

**Changes in possum behaviour at reduced density  
– a review**

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## Summary

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### Project and Client

At the request of the Animal Health Board (Project No. R-10557) Landcare Research reviewed what is currently known about changes in possum behaviour at reduced density. The review was completed in June 2002.

### Objectives

- To review changes in possum behaviour following reductions in density due to control, and at low density; and the relevance of those changes for ongoing maintenance control, monitoring and Tb epidemiology.
- To identify and prioritise research on key issues arising from the review.
- To produce a summary document for vector managers, in both hard copy and a format suitable for placement on the AHB web site, in addition to this report.

### Methods

- Information on possum behaviour was obtained from journals, books, conference proceedings and unpublished reports following searches of electronic databases.
- Simulation modelling was used to assess the likely impact of changes in behaviour on population monitoring.

### Main findings

- There is variation in possum movements at high densities, but there are few data on possum movements at low densities. There are also few data on changes in possum behaviour in response to control.
- Simulation modelling indicates biologically realistic changes in range size could influence population monitoring by changing encounter rates of possums with traps, and biologically realistic changes in trappability could influence population monitoring by changing interaction rates of possums with traps.
- The limited data available suggest possum behaviour could influence the success of future control, particularly if that behaviour is heritable.
- There is no evidence possum behaviour at low densities is likely to produce contact rates that will allow Tb to persist, other than possible increases in contact rates if possums enlarge their home range size following control.

### Recommendations

There is not enough reliable information available to recommend changes to current practices of possum control and monitoring, but our modelling and the information available indicate that changes in behaviour have the potential to substantially affect managers' ability to control and monitor possum populations. It is therefore crucial that the nature and size of such behavioural changes be determined under both 'initial' control (where populations are reduced from relatively high to low densities) and maintenance control (where populations are reduced from relatively low to lower densities) scenarios. Studies are therefore required to address the following questions:

- Do possums at lower population densities have sufficiently different movements to possums at higher population densities to result in different encounter rates with traps and baits that are large enough to influence population monitoring or the success of future control?
- If so, are these differences caused by control selectively removing animals that have high encounter rates with traps and baits thus changing the average behaviour of the post-control population; or by possums that remain post control changing their behaviour either in

response to the low population density or in response to the act of control? Some existing data are available to begin to address the question of how much individual variability there is likely to be in encounter rates with traps and baits in a given habitat type.

- If control selects for possums that have low encounter rates with traps and baits is this heritable? If so, this would have potentially serious implications for the success of long-term control. Studies comparing the behaviour of possums from populations that have been subjected to long-term control with the behaviour of those that have not should provide some insight into this.
- Do possums at lower population densities have sufficiently different interaction rates with devices/traps/baits to possums at higher population densities to influence population monitoring or the success of future control?
- If so, are these differences due to control selectively removing animals that have high interaction rates; or because possums change their interaction rates when at low density? Due to less competition for natural food for example.
- If control selects for possums that have low interaction rates with devices/traps/baits is this heritable?

To determine whether behavioural differences at low density are likely to maintain contact rates sufficient for the continued persistence of Tb, studies are required to address the following questions:

- What is the relative importance of the different contact behaviours and environmental pathways for the transmission of Tb?
- How do contact rates change with changing possum population density?

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## 1. Introduction

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This report reviews what is currently known about changes in possum behaviour as a consequence of control, and the degree to which behaviour differs between possums at high density and those at low density because of sustained control. It also explores the implications of those changes for population monitoring, the success of future control, and the transmission of bovine Tb. In addition simulation modelling was carried out to explore whether biologically realistic changes in behaviour are likely to influence population monitoring. The review and simulation modelling were carried out by Landcare Research between October 2001 and June 2002, and were funded by the Animal Health Board (Project No. R-10557).

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## 2. Background

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This review was motivated by the recognition that changes in possum behaviour at low densities could affect the results of possum population monitoring using the residual trap catch (RTC) method and the success of future control (AHB Workshop, Dec 2000). The RTC method (NPCA 2000) uses randomly placed traplines, with 10 (or 20) leghold traps set for 3 nights on each trapline, to produce a 'catch per unit effort' index that is presumed to relate directly to possum density, especially at low possum density. It is used to assess the effectiveness of possum control operations by providing a 'pass-or-fail' mean RTC target (originally <5%, AHB 1997) that the possum population must be reduced below. The targets also consider the RTC on individual lines to deal with the "patchiness" of control (Webster & Caley 2001). As with all index methods, RTC is affected by both the abundance of possums, and the average behaviour of the possum population. Average behaviour affects RTC because possums must first encounter traps, and then interact with them to be caught. Any detection technique that requires encounter and interaction (e.g. traps, wax blocks,) will be affected by average behaviour. Similar processes determine the effectiveness of baiting, i.e. possums must encounter baits and then consume them; and the transmission of Tb, i.e. a susceptible possum must encounter an infected possum and then interact with it in order to be infected by the disease. While the probability of encountering traps and baits is probably determined mainly by the movements of possums, additional social interactions may contribute to encounter rates between possums and hence transmission of Tb, so the latter will be considered separately in this review.

We first review the literature on possum behaviour and discuss how this may affect possum monitoring and the success of future control. We then use simulation modelling to explore further the likely impact of potential changes in behaviour on population monitoring using methods recently developed by Landcare Research staff (Efford, unpubl., Efford & Ramsey, unpubl.).

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### 3. Objectives

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- To review changes in possum behaviour following reductions in density due to control, and at low density; and the relevance of those changes for ongoing maintenance control, monitoring and Tb epidemiology.
  - To identify and prioritise research on key issues arising from the review.
  - To produce a summary document for vector managers, in both hard copy and a format suitable for placement on the AHB web site, in addition to this report.
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### 4. Methods

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- Information on possum behaviour was obtained from journals, books, conference proceedings and unpublished reports following searches of electronic databases.
  - Simulation modelling was used to assess the likely impact of changes in behaviour on population monitoring using methods recently developed by Landcare Research staff (Efford, unpubl., Efford & Ramsey, unpubl.). These methods are outlined in the body of the report.
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### 5. Main findings

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#### 5.1 Literature review

##### 5.1.1 Encounter rates and interactions with traps and baits

Possum population monitoring and control require that possums encounter and then interact with devices and baits. For any population of possums, the number of captures or poisonings will reflect the average behaviour of the possum population as well as its density. We are therefore interested in whether the average behaviour of the possum population differs enough between pre- and post-control populations to substantially affect encounter rates or interactions, because this will have implications for RTC monitoring and for bait uptake in future operations. For example, at a given population density a decrease in encounter rate with traps due to a change in average behaviour would result in a lower RTC. Similarly, at a given population density a decrease in the likelihood of being caught once a trap is encountered would result in a lower RTC. Average behaviour of the population could change either in response to the lower population density, or as a consequence of control, and both possibilities need to be considered.

