

Dispersal sinks and handling effects: interpreting the role of immigration in common brushtail possum populations

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Summary

1. An evaluation of the potentially adverse effects of measurement must be made before concluding that one is dealing with a 'dispersal sink'.

2. We conducted a spatially and temporally replicated removal experiment on common brushtail possums (*Trichosurus vulpecula*) in uniformly suitable old-growth eucalypt forest in south-eastern Australia, that was designed to address the question: does immigration 'rescue' populations from extinction?

3. Despite taking precautions to minimize potential harm, analyses indicated some evidence of an adverse effect of handling on the survival of pouch-young and strong evidence of effects on adult survival. In addition, symptoms of stress associated with handling observed at our site, corresponded to symptoms reported in connection with the long-term (15 + years) trapping study on possums conducted by Efford *et al.* in the Orongorongo Valley (OV) of New Zealand.

4. Initial projections from a demographic model indicated that the resident population at our site was not replacing itself (births < deaths), suggesting that the site was a dispersal sink. This was inconsistent with the fact that the site was in prime habitat. Moreover, the measured rate of *true* immigration in response to experimental removals was not sufficient to maintain the population density. Using data from Efford (1998), our model confirmed his suggestion that the OV site also appears to be a dispersal sink for possums, despite being in prime habitat.

5. When otherwise undiagnosable deaths among adults were assumed to be due to handling and 'right-censored' (excluded), the projection was that the resident population at our site was stable ($r \cong 0$), and therefore not in need of 'rescue' by immigration. Similarly, when survival estimates for the OV site were corrected by the same amounts, the projection was that the population at that site was also stable.

6. Most vacancies created by our experimental removals were filled by neighbouring residents that expanded their ranges into the removal areas. We suggest that the artificial 'removal' of residents as a consequence of deaths due to handling, may often induce an influx of such *apparent* immigrants, thereby giving the impression that immigration is 'rescuing' populations from extinction.

Key-words: demography, dispersal, metapopulations, removal experiments, rescue effect.

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Introduction

A 'dispersal sink' (Andrewartha & Birch 1954; Pulliam 1988; Stacey, Johnson & Taper 1997) may be defined as any habitat in which, in the absence of immigration, the resident population is expected to decline to extinction

($r < 0$), because local births are insufficient to compensate for local deaths (births < deaths). Dispersal sinks are cited in the literature on metapopulation dynamics as a case in which immigration is clearly important in 'rescuing' populations from extinction (Stacey *et al.* 1997). Dispersal sinks are assumed to occur in sub-optimal habitat, whereas 'source' populations (births > deaths) from which immigrants derive, are assumed to occur in optimal habitat.

Studies claiming to have demonstrated the existence of a dispersal sink were criticized by Watkinson &

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Sutherland (1995) because: (1) inferences regarding the demography of the resident population were often drawn from measurements of birth or death rates alone, rather than simultaneous measurements of both parameters; and (2) immigration was often inadequately measured, if at all. Only two studies on annual plants were judged by Watkinson & Sutherland (1995) to have adequately addressed these issues. Diffendorfer (1998) added a third study on another annual plant to the list, but otherwise drew the same conclusions as Watkinson & Sutherland (1995). Kadmon & Tielborger (1999) advocated an experimental approach to the evaluation of dispersal sinks because experiments they conducted on desert annuals failed to support the existence of dispersal sinks in conditions, where prior natural history studies had.

We propose that a third criterion should be added to those proposed by Watkinson & Sutherland (1995), namely an evaluation of the effects of measurement on immigration, births and deaths. The rigorous measurement of immigration in open populations in the field generally requires much more intensive handling and disturbance of the resident population than would otherwise be needed in a study of demography (Stenseth & Lidicker 1992; Clinchy 1999). If repeated capture and handling adversely effects either the birth or death rate of residents, then what might be a stable (births = deaths), or even a source (births > deaths) population in the absence of repeated capture and handling, may become a declining population ($r < 0$; Cypher 1997), that will then need to be 'rescued' from extinction by immigration. In addition, the artificial 'removal' of residents resulting from deaths due to capture and handling may actually induce an influx of immigrants (Stenseth & Lidicker 1992), leading to the conclusion that the site is a dispersal sink. Despite the logical necessity of testing for biases in demographic parameters attributable to handling effects, this is very rarely done in this or any other context (Wobeser 1994; Williams & Thorne 1996; Haydon *et al.* 1999).

Efford (1998) reported the existence of a dispersal sink among common brushtail possums (*Trichosurus vulpecula* Kerr) occupying optimal habitat in the Orongorongo Valley (OV) of New Zealand. Birth and death rates were both measured at the OV site, satisfying the first of the two criteria proposed by Watkinson & Sutherland (1995). However, the OV study did not adequately measure immigration. Since fewer than two-thirds of the resident young at the OV site were tagged while still with their mothers, 'almost all unmarked yearlings ... could be explained as surviving native young that had escaped tagging' (Efford 1998, p. 510). Moreover, territorial expansion (i.e. 'apparent recruitment of peripheral adults'; Efford 1998, p. 515) could not be distinguished from *true* immigration (defined by the new home range being disjunct from the abandoned one; Lidicker & Stenseth 1992, p. 23).

We conducted a spatially and temporally replicated removal experiment on common brushtail possums in

uniformly suitable old-growth eucalypt forest in south-eastern Australia, designed to address the question: does immigration 'rescue' populations from extinction? We took every possible step to ensure that our measurement of immigration was made *without error*. By using multiple methods of capture and identification we attempted to completely enumerate all residents in the removal areas and in a surrounding 'border zone', so we could unambiguously identify unmarked individuals as immigrants, and distinguish range expansion from *true* immigration (Stenseth & Lidicker 1992; Clinchy 1999). In conjunction with measuring immigration, we also measured both birth and death rates in the resident population. Consequently, our study meets both criteria proposed by Watkinson & Sutherland (1995).

