 female); whilst the experimental group contained nine offspring (four male, five female). Prior to the removal of mothers, control and experimental groups did not significantly differ for any of the four range estimates (Table 1). However, home range estimates for the experimental group became significantly larger (Mann–Whitney *U*-tests $P \leq 0.03$) for all range measures excluding the 50% KDE ($P = 0.06$), once mothers were absent. The median home range areas of experimental juveniles increased substantially from when mothers were present to when they were absent (Table 2). No significant change was recorded in the control group during this period.

Our longitudinal mixed effects model showed MCP home ranges of all individuals changed over time (Fig. 1). For the control group, there was a small, but significant, decrease in home range size over time ($\beta = -0.009$, $SE = 0.003$, $P = 0.005$), whereas for the experimental group home range size increased significantly ($\beta = 0.013$, $SE = 0.006$, $P < 0.001$). Sex ($P = 0.52$) or group membership ($P = 0.08$) did not have a significant effect on home range size. The same model including a first-order auto-regressive error structure for individuals did not perform significantly better (Likeli-

Table 1. Median (range) home range areas for control and experimental juvenile possums before and after mother removal. Range sizes are provided for 95%, 75% and 50% kernel density estimates (KDE) and 100% minimum convex polygons (MCP). *P*-values are results from Mann–Whitney *U*-tests comparing median home range sizes of control vs. experimental groups

Range estimate	Home range area (ha) mothers present			Home range area (ha) mothers absent		
	Control	Experimental	<i>P</i>	Control	Experimental	<i>P</i>
95% KDE	0.53 (0.27–16.4)	0.50 (0.21–1.40)	0.56	0.42 (0.11–4.78)	1.35 (0.58–2.14)	0.02
75% KDE	0.29 (0.10–6.65)	0.26 (0.13–0.88)	0.49	0.22 (0.07–3.14)	0.69 (0.29–1.24)	0.03
50% KDE	0.16 (0.05–3.29)	0.15 (0.07–0.29)	0.22	0.14 (0.04–1.87)	0.32 (0.09–0.83)	0.06
100% MCP	1.89 (0.41–95.2)	0.93 (0.36–6.83)	0.29	1.00 (0.38–33.34)	3.62 (2.43–32.79)	< 0.01

Table 2. Percentage change in home range areas for control and experimental juvenile possums after mother removal. Range sizes are provided for 95%, 75% and 50% kernel density estimates (KDE) and 100% minimum convex polygons (MCP). *P*-values are results from Wilcoxon test for matched pairs comparing median home range sizes before and after mother removal

Range estimate	Control		Experimental	
	% change	<i>P</i>	% change	<i>P</i>
95% KDE	–21	0.07	+ 170	0.01
75% KDE	–24	0.16	+ 172	0.01
50% KDE	–12	0.20	+ 113	0.03
100% MCP	–47	0.38	+ 289	0.02

hood ratio statistic < 0.01, *P* = 1.00) and estimated only a low auto-correlation of $r = 0.2$, which was not significant.

Discussion

The ability to manage animal species is dependent upon knowledge of the processes and parameters of animal spatio-temporal behaviour (Swingland & Greenwood 1983; Macdonald & Johnson 2001; Nathan *et al.* 2008; Patterson *et al.* 2008). Studying the space use of individuals subject to experimental manipulations provides unique opportunities to improve our understanding of the spatial organisation of populations. Our data indicate that the movements of brush-

tail possum offspring were influenced by the removal of mothers from the natal range, with juveniles expanding their home range areas shortly after mother absence. Changes in offspring space use when mothers are absent may be the result of factors such as subsequent social interactions and the reduction of maternal cues marking range areas.

Olfactory communication is prominent among marsupials (Russell 1985; Salamon 1996), with scent marks used by adults to label regularly occupied areas (Croft & Eisenberg 2006). Visual cues such as heavily chewed and gnawed objects are also frequently used to signal home range areas (Kean 1967; Biggins 1984). As juvenile brushtail possums are unlikely to scent mark (Biggins & Overstreet 1978), they may not be able to readily identify the previous extent of their maternal range as cues left by their mothers fade. Additionally, the lack of these cues may initiate the movements of conspecifics into the depleted area (Efford, Warburton & Spencer 2000; Clinchy, Krebs & Jarman 2001; Ji *et al.* 2001), where they may begin their own scent or visual marking. As subordinate possums will avoid areas recently marked by dominants (Winter 1976), this could result in the expansion of juvenile ranges away from the cues of dominant individuals. Accordingly, this will bring about the temporal and spatial avoidance behaviour previously observed between dominants and subordinates (Jolly 1973; Winter 1976).