There are three basic mechanisms that could lead to a change in the average behaviour of the population post-control that apply to both encounters and interactions:

1. Control selectively removes animals with high encounter rates or high interaction probabilities.
2. Individual possums change their encounter rates or interaction probabilities.
3. Animals with different encounter rates or interaction probabilities immigrate onto the site post-control.

##### 5.1.2 What determines encounter rates with traps and baits?

Both the RTC method and possum control largely require possums to come to the ground to

encounter traps or baits, although some aerially distributed bait may get caught in the canopy. Spotlight shooting can target possums up trees but is ineffective in continuous forest and so not used there. As a consequence, the amount of area per night possums cover moving on the ground will determine how often possums encounter traps and baits. What do we know about the movement of possums, and its likely affect on their encounter rates with traps and baits?

Few studies have made detailed observations on the movements of resident possums over short time scales, and most of these were based on small numbers of individuals (Ward 1978, MacLennan 1984, Winter 1976, Paterson et al. 1995, Jolly 1976). In contrast, a larger number of studies have looked at home range sizes of possums considering movements over longer time-scales ((Cowan & Clout 2000). To use the results from these studies to make predictions about whether they reflect likely contact rates with traps and baits, we need to establish that longer term movements are representative of short-term movements that occur over periods appropriate to baiting or trapping.

Ward (1978) followed four possums in the Orongorongo valley in native podocarp/hardwood forest. Three of the possums spent 15-20% of their time on the ground, but one female spent only 9% of her time on the ground in the first year of the study, and 4% in the second. Graphical depiction of daily range lengths suggested that movement patterns were reasonably consistent from day to day, indicating possums probably came to the ground on most days. Possums moved over an area of <math>900\text{m}^2</math> per night on average, but occasionally showed much larger movements. Average movements over 3 nights were correlated with seasonal home ranges ( $r = 0.79$ ), suggesting that longer-term home range estimates do provide an indication of relative movements over shorter time scales equivalent to a trapping period for individual possums.

Average nightly movements for possums inhabiting mixed woodland/scrub bordering pasture in a study in the Wairarapa were approximately ten times larger than in the Orongorongo valley (Paterson et al. 1995). Home range sizes were also considerable larger in the Wairarapa, providing further evidence that home range estimates provide a guide to the nightly activity of possums (Paterson 1993).

Possum range size will be determined by travel both on the ground and in the canopy. In Ward's (1978) study, the female possum that used the ground least (in terms of %time) also had the smallest home range, suggesting home range size may be determined largely by distance travelled on the ground. In a study conducted in Queensland (MacLennan 1984) found that possums spend about 9% of their time on the ground, on average travelling 104 metres between trees. Movements of this length must make a significant contribution to home range size, although it is not certain that observations on possum movements in a Queensland habitat are relevant to New Zealand conditions. Another study of six possums in Queensland (Winter 1976) found more time was spent travelling in trees than on the ground, but no data were provided on distances moved in terrestrial vs. arboreal habitats, so it is not possible to determine the relative contributions of terrestrial and arboreal movements to home range size from that study.

In summary, home range size probably provides a useful indicator of likely encounter rates of possums with traps and baits, but the evidence for this is weak.

### **5.1.3 Do some animals have higher encounter rates with traps and baits than others?**

The majority of studies on possum home range sizes have been carried out in populations at close to carrying capacity. Male home ranges are often twice as large as female home ranges (Ward 1978, Paterson et al. 1995, Jolly 1976), but in some habitats the ranges are similar (Cowan & Clout 2000). Males also spend a greater proportion of their time on the ground than females (Ward 1978, Winter 1976), and at pastoral ecotones males travel more often to pasture than females (Green & Coleman 1986), indicating they would be more likely to encounter both traps and baits in some habitats.

Sex-biases in trapping and poisoning have been observed (Coleman & Green 1984), suggesting the population that remains post-control may sometimes be female biased.

For baits distributed from the air the wider ranging behaviour, and greater use of the ground by males may result in more males being killed. (Clout 1977) provides some evidence that this may occur, with eight marked females and two marked males surviving a 1080 operation in a population where the pre-control sex ratio approximated parity. Fraser and Knightbridge (1995) also trapped a predominance of females during the post-control monitoring of aerial 1080 poisoning of pine forest, but Nugent et al. (2001a) found no difference in sex ratio between controlled (aerial 1080) and uncontrolled areas of native forest.

A female bias in survivors has been reported when widely spaced bait stations were used placed (Hickling 1995). In contrast, in a group of trials carried out in plantation forests (Henderson et al. 1997) where bait stations were placed 100m apart, the population post-control was male biased (Henderson unpubl. data quoted in (Henderson & Hickling 1997)). There is some evidence that home range sizes do not differ as much between males and females in pine plantations (Cowan & Clout 2000). Henderson and Hickling (1997) speculated that the bias may have been caused either by behavioural factors that cause females to be more susceptible to control by bait stations (presumably through their interaction with them), or by a male-biased recolonisation from surrounding areas. A study carried out in farmland, swamp and willow in Hawke's Bay indicated poison baiting targeted males and females equally (Brockie et al. 1997). In this area home ranges of males and females were similar (Brockie et al. 1987 quoted in Cowan & Clout 2000).

From a study conducted on a forest remnant in farmland near Dunedin, Efford (unpubl. data) has some evidence that home ranges of yearling possums are smaller than those of adults. The rank of home range size from smallest to largest was yearling females < adult females  $\leq$  yearling males < adult males. Presuming bait encounter rate is positively correlated with home range size, these findings suggest control would be biased towards killing males and older animals, which would, in turn, predict a population bias towards young animals and females following control. If these animals do not change their behaviour (i.e. they maintain their home ranges and ground use) then RTC is likely to underestimate population density immediately post-control. A female-biased population would also have a greater rate of increase ( $r$ ) than a population of equivalent density with an equal sex ratio. In addition the sex ratio is likely to return to parity as the population increases, and the relative increase in the proportion of males would spuriously increase the RTC estimate if there was a higher contact rate of males with traps. This may partially explain apparent high rates of increase over a period of 1 or 2 years following control in some areas, but there are instances of apparently rapid population increase where this mechanism does not apply (Nugent et al 2001a).