In this paper, we report: (1) evidence of handling effects resulting from our intensive efforts to measure immigration *without error*; and (2) the errors that may be introduced into population projections, as a consequence of such efforts. We use demographic estimates from our study, and the OV study, to demonstrate that whether or not a site is judged to be a dispersal sink ($r < 0$) may largely depend on whether or not deaths in association with handling are assumed to be 'natural'. Because we distinguished between *true* immigration and range expansion in response to removals, we are able to evaluate the relative contribution of each of these processes to the apparent 'rescue' of our study populations from extinction. We discuss the process whereby apparent dispersal sinks may actually be the result of our efforts to accurately measure immigration, births and deaths.

Methods

STUDY SITE

The study was conducted in the eastern arm of Paddys Land State Forest (30°06'00" S, 152°10'20" E; elevation 940–1040 m), which lies near the centre of the 121 000 ha Guy Fawkes Wilderness Area (GFWA) in north-eastern New South Wales (NSW), Australia. The GFWA contains 'the highest concentration of arboreal mammals found in NSW' (NPWS 1992, p. 20), and has been described as 'very important for arboreal mammals ... at all scales (i.e. regional, state and continental)' (NPWS 1992, p. 35). According to a regional species distribution model developed by the NSW National Parks and Wildlife Service, the GFWA consists of uniformly suitable habitat for common brushtail possums, and possums are predicted to occur at moderate to high densities throughout the GFWA (NPWS 1994).

GENERAL PROCEDURES

All procedures were similar to those used by other researchers. We established two 36 ha study grids, approximately 2 km apart, in September 1994. On each grid we marked out 49 permanent trap locations at 100 m intervals in a 7 × 7 matrix. Possums were live-trapped

Table 1. Seasonal survival estimates and projected population growth rates (r) for the Paddys Land (PL) and Orongorongo Valley (OV) sites, under three scenarios regarding the treatment of deaths in association with capture and handling. See Table 2 regarding proximate causes and symptoms preceding death. Animals found moribund in traps at the PL site demonstrated all likely symptoms of handling stress (W + B + R). Survival estimates for 1-year-olds are not reported for the PL site because these were assumed to be equivalent to those for adults (Efford 1998, p. 510; Clinchy 1999)

	Scenario 1		Scenario 2		Scenario 3	
	Only obviously anthropogenic deaths excluded		Deaths where animals were found moribund in traps, also excluded		Deaths where cause undiagnosable and prior probable symptoms of handling stress, also excluded	
	PL	OV	PL	OV	PL	OV
Seasonal survival estimates						
Adults						
Autumn	0.9706	0.9680	0.9889	0.9720	0.9889	0.9863
Winter	0.8957	0.9130	0.9061	0.9290	0.9610	0.9782
Spring	0.9740	0.9623	0.9740	0.9654	0.9740	0.9623
Summer	0.9600	0.9623	0.9600	0.9654	0.9733	0.9756
1-year-olds						
Autumn	–	0.8490	–	0.8530	–	0.8673
Winter	–	0.8600	–	0.8760	–	0.9252
Spring	–	0.9439	–	0.9471	–	0.9439
Summer	–	0.9439	–	0.9471	–	0.9573
Population growth rates (r)	–0.1005	–0.0965	–0.0706	–0.0689	0.0008	0.0042

using 30 × 30 × 60-cm wire mesh cage traps baited with apple. Traps were set for 3 nights at each grid point in each month from March to September. We captured particular individuals by setting traps at den trees and captured trap-shy individuals using a Montech Model 2 CO₂-powered dart-gun (Montech Pty Ltd, Melbourne, Australia) that fired a modified 0.5 mL insulin syringe filled with Zoletil 100 (active ingredients include Tiletamine and Zolazepam; Virbac Pty Ltd, Sydney, Australia) at a concentration of 30 mg per 0.15 mL.

We define handling as measurement of a male's testes, or examination of the interior of a female's pouch. Prior to handling, animals were weighed to the nearest 50 g using a spring scale. Males were classified as adult if testis length (measured to the nearest 0.1 mm using vernier calipers) was ≥ 18.0 mm, and females were classified as adult if their pouch was invaginated (Clout & Efford 1984). The same person (MC) handled and measured all the animals. Animals trapped overnight were processed and released beginning at dawn the next day. To reduce the level of stress on the animals, individuals were handled only once during a 3-night trapping session. Aside from those captured using the dart-gun, animals were generally not tranquillized prior to handling.

All animals ($N = 354$), including pouch-young, were marked with individually numbered monel metal ear-tags. Tissue samples for genetic analyses were obtained by cutting a small notch (< 5 mm on a side) in the distal part of an animal's ear (once per animal). Beginning in March 1995, every adult female was fitted with a radio-collar equipped with a mortality switch ($N = 78$). Radio-signals were checked weekly.

Survival of radio-collared adult females was estimated using Pollock *et al.*'s (1989) staggered-entry design. Initial survival estimates (Scenario 1, Table 1) 'right-censor' (exclude) only obviously anthropogenic deaths. Subsequent estimates also right-censor deaths that were most probably due to capture and handling (Scenarios 2 and 3, Table 1). To test for differences in survival, individuals were assigned to groups following Lee (1992, pp. 245–246), and comparisons between groups were made using the most conservative version of the log-rank test (Pollock *et al.* 1989). All other statistical procedures follow Sokal & Rohlf (1995) and Zar (1996). Descriptive statistics are means ± standard errors, unless otherwise stated. Results are reported as statistically significant based on Bonferroni-corrected α values (Rice 1989).

REMOVAL EXPERIMENT

On 1 August 1995, we removed 10 adult resident females from the core of one grid and nine from the other. We refer to these 19 females as the group of 'core residents'. The immigration rate was measured by the number of artificially created vacancies (out of 19) occupied by unmarked females over 1 year. We temporally replicated the experiment on 1 August 1996, by removing any females that had settled in the vacancies, and monitoring for a second year (until 1 August 1997).