Several studies on small species of mammals have documented the recolonisation of depopulated areas by immediate neighbours (Stickel 1946; Van Vleck 1968; Verts & Carraway

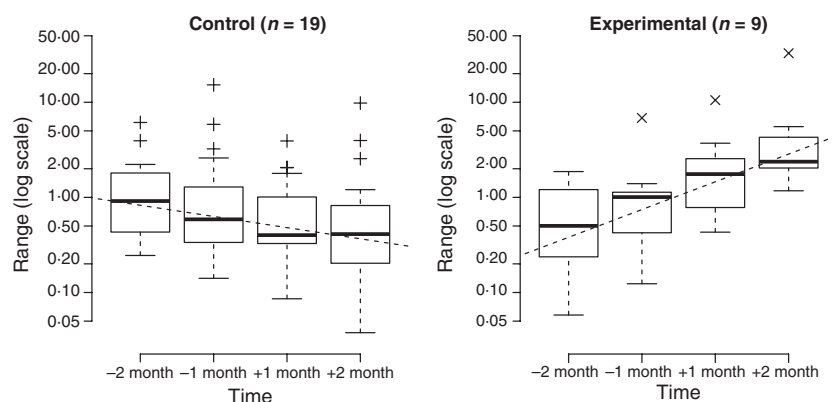


Fig. 1. Change in 100% minimum convex polygons (MCP) home range areas for control and experimental juvenile possums before and after mother removal. Bar lengths correspond to 75 and 25 percentiles, dark lines within bars medians, and whiskers 1.5 times the inter-quartile range.

1986; Nakata & Satoh 1994). In brushtail possums, the removal of neighbours has been shown to induce home range shifts of individuals from the surrounding area towards this vacant space within a matter of weeks (Efford, Warburton & Spencer 2000; Clinchy, Krebs & Jarman 2001; Ji *et al.* 2001). Adult possums appear to adjust their home ranges to increase usage of the area of reduced density, potentially maximising their access to resources which are no longer constrained by the behaviour of neighbours (Efford, Warburton & Spencer 2000). Based on these findings it appears that by removing mothers, neighbouring resident possums may have expanded their ranges to overlap more extensively with the area occupied by remaining offspring. In addition to the possible impacts of marking their new range, this overlapping of areas may result in aggressive encounters between offspring and recently immigrated dominant adults. As subordinate juveniles can be excluded from their home ranges or den sites during encounters with dominants (Biggins & Overstreet 1978; Ward 1978; Green 1984; Cowan 1989; Day, O'Connor & Matthews 2000), offspring will have little chance of successfully defending these areas when their mothers are absent, and consequently range expansion may be driven by exclusion from original home range areas.

Our results illustrated a clear trend for offspring range expansion after mother absence regardless of sex. This was in contrast to findings by Steinmann *et al.* (2006), who observed that experimental removal of adult female corn mice (*Calomys musculus*) resulted in a decrease in home range area for juvenile males but not females. During our study, there was also one recorded instance of natural mother mortality and it was noted that her offspring demonstrated similar changes in space use to the experimental group, indicating that regardless of the cause of mother absence the resultant behavioural changes in offspring are likely to be similar.

These findings have particular importance when considering the impacts which population control activities may have on the behaviour of survivors. Our research suggests that young surviving possums may expand their ranges following control operations, particularly if their mothers have been successfully removed. Similar disruptions in the spatial organisation of populations, including considerable home range expansions, have been noted in other mammalian species subject to population culling (Tuytens *et al.* 2000; Coulson *et al.* 2004; Woodroffe *et al.* 2006). Expansions in home range areas following control may lead to increased encounter rates with conspecifics resulting in the persistence of bovine tuberculosis in remaining populations. Thus, control operations which insufficiently target juvenile possums have the potential to counteract the benefits of disease management strategies. Understanding the spatial dynamics of species which act as vectors for infectious diseases is vital for predicting transmission scenarios and has important implications for designing effective control strategies. Studies involving experimental removals are extremely valuable for providing further insight into the consequences of control operations on the spatial structure of populations.

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