Two studies suggest some possums spend more time than others in the canopy and are less susceptible to aerial baiting because they fail to encounter baits ((Morgan 1994). In both studies dyed baits were delivered from planes and uptake of baits by possums shot from the canopy was compared with uptake of baits by possums caught on the ground. In both cases a smaller proportion of possums shot from the canopy had consumed baits, although the sample size in Morgan (1994) was small.

Almost all the information we have on possum movements will be biased towards possums that use the ground, because possums must come to the ground to be trapped and to have radio-collars fitted, so whether some possums are predominantly canopy dwellers is still an open question. Control operations often kill about 90% of the population (Morgan & Hickling 2000) but that still leaves a substantial number of survivors. Furthermore, this assessment is based largely on RTC, a ground based technique, and it could be argued that the estimated reductions apply only to the susceptible

population of possums that use the ground. Similar estimates of population reduction using pellet counts (eg Coleman et al. 2000), which should detect both ground-using and canopy-based possums, would suggest most possums use the ground. Further, based on pellet counts, ground-based kill trapping removed all possums from an area at Mt Bryan O'Lynn in Westland (Coleman et al. 1980). In addition, eradication of possums from islands has been achieved using predominantly ground-based techniques (Cowan 1992, Clout & Ericksen 2000), consistent with all possums using the ground. However, in these cases control was applied over extended periods, and it is possible some possums use the ground only occasionally or for brief periods and would be missed in the short time frame of regular control.

There is significant individual variation in home range size among possums, e.g. podocarp-mixed broadleaf forest - males 0.1-3.0ha and females 0.03-3.8ha (Crawley 1973); and in nightly activity, e.g. pasture/scrub/remnant forest – males 0.1-8.8ha and females 0.05-2.32ha (Paterson et al. 1995). If encounter rates of possums with baits and traps are correlated with home range size, then survivors are highly likely to include the possums that have small ranges, and/or shortest daily movements within their range. It is not known whether this variation is determined by genetic reasons, prevailing conditions, e.g. population density, social or reproductive status, local food availability, or a combination of factors.

Finally there is also seasonal variation in home range size (Cowan & Clout 2000), indicating that the relationship between RTC and possum population density may be expected to change with season.

#### **5.1.4 Do the movement patterns of possums change in response to control, or due to reduced population density?**

Possums may expand their range sizes and hence potentially increase encounter rates with traps and baits in response to the removal of neighbours (Clinchy et al. 2001, Hynes 1999). However, (Efford et al. 2000) reported that possums that shifted their home range into an area made vacant by a removal experiment did not change the size of their home ranges.

If home range sizes were larger at lower densities then RTC would overestimate population density. This would increase the efficacy of possum control because possums would be more likely to encounter baits. As already noted there is some evidence that yearling possums have smaller home ranges than adults of the same sex (Efford, unpubl. data), but it is not clear whether these smaller ranges are a feature of being young and small-bodied, or whether the presence of older possums restricts the range size of young possums. If the latter, then it is possible that young possums expand their ranges following control. Similarly, it is not known whether individuals with small home ranges would expand their home ranges following population reduction. There is some evidence that possums in low-carrying-capacity habitats have larger home ranges than those in naturally high density populations (Cowan & Clout 2000, Ward 1978, Clout & Gaze 1984), but it is not clear whether range size differs in response to social pressures related to population density, or the greater concentration of resources in better habitats.

Alternatively, possums may reduce their ranging activity post-control if the increase in per capita availability of scarce resources means they have to range less widely to find them. There are no data on the relationship between home range size and the availability of resources for possums.

Possums may reduce their ranging activity immediately post-control if they associate the rapid disappearance of their neighbours, or the activity associated with control, with an increase in predation risk. A response of this nature would presumably be temporary. Across a diverse range of taxa prey have been shown to select for refuges or areas of more complex habitat structure, or to reduce their activity, when confronted with the risk of predation (Lima & Dill 1989, Sih 1987, Lima 1998). The brushtail possum reduces its activity on the ground, and avoids open areas, when

confronted with the risk of fox predation (Gresser 1996, Pickett 1999). The significance of natural predation for New Zealand possums is unknown, but is thought to be low (Cowan et al. 2000). Whether possums do perceive a rapid reduction in density as increased predation risk is uncertain, but a decrease in ranging activity would result in RTC underestimating population density immediately after control. The short-term nature of this type of response should have no impact on future control operations after behaviour has returned to normal. There are no empirical data to support this possibility.

### **5.1.5 Do the movement patterns of immigrants differ from those of residents?**

The increasingly broad scale and comprehensive coverage of possum control limits the potential for immigration to explain changes in the average behaviour of possum populations over short time frames. Most evidence suggests the movement of animals into controlled areas occurs over a relatively long period of time (Cowan & Clout 2000, Green & Coleman 1984), except on the very edges of controlled areas, where possums from adjacent uncontrolled areas rapidly shift their range (Efford et al. 2000, Ji et al. 2001). In the longer term recently matured males are the major colonists of controlled areas (Clout & Efford 1984). These may have smaller home ranges than older males, but may increase home ranges in response to the lower population density. Dispersal of juveniles away from the natal range does not appear to be affected by local population density (Cowan et al. 1997), suggesting a local accumulation of juveniles due to reduced dispersal in response to lower population densities achieved by control does not occur.

### **5.1.6 Do individual animals have different interaction rates with traps and baits?**

Once traps or baits are encountered, individuals must interact with them to be captured or killed. In most cases, individuals will be interacting with a novel object or food. Wariness of novel objects is termed neophobia, and there is probably individual variation in how neophobic different individuals are (Mitchell 1976, Greenberg 1990). For example, blackbirds and robins show extremely variable responses to novel food items, with some birds taking up to 100 exposures to a novel food before they consume it regularly (Marples et al. 1998). Possums also show neophobia towards novel foods (O'Connor & Matthews 1996). If some individual possums are more neophobic than others, then they are more likely to survive control efforts. If this neophobia is heritable, then as a whole the population will become more neophobic, and future control will be more difficult. Behavioural resistance to control has been observed in populations of brown rats (Brunton et al. 1993).