Analyses reported in Clinchy (1999) confirm that our combination of intensive live-trapping, capture with a tranquillizer dart-gun, and identification of parentage using microsatellite DNA ensured that elusive residents were not misidentified as immigrants. Moreover, since

all residents in the 'border zones' surrounding the removal areas were radio-collared, we could unambiguously distinguish range expansion from *true* immigration (Stenseth & Lidicker 1992; Clinchy 1999).

ANALYSES OF THE EFFECTS OF HANDLING

The total number of times an animal was handled is not an adequate measure of the potentially adverse effects of handling. If every animal was handled every month, and handling was innocuous, animals that survived longer would be handled more. Instead, we estimated the *frequency* with which each individual was handled by calculating the interval in days between each occasion on which it was handled, and then calculating the mean and median of these intervals. If the means and medians differed significantly, we judged the median to be more representative of the 'typical' handling frequency (Sokal & Rohlf 1995).

Core residents were handled significantly more frequently (Mann-Whitney $U_{15,54} = 108.5$, $P < 0.001$) than other females, as is to be expected given their central location on the grids. Since most deaths occurred in late winter (Table 1; 1 August = mid-winter in the antipodes) and the first manifestation of probable symptoms of handling stress ('wobbliness', 'boniness' and 'rumpiness'; next section) did not occur until *after* the core residents had been removed (Clinchy 1999, his Fig. 5-5), these females did not have the 'opportunity' to demonstrate either symptoms of handling stress or poorer survival. Given these structural biases, core residents are not included in tests of association between the frequency of handling and the presence of symptoms, or poorer survival.

To evaluate the effects of handling on the survival of pouch-young, we tested whether the fate of 54 pouch-young whose fate was known for certain was associated with the frequency with which their mother was handled, up to the time the young was 175 days old (weaning). To evaluate effects on the survival of adults, we tested: (1) whether a female's probability of survival was associated with the frequency with which she was handled; and (2) whether our survival estimate based on two years of telemetry data (Scenario 1, Table 1) differed from the long-term average survival, as indicated by the age structure (Krebs 1999) among 38 adults aged from cementum annuli (details below). Females were ranked according to median handling interval and divided into two equal-sized subgroups consisting of those handled more, or less, frequently. Our sample of 38 known-age adults included 25 females and 13 males. There was no significant difference ($t_{36} = 0.87$, $P = 0.387$) in the mean age of males (6.0 ± 0.6) and females (7.4 ± 0.8) in this sample. None the less, we calculated the expected age distribution among both 25 and 38 individuals, given our initial per annum survival estimate from radio-telemetry (Scenario 1, Table 1), and compared this to the observed age distribution among known-age females only, and all known-age adults, respectively.

ANALYSES OF LIKELY SYMPTOMS OF HANDLING STRESS

Every year at the Orongorongo Valley (OV) site a few possums are found moribund or dead in traps. Most moribund animals manifest behavioural symptoms of wobbliness (loss of motor control; Mackintosh *et al.* 1995) prior to death (P. E. Cowan, unpublished). When necropsied, these animals are generally observed to be in poor physical condition, being 'bony' and emaciated and possessing little or no body or bone marrow fat, although gross pathology is otherwise absent (P. E. Cowan, unpublished). Animals in poor condition possess significantly greater numbers of intestinal nematodes (*Parastrongyloides trichosuri*, *Paraastrostrongylus trichosuri* and *Trichostrongylus* spp.; Heath *et al.* 1998; Stankiewicz, Cowan & Heath 1998), and typically demonstrate symptoms of rumpiness (fur loss, lesions and scab formation, principally on the lower back and base of the tail; Humphreys *et al.* 1984; Presidente 1984; Clark 1995) in association with heavy ectoparasitic mite (*Trichosuroloaelaps crassipes*) infections (Cowan 1990). The majority of such trap-deaths occur in winter ($\cong 1.6\%$ of the total number of individuals trapped) but some do also occur in summer and autumn (0.6% and 0.4%; P. E. Cowan, unpublished; M. G. Efford, unpublished).

We observed similar symptoms of wobbliness (W), boniness (B) and rumpiness (R) at the Paddys Land (PL) site both among animals found moribund or dead in traps and among animals that were apparently healthy enough to exit the trap and find shelter on their own. To verify that these symptoms were reliable indicators of a similar syndrome to that described in association with trap-deaths at the OV site, we tested whether these symptoms were observed more often in autumn and winter than expected by chance, and whether symptoms co-occurred more often than expected by chance with: (1) each other; (2) weight loss; and (3) heavy intestinal nematode and ectoparasitic mite burdens. While death was immediate in cases of animals found moribund in traps, we tested whether survival was significantly poorer among females observed with symptoms at any time, compared to those never observed with such symptoms. Finally, we tested whether females observed with symptoms at any time were handled more frequently than females that were never observed with symptoms.

DIAGNOSIS OF PROXIMATE CAUSE OF DEATH

Where deaths occurred, we first classified the proximate cause as being either obviously anthropogenic or apparently 'natural'. Anthropogenic deaths included all those that were either accidental (e.g. attacked by a predator while in a trap) or intentional results of the experimental protocols. In subsequent comparisons we assume that anthropogenic deaths were independent of condition or age and thus represent a random sample from the population. Apparently 'natural' deaths were divided

Table 2. Proximate causes of all apparently 'natural' (not obviously anthropogenic) deaths of radio-collared adult females. Data are from the entire period during which females were radio-collared (March 1995–August 1997). Symptoms are wobbliness (W), boniness (B) and rumpiness (R)

Proximate cause of death	Number dead
Heterospecifics	
Predator (blood on the collar)	8
Parasitic infection	1
Undiagnosable	
Likely symptoms of handling stress:	
None	5
Not associated with survival	R
Associated with poorer survival	W
	B + R
	W + B + R

further into those due to heterospecifics (predators or parasites) and those for which the cause was undiagnosable. Categorization into these two classes was possible in all cases of apparently 'natural' deaths of radio-collared adult females (Table 2), following tests for the presence of blood on the collar (see below) and necropsies of intact carcasses. Categorization of the deaths of males was only possible in cases of trap-deaths.