If animals neophobic towards novel foods are also neophobic towards lures or traps, then RTC will be affected also, and will underestimate population density. Possums react to the lure at trap sites and neophobic responses could occur towards the lure, but possums may be unaware of traps set on the ground, reducing the potential for neophobic reactions (B. Warburton unpubl. data). Catch rates on raised sets are lower than for ground sets, which may, in part, be because the trap is much more apparent with raised sets. The success of this form of trapping may be more sensitive to neophobic reactions by possums. (Sunnucks 1998) found individual rabbits tended to have similar ranked avoidance of different novel visual stimuli, suggesting neophobic individuals may be wary of most novel things. However, there was no apparent relationship between trappability and neophobia in rabbits in the field (Sunnucks 1998). This contrasted with results obtained in the laboratory, where rabbits obtained by trapping consumed more novel foods than those obtained by ferreting (Sunnucks 1995 unpubl. PhD thesis, quoted in Sunnucks 1998).

### **5.1.7 Do the interaction rates of possums with traps and baits change in response to control, or due to reduced population density?**

The development of bait shyness following lethal baiting (Hickling 1995) is now well documented. This type of behavioural response is not the main focus of this review and will be addressed here only briefly. Considerable evidence now exists that long-lasting aversion to baits can be induced in possums both in the laboratory (Morgan et al. 1996, O'Connor & Matthews 1996, Morgan & Milne 1997, O'Connor & Matthews 1997), and in control operations in the field (O'Connor & Matthews 1999, Ogilvie et al. 2000). Aversion can largely be overcome by changing the bait type and flavour

(Morgan et al. 1996, O'Connor & Matthews 1999). Follow-up control with a slow-acting toxin, such as brodifacoum, can also overcome shyness, and is probably more effective if maintenance control is not started until at least 2 months after initial control (Henderson et al. 1997). Pre-feeding with non-toxic bait of the same type to be used in the control operation greatly reduces the development of bait aversion (Ross et al. 2000, Moss et al. 1998), but increases the cost of control.

The potential for possum behaviour to contribute to the risk of sublethal poisoning during control operations with cereal baits was reviewed by (Henderson & Hickling 1997). They suggested that at high population densities, social interactions at bait stations could decrease the feeding time of subordinate individuals, increasing the risk of sub-lethal dosing. At very low densities this seems certain to be less of a problem, and interaction rates per possum should increase. It has been suggested that pre-feeding with non-toxic baits at bait stations may result in possums feeding there attracting other possums to feed ((Hickling et al. 1991). This effect would presumably be reduced at low population densities, as possums would be less likely to encounter other possums feeding at bait stations.

Enhanced neophobia occurs when a bad experience increases wariness of all novel objects. Possums fed a sub-lethal dose of cyanide in a novel food show increased wariness of other novel foods (O'Connor & Matthews 1996). If this wariness is also displayed towards lures or traps, then individual possums will decrease their interaction rates and RTC will underestimate population density. Thus sub-lethal poisoning may affect monitoring immediately after control. Pre-feeding with non-toxic bait of the same type to be used in the control operation greatly reduces the development of bait aversion (Ross et al. 2000, Moss et al. 1998) and presumably the potential for enhanced neophobia.

Possums may consume less bait if lower population densities result in less competition for natural food and hence decreased attractiveness of baits. This would occur if possums have a significant impact on their food supply at higher densities, but this is not certain (Efford 2000). It may occur also if interference competition restricts access to natural food at higher densities. Nugent et al. (2001b) reported a major shift in diet following control of possums at Waihaha, with increased usage of fruits and insects and decreased use of foliage, suggesting that the relative attractiveness of baits may have reduced after control. Bait uptake by other species has been shown to decrease with increasing availability of natural food (e.g., pigs (Choquenot & Lukins 1996). For possums, the results are equivocal. (Morgan 1982) found the percentage of possums consuming non-toxic baits was much lower in summer than in winter, possibly due to food availability, but food availability was not quantified. However, in another experiment, the percentage of possums eating at least one bait was high in all seasons (Morgan et al. 2000). It is not clear whether bait acceptance would decrease at lower population densities.

### **5.1.8 Summary**

Changes in both encounter rates and interaction rates have the potential to affect both population monitoring and the success of future control operations. Such changes in the average behaviour could occur either by selective survival of 'unusual' individuals, or by individuals changing their behaviour in response to either the act of control or lower population densities. However, it is unclear from the limited evidence for these changes whether they are of sufficient magnitude to substantially affect the results of population monitoring or future control. Observations that RTC can be low immediately post-control and then increase rapidly (Nugent et al. 2001a) suggest that, at least in the short term, behavioural changes are of sufficient magnitude to affect the results of RTC monitoring. The rapid increase in RTC could be due to immigration of animals into the area following control, but this appears unlikely due to the large scale over which control is usually applied, and is also argued against by most of the available data on colonisation (Cowan & Clout 2000, Green & Coleman 1984).

This leaves two behavioural scenarios that might explain the accumulating circumstantial evidence that there is relatively rapid change in RTC after control, with different implications for monitoring. Either possums have the same average behaviour immediately post-control, but then change that behaviour so that they are trapped more easily (i.e., the relationship between RTC and possum density differs between higher and reduced density populations), or the average behaviour of survivors is different initially then returns to ‘normal’.

Under the first scenario an immediate post-control RTC (taken prior to the behaviour change) accurately reflects the actual density of the population based on the RTC-density relationship for high-density populations, and is the appropriate index to reflect the effectiveness of control in terms of percent reduction, at least when populations are being reduced from high to low levels. Subsequent RTCs provide an index of possum density that overstates residual density relative to the original high density.

Under the second scenario individuals remaining after control are trapped less easily, but the difference in average behaviour may be short-lived, and individuals subsequently change their behaviour so that the increase in RTC will reflect a return to ‘normal’ behaviour. Alternatively, individual behaviour may not change, but the offspring of survivors may have normal behaviour, so the average behaviour gradually returns to ‘normal’, and the RTC index therefore increases faster than the population itself. Under either possibility the later indices would more accurately reflect the actual density of the population while the index immediately post-control would not provide an accurate assessment of the effectiveness of control. Either of the above scenarios is plausible, both may apply, and the answer may differ in different habitat types, but there are no empirical studies that distinguish between them.

The above discussion has focussed on large population reductions typical of initial control. For maintenance control, where already low populations are reduced to even lower densities, it is unknown whether there is any change in average behaviour affecting RTC. This may depend on why behavioural changes occur. For example, if possum movements are determined mainly in response to limiting factors that only exert significant impact on possum movements when the population is near carrying capacity, then further reducing an already low population may not have much impact on possum behaviour and the RTC-density may be close to linear at lower densities, but different from the relationship at higher densities. In the next section we use simulation modelling to explore the magnitude of behavioural changes required to significantly affect RTC.