Each female's radio-collar was wrapped with adhesive bandaging to distinguish between animals actually killed by a predator (causing the bandaging to be inundated with fresh blood) and those scavenged after dying of another cause (accuracy verified in Clinchy 1999). The presence of blood was confirmed using the SKD Hemocult II SENSAs, Sensitive Serial Test for Enhanced Detection of Fecal Occult Blood (SmithKline Diagnostics, Inc., San Jose, California, USA).

Necropsies were conducted following each of 12 anthropogenic (eight females, four males) and 12 non-anthropogenic (seven females, five males) deaths. In all cases the carcass was examined for gross pathology and in all but one case (a non-anthropogenic female) the presence and intensity of parasitic infections was also evaluated. Histopathology was evaluated in three (all females) of the 12 non-anthropogenic cases, and a biochemical analysis of the blood was conducted in an additional case (a male). Serological evaluations were conducted on blood samples from one non-anthropogenic and five anthropogenic females. Tests were conducted for the presence of antibodies to the Eimeriid protozoan *Toxoplasma gondii*, the spirochaete bacterium *Leptospira interrogans* (serovar *hardjo* and serovar *pomona*) and five arboviruses: Ross River Virus, Murray Valley Encephalitis Virus, Kunjin Virus, Sindbis Virus and Barmah Forest Virus. Further details regarding methodologies are reported in Obendorf *et al.* (1998).

Whenever we could retrieve the lower jaw we used counts from the microscopic examination of the number

of cementum annuli in serial sections of both the first premolar (PM1) and third molar (M3) to estimate the animal's age in years (Clout 1982; Clinchy 1999). This gave us a sample of 38 known-age adults. The cause of death was anthropogenic in 14 cases, heterospecific in three and undiagnosable in 17. Teeth were also collected from four males whose carcasses were discovered opportunistically, the cause of death being unknown. To determine if undiagnosable deaths were due to 'old-age' (senescence), we tested whether the mean age of this group differed from that of the anthropogenic group. We also tested whether age differed among all four groups.

MODEL OF POSSUM DEMOGRAPHY

To evaluate the role of immigration and the potentially adverse effects of measurement on projected population growth rates, we constructed a deterministic, stage-based model of the demography of the possums at the PL site. Copies of the model (in Microsoft Excel format), together with details regarding assumptions and values used in the model, are available at <http://www.zoology.ubc.ca/~clinchy>. As is conventionally the case when modelling demography (Beissinger & Westphal 1998), both the parameters and the results produced by the model concern females only. We report projected population growth rates, r , based on a stable age distribution, and calculated as $\ln(N_{t+1}/N_t)$, where N is the number of adult females alive at the beginning of each autumn. The sensitivity of r to changes in a given parameter was evaluated by varying the parameter by 0.1 (i.e. 10%) about its observed value at the PL site (e.g. from 0.35 to 0.45, if the observed value = 0.30), while all other parameters were kept constant (Caswell 1989, p. 119). Parameter values for the PL site were based on pooled data from two complete annual breeding cycles (from the beginning of autumn 1995 to the end of summer 1996). We evaluated the effect of immigration on the projected population growth rate by beginning with an initial population of 19 (equal to the number of removals) and adding immigrants at the observed rate. The model was then run until a new stable population size was reached.

We ran model projections for the PL site under three scenarios regarding the treatment of 'censored' deaths among adults (Table 1): (1) only obviously anthropogenic deaths were right-censored; (2) in addition, deaths of animals found moribund in traps were also right-censored; and (3) in addition, deaths were also right-censored in cases where the cause was undiagnosable and the animal had previously demonstrated probable symptoms of handling stress associated with poorer survival. The demography of possums at the OV site is described in Efford (1998) and Humphreys *et al.* (1984), and closely resembles that of possums at the PL site. We ran model projections for the OV site under three equivalent scenarios (Table 1): (1) we used Efford's (1998) estimates of survival (without modification) which, as

in Scenario 1 for the PL site, exclude only obviously anthropogenic deaths (M. G. Efford, unpublished); (2) we assumed that deaths of animals found moribund in traps at the OV site were the direct result of capture and handling, and modified Efford's (1998) estimates of survival by the percentages reported in the section on 'analyses of likely symptoms of handling stress' (above); and (3) we added the differences in survival between our own estimates under Scenarios 1 and 3, to Efford's (1998) estimates of survival.

Results

EFFECTS OF HANDLING ON REPRODUCTION AND SURVIVAL

Almost all (98%) adult females gave birth to a single pouch-young in autumn or winter in each year. Four of the five females that did not breed demonstrated probable symptoms of handling stress, being either wobbly (W) or both bony *and* rumpy (B + R) or all three (W + B + R).

The frequency with which their mothers were handled differed significantly between pouch-young that died prior to weaning (175 days) and those that survived (handling $F_{1,50} = 7.29$, $P = 0.009$; year $F_{1,50} = 0.08$, $P = 0.774$; interaction $F_{1,50} = 0.01$, $P = 0.929$). The mothers of young that died were handled about once a month, while mothers of surviving young were handled about once every second month (Table 3). Similarly, radio-collared adult females that were handled more frequently had a significantly lower probability of survival ($\chi^2_1 = 7.11$, $P = 0.008$) than those that were handled less frequently (Fig. 1).