## **5.2 Simulation modelling to assess the likely impact of changes in behaviour on RTC**

### **5.2.1 Simulation method**

Efford (unpubl.) has developed a new method for estimating population density ( $D$ ) based on simulation and inverse prediction, which also generates estimates for two behavioural parameters ( $g_0$  and  $\sigma$ ). Estimates for these parameters are obtained by using simulation to identify the combination of  $D$ ,  $g_0$ , and  $\sigma$  that best predict the sample data (i.e. population size, capture probability and recapture distance) empirically obtained from a particular capture-mark-recapture study with a specific trap layout. The parameters ( $g_0$  and  $\sigma$ ) relate to a statistical model for trap catch, where the probability that an animal is caught in a particular trap is assumed to decline with increasing distance ( $d$ ) between the trap and the centre of the animal’s range. The maximum probability,  $g_0$ , occurs when the trap is exactly in the centre of the range ( $d = 0$ ), and declines according to a half-normal curve, reaching  $0.606g_0$  when  $d = \sigma$ . The parameter  $\sigma$  provides an estimate of ranging activity over a period equivalent to the trapping period, while  $g_0$  is influenced by the inherent trappability of animals (the probability of being caught once a trap is encountered), and the size of the range. There is a negative correlation between  $\sigma$  and  $g_0$  because if an animal increases its range size, the amount of time spent in the centre of its range is expected to decrease.

However, if we assume most animals are almost certain to visit the centre of their range on any one night, then  $g_0$  will mainly reflect inherent trappability. On this assumption, we have explored the effect of these parameters on RTC using simulation modelling, but it should be noted that this assumption needs testing.

Capture-mark-recapture data from Castlepoint (R. Jackson, L. Corner, J. McKenzie, R. Morris, unpubl. data) suggests that values of  $g_0 = 0.2$  and  $\sigma = 30$  metres represents standard behaviour of possums in a population at close to carrying capacity in scrub/farmland habitat. The uncontrolled mean possum density was approximately 6/ha. Assuming a circular normal home range, the area that includes 95% of locations is  $6\pi\sigma^2$  (Jennrich & Turner 1969), so a value of 30m for  $\sigma$  equates to a 95% range area of 1.7 ha.

### 5.2.2 Simulating the effects of behavioural differences on RTC

We simulated RTC using the standard protocol (NPCA 2000) and sampled a virtual population of possums at different values of  $\sigma$  holding  $g_0$  constant at 0.05 and 0.2, and at different values of  $g_0$  holding  $\sigma$  constant at 30m and 60m, at two different possum densities (0.2/ha and 0.8/ha; Efford & Ramsey, unpubl. Fig. 1). The index was more sensitive to changes in  $\sigma$  than  $g_0$ , but both had an influence on RTC.

For a population of 0.2 possums/ha (<5% of uncontrolled mean density), the change in movement behaviour required to shift the RTC index from 2% RTC to 5% RTC would require a change in  $\sigma$  from c. 40m to >60m (95% range c. 3.2ha to >6.8ha). For a constant  $\sigma$  of 30m, changes in intrinsic trappability had almost no effect on RTC for a low-density population.

For a population of 0.8 possums/ha (~13% of uncontrolled mean density) to go from 2% RTC to 5% RTC would require a change in  $\sigma$  from 20m to 30m (95% range 0.75ha to 1.7ha). For a constant  $\sigma$  of 30m, changes in intrinsic trappability from 0.05 to 0.2 would produce a similar effect. The simulation thus suggests that smaller changes in behaviour are required to produce significant changes in RTC when population density is higher, but the changes required at either density are well within the range of behaviour in individual movements.

### 5.2.3 Applying the method to an actual population reduction

We estimated  $g_0$  and  $\sigma$  for the Castlepoint population at high density and then following a cull of the population, using capture-mark-recapture data (Fig. 2). Virtually all resident possums were removed from the Castlepoint study site by cage trapping and follow-up leghold trapping over August to October 1994 based on the absence of marked possums in subsequent samples (J. McKenzie pers. comm.), although we cannot rule out the possibility that animals with low trappability avoided both pre-control capture and removal. When live trapping resumed in November 1994 there was a low-density population of recent colonists or untagged survivors in the 21ha removal area (1.3/ha or 21% of the mean density over the previous 2 years). The population rose steadily over the next 2 years but remained below the previous mean (6.1/ha).

In the pre-cull period at Castlepoint  $g_0$  varied greatly for reasons we cannot fully explain, but which possibly include seasonal effects. Population size and recapture distance fell, and capture probability rose, in the 2 months immediately before the cull (Fig. 2); these effects are probably due to culling on an adjacent property (J. McKenzie and R. Jackson pers. comm.). The colonising population at Castlepoint was marked by very low  $g_0$  (< 0.1) and enlarged ranges ( $\sigma > 40$ m) compared with the previous 2 years (Fig. 2). These effects had largely disappeared 12 months later (October 1995) when density had reached 57% of its previous mean. Through the following year  $g_0$  remained at the lower end of the 1992-1994 range.

We cannot strictly distinguish enlargement of ranges from greater mobility within the same range boundary with the present data. The ( $g_0$ ,  $\sigma$ ) model fits a distribution model with constant shape

(probability profile) and no definite boundary. However, it seems likely increased recapture distances and  $\sigma$  do imply that each possum tends to be active over a greater area, and that there is general enlargement of ranges. Assuming a circular normal range, the pre-cull values of  $\sigma$  correspond to a mean 95% area of  $2.06 \pm 0.07$  ha. Immediately post-cull (November and December 1994) these estimates rose to 5.5 ha and 3.8 ha, but with large prediction errors that included the previous mean (Fig. 2). While this analysis appears to suggest that RTC could increase post-control due to expansion of home ranges, it is important to note that these results are thought to apply to behavioural changes of recent colonists, which may not reflect behavioural changes of survivors when control is applied over larger areas. In addition, the model also suggested a decrease in  $g_0$ . At a population density of 1.3/ha, simulation of RTC using standard behaviour before control ( $g_0 = 0.2$ ,  $\sigma = 35$ ) and after control ( $g_0 = 0.05$ ,  $\sigma = 55$ ) gave indistinguishable estimates of RTC of  $\sim 7.5\%$ . In other words, the increase in range size was offset by the decrease in  $g_0$  for the purposes of estimating RTC. It is not clear how much of the reduction in  $g_0$  was due to a reduction in inherent trappability, and how much if any was due to the possible negative correlation between  $g_0$  and  $\sigma$ .

### 5.3 Possum behaviour and Tb

#### 5.3.1 Contact rates and epidemiology of bovine Tb

In brushtail possums, Tb infection is thought to be transmitted predominantly by aerosols, which requires close contact for transmission (Jackson *et al.* 1995), but there is some suggestion that environmental pathways are important also (Cooke 2000). The overall Tb transmission rate will be a function of the relative contributions of (i) the various contact behaviours, which are categorised into two main pathways: pseudo-vertical (mother-offspring); and horizontal-direct (e.g., agonistic/affiliative interactions, mating, den-sharing) (Morris & Pfeiffer 1995); and (ii) the environmental pathways not requiring close contact between individuals (horizontal-indirect, e.g., sequential den-sharing, consumption of contaminated pasture).

The rate of contacts between possums and hence the rate of Tb transmission is assumed to have some functional relationship with population density (McCallum *et al.* 2001). How contacts between animals change with population density is termed the contact rate function ( $c(N)$ ). Model predictions of the dynamics of bovine Tb in possum populations are all sensitive to the form of the contact rate function, but there are few data. All existing possum Tb models assume the overall contact rate is either linearly related to population density (Barlow 1991, Barlow 1991) or takes a convex-up form (Barlow 1996, Roberts 1996, Barlow 2000). These later models of possums/bovine Tb which include non-linear transmission of disease appear to better reproduce the dynamics of disease observed in the field, i.e. low prevalence and persistence of disease in aggregated patches at low density (Barlow 2000).

The convex-up form for the contact rate function is assumed to represent contacts between possums due to mating, as it is believed mating contacts are relatively independent of population density (Barlow 2000). A non-linear convex-up contact rate implies a lower threshold density for disease elimination and at the extreme case where the contact rate is independent of population density the population must be eradicated to eliminate disease (Roberts 1996; Barlow 2000). However, little is known about mating contact rates between possums and only a few studies have either estimated the disease transmission rates in possums, or investigated how contact rates relate to changes in possum population density.

#### 5.3.2 Mating contact rate

Interactions between possums during mating have been proposed as the most important behaviour for Tb transmission (Pfeiffer 1994; Morris and Pfeiffer 1995). The most comprehensive study that investigated the interactions between possums during mating found that some male possums formed 'consort' relationships with reproductively active females (Winter 1976). This involved the pairing of a male with a female in reproductive condition, often for extended periods of time, and is thought

to reduce the probability that the female would be mated by other males (Winter 1976). This consort period was observed to last for between 30 to 40 days (Winter 1976). Following mating, consort behaviour usually ceases (Winter 1976). This type of mating system produces a mating contact rate largely independent of population density, unless the amount of time devoted to the consort period varies with population density, i.e. in a low-density population a male may only spend 20 days with a female, while he may spend 40 days with a female if the population density is high. The effect this type of mating system would have on the shape of the overall contact rate function (incorporating non-mating contacts) for the purposes of disease transmission, would depend on the proportion of total contacts mating contact comprised, and the probability of transferring the disease during the different types of contacts.

The study by Winter (1976) was conducted on a low-density population at carrying capacity ( $K$ ) inhabiting eucalypt woodland near Brisbane, Australia and the patterns of interactive behaviour may not reflect those in New Zealand populations where population density is generally much higher. Genetic studies of paternity in New Zealand possum populations by Taylor et al. (2000) and Sarre et al. (2000) found the mating system is largely polygynous, suggesting a lack of formal bonding between males and females during mating. Furthermore, genetic studies underestimate the rate of sexual contacts, because unsuccessful mating attempts are not included. (Ji et al. 2001) found that a polygynous mating system was maintained in a population at low density in a site near Auckland. A polygynous mating system where males and females do not form bonds during mating would more likely produce a linear density-dependent mating contact rate.

A study to determine how the mating contact rate may be affected by changes in population density was undertaken by Ramsey et al. (submitted) on a possum population inhabiting a 13-ha, semi-isolated patch of remnant native forest on farmland at Pigeon Flat near Dunedin. The study involved estimating the contact rate of males with oestrus and non-oestrus females, using intensive monitoring of radio-collared animals. The contact rates were estimated, first at high density and then following a c. 70% reduction in population density. Reducing population density did not substantially change the contact rates of males with either the oestrus or non-oestrus females, indicating mating contacts may not be any more important than other affiliative/agonistic contact behaviours. The relationship between the mating and non-mating contact rate and population density was found to be linear. A linear form for  $c(N)$  assumes contacts between individual male and female possums are essentially random and, hence, density-dependent. Thus, the results of Ramsey et al. (submitted) support the assumption of simple density-dependent contact rates assumed in the earliest models of possums and bovine Tb (Barlow 1991a,b).

Further support for the assumption of linear density-dependent contact rates was provided in a study by Caley and Ramsey (2001). This study estimated the effect of altering mating behaviour on the transmission rate of *Leptospiriosis interrogans* serovar *balcanica*. A proportion of female possums (80%) at particular sites were subjected to sterilisation by tubal ligation. This treatment effectively increased the frequency of oestrous during the breeding season, which was hypothesised to result in an increase in mating contacts compared with those with unsterilised females in control sites. Estimation of the disease transmission coefficient ( $\beta$ ) assuming either linear density-dependent or frequency-dependent transmission determined linear density-dependent transmission was the most appropriate form for the transmission of *L. balcanica*. Another study is currently in progress to test the importance of mating contacts to Tb transmission by comparing infection rates between sterilised and intact possums (D. Ramsey pers. comm.).

A study by (Caley et al. 1999) was designed to test the predictions of the Barlow (1991a,b) model and hence indirectly, the assumption of linear density-dependent disease transmission. Their study maintained an endemically infected possum population at an average of 22% of its pre-control density for 10 years. The prevalence of Tb in the population declined to zero after the sixth year of maintenance control, indicating support for the threshold density predicted by the Barlow (1991a)

model. However, this does not necessarily prove a linear form for the contact rate as Tb could theoretically still be eliminated from a possum population held to 22% of  $K$  if a non-linear contact rate is assumed (Barlow 2000). The results of Caley et al. (1999) do, however, provide an upper limit to the estimate of non-linearity in the contact rate function, all else being equal.