When only obviously anthropogenic deaths were right-censored, per annum adult survival was estimated to be 81.3% (Scenario 1, Table 1). Since age at death was independent of the proximate cause in our sample of 38 known-age adults (details in subsequent section), the observed age distribution can be treated as a random sample from the population (Krebs 1999). When categorized into just two age classes (ages 2–8 and 8–14), the expected age distribution based on our initial estimate of survival from radio-telemetry (Scenario 1, Table 1) differed significantly from the observed age distribution, independent of whether only females (binomial $P = 0.026$)

Table 3. Mean interval in days between occasions on which their mother was handled, compared between pouch-young that died prior to the onset of weaning (175 days), and those that survived

Pouch-young survived to weaning	Interval (in days) between occasions on which mother was handled					
	N	1995 Mean	1995 SE	N	1996 Mean	1996 SE
No	17	37	3.4	6	37	4.8
Yes	8	54	11.9	23	51	3.7

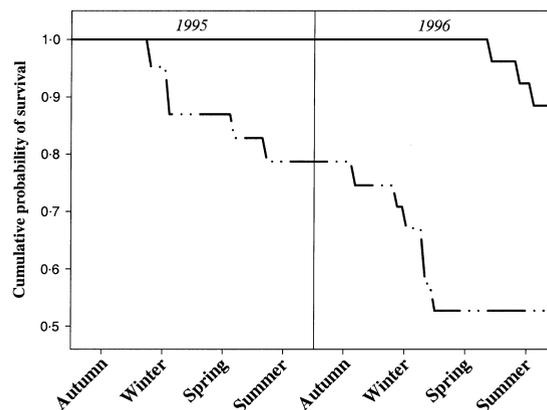


Fig. 1. Effect of handling on the survival of radio-collared adult females. The solid line indicates survivorship among females handled less frequently (median handling interval ≥ 45 days, $N = 27$), while the dashed line signifies survivorship among females handled more frequently (median handling interval < 45 days, $N = 27$).

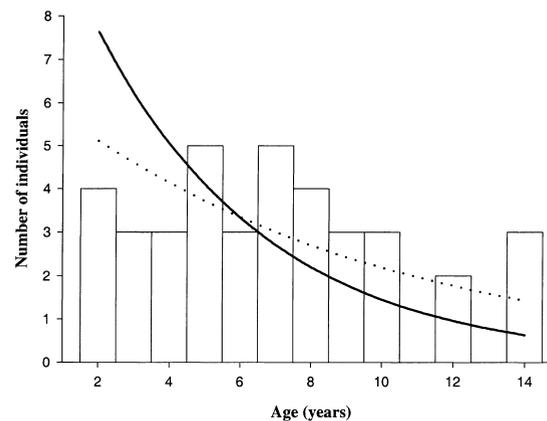


Fig. 2. Observed age structure among 38 known-age adults (open bars), compared to the expected age distribution if per annum survival is either 81.3% (solid line; Scenario 1, Table 1), or 90.1% (dotted line; Scenario 3, Table 1).

or both males and females (binomial $P = 0.047$) were considered. Categorization into more age classes made no difference (Clinchy 1999). There were many more older animals than expected given a long-term per annum average survival rate of 81.3% (Fig. 2).

PROBABLE SYMPTOMS OF HANDLING STRESS

Seven animals were found moribund (two females and four males) or dead (one male) in traps at the PL site. Just as at the OV site, all six moribund animals were wobbly (W), all seven were bony (B), and all but one (a male) were rumpy (R). Among the 78 radio-collared adult females (including those found moribund) there were 10 cases of wobbliness, 15 cases of boniness and 22 cases of rumpiness. Compared to the overall frequency of capture and handling in each season (Clinchy 1999, his Tables 6.5 and 6.7), symptoms of wobbliness (partial $\chi^2_1 = 14.44$, $P = 0.002$; marginal $\chi^2_1 = 14.10$,

Table 4. Co-occurrence of probable symptoms of handling stress. Symptoms are wobbliness (W), boniness (B) and rumpiness (R). The observed proportion of radio-collared adult females (of 78) with > 1 symptom, was compared to that expected if symptoms bore no relation to one another. Expected frequencies of chance co-occurrence were determined by calculating the proportion showing each symptom (e.g. 10/78 W = 0.128; 15/78 B = 0.192) and multiplying these together (e.g. expected co-occurrence of W + B = 0.128 × 0.025 ≈ 1.9 of 78). Observed and expected frequencies were compared using the binomial test

Number and probability	Combination of symptoms			
	W + B	W + R	B + R	W + B + R
Observed	8	9	13	8
Expected	1.9	2.8	4.2	0.5
Binomial <i>P</i>	0.001	0.002	< 0.001	< 0.001

$P = 0.003$) and boniness (partial $\chi^2_1 = 15.10$, $P = 0.002$; marginal $\chi^2_1 = 14.76$, $P = 0.002$) were both observed significantly more often than expected during the colder months in autumn and winter; dyadic and triadic combinations of symptoms occurred much more frequently than expected by chance (Table 4); and symptoms of wobbliness (partial $\chi^2_1 = 8.83$, $P = 0.003$; marginal $\chi^2_1 = 6.39$, $P = 0.012$), or the combination of being both bony and rumpy (B + R: partial $\chi^2_1 = 6.80$, $P = 0.009$; marginal $\chi^2_1 = 5.71$, $P = 0.017$), were both preceded by weight loss significantly more often than expected from the overall frequency of weight loss among animals weighed on successive occasions (Clinchy 1999, his Table 6.6). The seasonal occurrence of these symptoms and their co-occurrence both with each other and observable weight loss are all clear indications of a syndrome similar to that described in association with trap-deaths at the OV site.