### 5.3.3 Non-mating contact rate

The simultaneous sharing of dens has been proposed as one of the major mechanisms for Tb transmission between possums (Morris & Pfeiffer 1995). A study by (Caley et al. 1998) investigated the effect of reducing population density on the simultaneous den-sharing contact rate in a native forest remnant dominated by fuchsia and mahoe. Reducing population density significantly lowered the probability of simultaneous den sharing between possums, with reductions of greater than 60% of  $K$  estimated to eliminate simultaneous den-sharing altogether in that habitat type. Thus, the den-sharing contact rate was density-dependent, taking a convex-down form for the contact rate/density function. Based on these data, current control targets should eliminate den sharing, although it is not known how den sharing rates vary in other habitat types.

Pseudo-vertical transmission between mother and offspring is assumed constant in all models of possums and bovine Tb, because contact rates between them are not thought to be influenced by population density. However, Caley et al. (1998) showed that as young possums neared independence the mother-daughter den-sharing probability was reduced at low density. This suggests the rate of pseudo-vertical transmission may also be reduced at low density and, hence, a convex-down relationship for the pseudo-vertical transmission rate and population density may not be an unreasonable assumption.

If possums in a given habitat increase their movements at reduced densities, then contact rates may increase, and the contact rate function for that habitat type would be convex up. Indeed Barlow (1991a) has argued that one explanation for the control target for the elimination of Tb being a percentage of  $K$  (regardless of habitat) rather than a target population density, is that possums in naturally low-density populations have larger ranges and hence contact rate is independent of  $K$ . Increases in possum range size at reduced densities may also increase the chances of sequential den sharing.

In summary, investigations of contact behaviours presumed important in the transmission of bovine Tb between possums, and their relationship with population density, have not revealed any mechanism that may result in the persistence of disease at low (reduced) density, other than possible increases in contact rates and sequential den sharing due to increased movements. However, we still know relatively little about the importance of the various contact behaviours for the transmission of Tb between possums.

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## 6. Recommendations

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There is not enough reliable information available to recommend changes to current practices of possum control and monitoring, but our modelling and the information available indicates that changes in behaviour have the potential to substantially affect managers' ability to control and monitor possum populations. It is therefore crucial that the nature and size of such behavioural changes be determined under both 'initial' control (where populations are reduced from relatively high to low densities) and maintenance control (where populations are reduced from relatively low to lower densities) scenarios. Studies are therefore required to address the following questions:

- Do possums at lower population densities have sufficiently different movements to possums at higher population densities to result in different encounter rates with traps and baits that are large enough to influence population monitoring or the success of future control?
- If so, are these differences caused by control selectively removing animals that have high encounter rates with traps and baits thus changing the average behaviour of the post-control population; or by possums that remain post control changing their behaviour either in response to the low population density or in response to the act of control? Some existing data are available to begin to address the question of how much individual variability there is likely to be in encounter rates with traps and baits in a given habitat type.
- If control selects for possums that have low encounter rates with traps and baits is this heritable? If so, this would have potentially serious implications for the success of long-term control. Studies comparing the behaviour of possums from populations that had been subjected to long-term control with the behaviour of those that had not should provide some insight into this.
- Do possums at lower population densities have sufficiently different interaction rates with devices/traps/baits to possums at higher population densities to influence population monitoring or the success of future control?
- If so, are these differences due to control selectively removing animals that have high interaction rates; or because possums change their interaction rates when at low density? Due to less competition for natural food for example.
- If control selects for possums that have low interaction rates with devices/traps/baits is this heritable?

To determine whether behavioural differences at low density are likely to maintain contact rates sufficient for the continued persistence of Tb, studies are required to address the following questions:

- What is the relative importance of the different contact behaviours and environmental pathways for the transmission of Tb?
- How do contact rates change with changing possum population density?