Possums at the PL and OV sites possessed the same intestinal nematodes (*Parastrongyloides trichosuri*, *Paraastrostrongylus trichosuri* and *Trichostrongylus* spp.) and the same ectoparasitic mite (*Trichosurolaelaps crassipes*). Just as at the OV site, animals in poor condition at the PL site possessed significantly greater numbers of both intestinal nematodes and ectoparasitic mites. *Parastrongyloides trichosuri* and *T. crassipes* burdens were significantly greater ($t_{16} = 4.07$, $P < 0.001$; $t_{15} = 2.31$, $P = 0.035$) in animals found moribund or dead in traps (median = 338, range = 19–1183; median = 34, range = 7–225) compared to those whose deaths were obviously anthropogenic (median = 9, range = 2–146; median = 15, range = 1–34), and the same was true when all undiagnosable deaths were considered ($t_{18} = 3.19$, $P = 0.005$; $t_{18} = 2.78$, $P = 0.012$). *Parastrongyloides trichosuri* and *T. crassipes* burdens were also significantly greater ($P < 0.05$ in all cases) when contrasts were restricted to individuals that showed symptoms of wobbliness or boniness or rumpiness prior to an undiagnosable death, compared to those that did not demonstrate symptoms prior to an obviously anthropogenic death (i.e. apparently healthy animals).

Females that were either wobbly (Mann–Whitney $U_{10,44} = 93.5$, $P = 0.005$), or both bony and rumpy (B + R; Mann–Whitney $U_{13,41} = 134.5$, $P = 0.032$) or any other combination (Table 4; $P < 0.01$ in all cases), were handled significantly more frequently than females

without these symptoms. Females that showed these symptoms were also significantly less likely to survive (W, $\chi^2_1 = 13.51$, $P < 0.001$; B + R, $\chi^2_1 = 6.59$, $P = 0.010$; any other combination, $P < 0.01$ in all cases) than those without these symptoms. All eight females that demonstrated all three symptoms (W + B + R, Table 4) died. In most (9/11) cases when females with these symptoms (W, B + R, any other combination) died, the cause was undiagnosable (Table 2).

PROXIMATE CAUSES OF DEATH

Eight radio-collared adult females were killed by predators and a ninth died from a massive *Ophidascaris robertsi* (Viggers & Spratt 1995) infection (Table 2). The almost two-thirds of all apparently 'natural' deaths remaining were undiagnosable (Table 2). As already noted, two females were found moribund in traps. In another 10 cases the animal appeared to have simply 'dropped dead', since the carcass was found intact, either lying on the ground (9) or hanging by its tail from a tree branch (1).

Undiagnosable deaths were not the result of an infectious disease. Necropsies of these animals revealed no evidence of gross pathology associated with parasitic infections, nor any evidence of the viral disease described by Mackintosh *et al.* (1995), and all serological tests for antibodies were negative. These same necropsies also clearly indicated that undiagnosable deaths were not the result of starvation. While most of the animals examined had little or no subcutaneous or peritoneal fat, all had food in their guts, and there was no gross pathology indicative of starvation observable in the liver or kidneys.

Undiagnosable deaths were also not simply due to 'old age' (senescence). Animals whose deaths were undiagnosable (mean age = 7.4 ± 0.9 years) were not significantly older (cause $F_{1,28} = 0.72$, $P = 0.402$; sex $F_{1,28} = 0.30$, $P = 0.586$; interaction $F_{1,28} = 0.41$, $P = 0.526$) than those whose deaths were obviously anthropogenic (mean age = 5.8 ± 0.9 years). There was also no significant difference in age when all four groups from which teeth were collected were considered ($F_{3,34} = 1.21$, $P = 0.320$).

Undiagnosable deaths were associated with handling stress. In all cases where histopathology was evaluated the 'white pulp' of the spleen appeared diffuse and

Table 5. Sensitivity of the projected population growth rate (r) to changes in each of the parameters included in the deterministic, stage-based model of possum demography described in the text

Sensitivity of r to:	Birth order	Stage	Born in:	To end of:	Δr
Proportion of adults bearing:	Primary	Young-of-the-year	Autumn		0.0068
	Primary	Young-of-the-year	Winter		0.0004
	Replacement	Young-of-the-year	Winter		0.0002
Sex ratio at birth		Young-of-the-year			0.0241
Proportion 1st breeding as:		1-year-olds			0.0012
		2-year-olds			0.0006
		1–3-year-olds			0.0009
Success of 1st-time breeders		Adults		Autumn	0.1045
		Adults		Winter	0.1118
		Adults		Spring	0.0971
		Adults		Summer	0.0973
Survival of:		1-year-olds		Autumn	0.0086
		1-year-olds		Winter	0.0091
		1-year-olds		Spring	0.0086
		1-year-olds		Summer	0.0087
	Primary	Young-of-the-year	Autumn	Autumn	0.0009
	Primary	Young-of-the-year	Autumn	Winter	0.0102
	Primary	Young-of-the-year	Autumn	Spring	0.0121
	Primary	Young-of-the-year	Autumn	Summer	0.0121
	Primary	Young-of-the-year	Winter	Winter	0.0001
	Primary	Young-of-the-year	Winter	Spring	0.0001
	Primary	Young-of-the-year	Winter	Summer	0.0002
	Replacement	Young-of-the-year	Winter	Winter	0.0002
	Replacement	Young-of-the-year	Winter	Spring	0.0002
	Replacement	Young-of-the-year	Winter	Summer	0.0003

depleted (lymphoid follicular involution), indicative of a response to stress (Humphreys *et al.* 1984; Obendorf *et al.* 1998). Moreover, where a biochemical analysis of the blood was conducted the results revealed a 'stress haemogram' (D. Obendorf, unpublished) with elevated creatine phosphokinase (CPK) levels ($> 6000 \text{ U L}^{-1}$), consistent with a diagnosis of capture myopathy (Williams & Thorne 1996).

MODEL PROJECTIONS

Sensitivity analysis of our demographic model (Table 5) indicated that: (1) adult survival is an order of magnitude more important than almost any other parameter in determining the population growth rate; and (2) any change in adult survival produces a directly proportional change in r . Consequently, in the following analyses we focus solely on the errors that may be introduced into population projections as a result of adult deaths due to handling.

When only obviously anthropogenic deaths are excluded (right-censored) when estimating survival, the projection for the PL site is that the resident population will decline by 9.6% per year (Scenario 1, Table 1, Fig. 3), suggesting that the site is a dispersal sink. However, based on the rate of *true* immigration measured in response to our experimental removals, an initial population of 19 adult females is projected to decline to a new stable equilibrium of just three females (Fig. 3), an 84% reduction in density. This suggests that the site is *not* a dispersal sink, in so far as immigration is not sufficient to balance local losses.

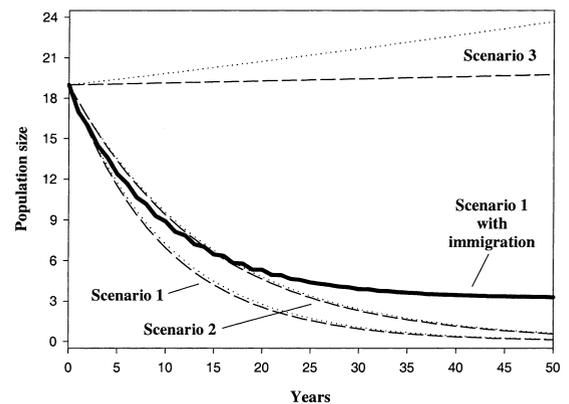


Fig. 3. Projected changes in population size given three scenarios regarding the treatment of deaths in association with capture and handling (Table 1). Initial population size = 19 adult females in all cases. The dashed line indicates projections concerning the Paddys Land (PL) site, while the dotted line signifies projections concerning the Orongorongo Valley (OV) site.

Based on published estimates, the projection for the OV site is that the resident population will decline by 9.2% per year (Scenario 1, Table 1, Fig. 3). This corresponds with Efford's (1998) suggestion that the OV site appears to be a dispersal sink for possums.

If the deaths of animals found moribund in traps are assumed to be a *direct* result of capture and handling and correspondingly right-censored (Scenario 2, Table 1), the resident populations at both the PL and OV sites are still projected to decline, but at a noticeably slower rate ($\cong 7\%$ per year; Scenario 2, Table 1, Fig. 3). If, in

addition, deaths are also right-censored where the cause was undiagnosable and the animal had previously demonstrated those probable symptoms of handling stress associated with poorer survival (W, B + R, any other combination; Table 2), the resident population at the PL site is projected to be *stable* ($r \equiv 0.0$; Scenario 3, Table 1, Fig. 3). Similarly, if the differences between our estimates of survival at the PL site under scenarios 1 and 3 are added to Efford's (1998) estimates of survival, the resident population at the OV site is also projected to be *stable* ($r \equiv 0.0$; Scenario 3, Table 1, Fig. 3).

Discussion

Demonstrating the existence of a dispersal sink requires accurate measurements of immigration, births and deaths (Watkinson & Sutherland 1995). Accurately measuring immigration presents special problems (Stenseth & Lidicker 1992), which we overcame by extensive and intensive sampling and re-sampling (Clinchy 1999). In addition to evidence of an effect of handling on the survival of pouch-young (Table 3), several independent lines of evidence indicated that our intensive efforts to measure immigration *without error* also had an adverse effect on adult survival (Figs 1 and 2, Table 2). Whether or not our study site appears to be a dispersal sink ($r < 0$) depends on whether deaths associated with capture and handling are assumed to be 'natural' or not (Scenarios 1 vs. 3, Table 1, Fig. 3).

Females that were handled more frequently were less likely to survive (Fig. 1). This could be because handling stress directly affected survival or because animals that were already in poorer condition were more trappable (Sedinger *et al.* 1997). In the latter case, the survival rate ought to be the same in the presence or absence of handling. In comparatively long-lived animals, such as common brushtail possums, the observed age structure is a function of the average survival rate over many preceding years (Krebs 1999). Based on the observed age structure (Fig. 2), the long-term average survival rate was clearly higher *prior* to the study than it was *during* the study (= 81.3% when likely handling deaths are included; Scenario 1, Table 1), suggesting that the stress of handling *was* directly affecting survival. Our estimate of the 'background' survival rate (= 90.1% when probable handling deaths are excluded; Scenario 3, Table 1) corresponds much more closely with the observed age structure (Fig. 2).

Just as at the OV site, symptoms of wobbliness and boniness and rumpiness were observed at the PL site, in association with: (1) trap-deaths; (2) changes in ambient temperature (season); (3) each other (Table 4); (4) weight loss; and (5) heavy intestinal nematode and ectoparasitic mite infections. These commonalities clearly suggest a common cause at both sites. This cause could be handling stress or some other underlying disease state. The fact that females with 'terminal' symptoms (W, B + R, any other combination) were handled more frequently is not conclusive since, as noted above, animals *already*

in poorer condition may have been more trappable. However, four lines of evidence indicate that handling stress was in fact the cause: (1) this suite of symptoms (W, B, R) closely resembles those (ataxia, muscular degeneration and fur loss) typically observed in association with capture myopathy and handling stress in other species (Fiennes 1982; Mann & Helmick 1996; Williams & Thorne 1996); (2) these same symptoms have all been reported in response to stress in captive common brushtail possums (Humphreys *et al.* 1984; Presidente 1984); (3) necropsies revealed evidence of histopathology and biochemical anomalies consistent with a diagnosis of handling stress; and (4) most importantly, our diagnoses of the proximate causes did not reveal any evidence that the deaths of animals with these symptoms were due to 'old-age' (senescence), starvation or any other underlying disease state.

We conclude that there is clear statistical (Figs 1 and 2) and symptomatological (Table 2) evidence of handling effects. To gauge the scope of the errors introduced into our population projections as a result of these handling effects, it was necessary to identify *which* individuals most probably died as a direct result of capture and handling (Table 1). Our estimate of the scope of these errors is doubly conservative, since inclusion in this category was restricted to: (1) only those individuals that showed those likely symptoms of handling stress that were known to be associated with poorer survival (W, B + R, any other combination); from among (2) only those individuals whose deaths were otherwise undiagnosable (Table 2).