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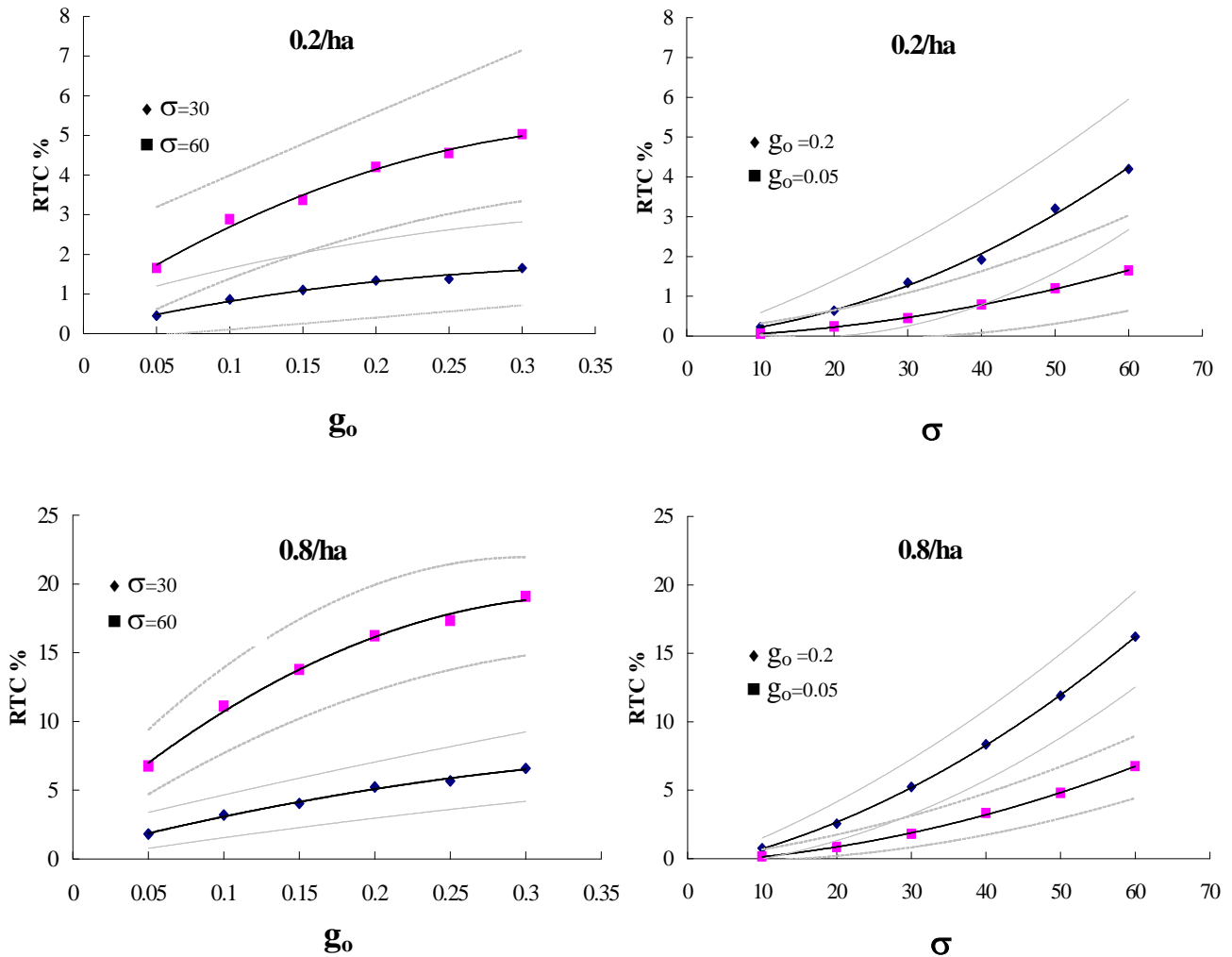
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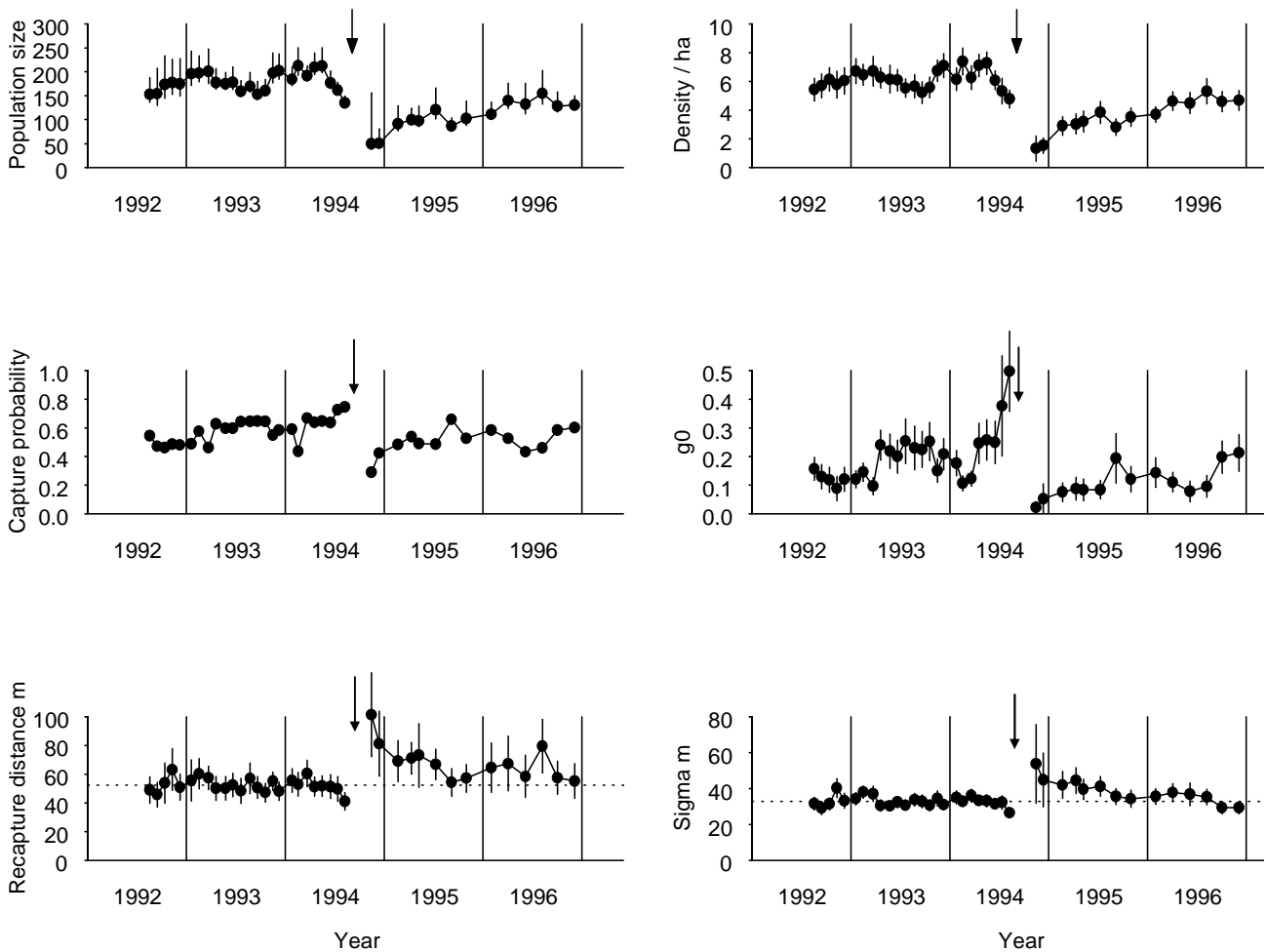
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**Figure 1.** Simulation modelling of RTC at different possum population densities for different values of  $\sigma$  and  $g_0$ . 95% confidence intervals are shown (dotted lines). For a population of 0.2 possums/ha to go from a near zero RTC to a 5% RTC would require a change in  $\sigma$  from <20m to >60m. For a constant  $\sigma$  of 30m, changes in intrinsic trappability have almost no effect on RTC for a very low-density population. In other words, for a very low-density population only very large changes in range size would have a significant impact on RTC. For a population of 0.8 possums/ha to go from a near zero RTC to a 5% RTC would require a change in  $\sigma$  from 10m to 30m. For a constant  $\sigma$  of 30m, changes in intrinsic trappability from 0.05 to 0.3 would produce a similar effect.



**Figure 2.** Population dynamics of possums live trapped at Castlepoint, Wairarapa, before and after a cull in August-October 1994 (arrows). Data of R. Jackson, L. Corner, J. McKenzie, R. Morris and coworkers. All variables except capture probability shown with 95% confidence intervals for the mean. Population size and daily capture probability were estimated by Chao's (1987) method. Density ( $D$ ),  $g_0$ , and range scale ( $\sigma$ ) estimated jointly by simulation and inverse prediction (Efford unpubl.). The method entails a search for the values of  $D$ ,  $g_0$ , and  $\sigma$  that jointly generate (by simulation) population samples (i.e. population size, capture probability and recapture distance) similar to those observed, given the trap layout that was used to collect the data. Dashed lines show pre-cull mean. The post-cull population was marked by very low  $g_0$  and enlarged ranges compared to the previous 2 years.