If our conclusions about the adverse effects of handling are incorrect, then the PL site would appear to be a dispersal sink (Scenario 1, Table 1, Fig. 3). This is clearly inconsistent with the modelled prediction that the PL site represents optimal habitat for possums (NPWS 1994), since dispersal sinks are generally assumed to occur in suboptimal habitat. Moreover, the measured rate of *true* immigration is not sufficient to maintain the population size under this scenario (Scenario 1 with immigration, Fig. 3), in which case the observed densities are inexplicable.

While the demographic results from the PL site could be dismissed as the consequence of 'a couple of bad years', results from the OV site are based on more than 15 years of data (Efford 1998). Under the assumption that handling is innocuous (Scenario 1), the resident population at the OV site is projected to decline at virtually the same rate as the resident population at the PL site (Table 1, Fig. 3). As with the PL site, the projected decline at the OV site is clearly inconsistent with the fact that it too appears to be in optimal habitat (Efford 1998).

The remarkable similarities in the projections for both the PL and OV sites (Table 1, Fig. 3) may at first seem surprising. Common brushtail possums were introduced into New Zealand from Australia (Cowan 1990), and the two countries are ecologically very different. The similarities in projections are less surprising, however,

considering the overwhelming importance of adult survival to the projected population growth rate (Table 5). As a consequence, similarities in the factors affecting adult survival are largely sufficient to explain the similarities in the projections. Since predator densities (Fitzgerald & Karl 1979; Catling & Burt 1995; Efford 1998; Clinchy 1999) and parasite burdens (Heath *et al.* 1998; Obendorf *et al.* 1998; Stankiewicz *et al.* 1998; Clinchy 1999) are comparable at both sites, and deaths due to predators and parasites were not numerous enough to have created a dispersal sink at the PL site (Table 2), it seems likely that an additional factor must also have been at work at the OV site. We suggest that, just as at the PL site, that other factor is handling stress.

Logically, animals found moribund in traps represent observable deaths *in association with* capture and handling that may or may not be the direct *result* of capture and handling. As is typical of animals that die during capture (Fiennes 1982; Williams & Thorne 1996), no gross pathology was evident in animals found moribund in traps at either the PL or OV sites. Where there is no other evidence it will not be possible to say definitively whether such deaths are 'natural' or not. Since this may affect whether a site is judged to be a dispersal sink, we propose that all studies reporting the existence of an apparent dispersal sink should also report the frequency of all observable deaths that occur *in association with* capture and handling.

The PL and OV sites would both appear to be dispersal sinks if animals found moribund in traps were the only ones deemed to have died as a direct *result* of capture and handling (Scenario 2, Table 1, Fig. 3). Of course, deaths due to handling may not always occur in the presence of the researcher. Animals may be released, apparently unharmed, that may not die until days or weeks later (Fiennes 1982; Williams & Thorne 1996). The perplexing fact that females at our site were 'dropping dead' for no apparent reason (Table 2) would not have been evident if these animals had not been radio-collared. In addition, the scarcity of both predators and scavengers meant that we were often able to retrieve intact carcasses for diagnosis, something that is rarely feasible (Wobeser 1994). Since results regarding the OV site were based solely on trapping (Efford 1998), it is not possible to evaluate how many animals at that site may have been 'dropping dead' following their release. If we assume that such deaths occurred with the same frequency at both sites, the resident population at the OV site is projected to be stable ($r \approx 0.0$; Scenario 3, Table 1, Fig. 3).

Given the strikingly similar symptoms of handling stress and the parallels in projected outcomes at both the PL and OV sites, it seems reasonable to conclude that the resident population at the OV site was unable to replace itself (births < deaths) *largely because* of the trapping study. Since numbers remained stable at the OV site (Efford 1998, his Fig. 3), new animals must have been continually entering from outside the study area. The results from our experimental removals indicate

that the reason why these new recruits were drawn into the area *may also* have been largely because of the trapping study.

In the 2 years following our 'pulsed' experimental removal of the 19 core residents, 15 females that were originally resident in the surrounding 'border zones' expanded their ranges into the core and re-occupied many of the dens of the core residents (Clinchy 1999). Range expansion in response to the disappearance of a neighbour is common in territorial species (Carpenter 1987). Efford, Warburton & Spencer (2000) called this the 'vacuum effect'. Given that deaths due to capture and handling are analogous to removals, the OV study may be viewed as a low-intensity, 'press' (continuous) removal experiment. Reproduction (Table 3) and survival (Fig. 1) will be higher among animals living just outside of the study area precisely because they are *not* repeatedly captured and handled. The creation of vacancies on the study grid as a *result* of deaths due to capture and handling presumably draws in these neighbours from just off the grid (i.e. the vacuum effect), and numbers therefore remain stable. Efford (1998, p. 515) acknowledged that such 'apparent recruitment of peripheral adults' at the OV site, could not be ruled out.

We caution against dispersal sink studies becoming self-fulfilling prophecies: (1) deaths due to capture and handling create a declining population ($r < 0$) fit to be 'rescued' from extinction by immigration; (2) the resulting 'removal' of residents creates vacancies that draw in *apparent* immigrants in the form of neighbours intent on securing all or part of the empty ranges (i.e. the vacuum effect); and (3) thus is the population 'rescued' from extinction by 'immigration'. This conundrum is not easily resolved. Distinguishing between *true* immigration and the *apparent* immigration entailed by the vacuum effect (Lidicker & Stenseth 1992, p. 23) will probably require even more intensive capture and handling.

How often do handling effects generate apparent dispersal sinks? At present this is unanswerable, because so few studies have tested for biases in demographic parameters attributable to handling effects (Wobeser 1994; Williams & Thorne 1996; Haydon *et al.* 1999). Haydon *et al.* (1999) recently reported that significant biases in population projections for snowshoe hares were the result of handling effects. Biases in population projections resulted from comparatively small effects on adult survival in both possums ($\approx 8.8\%$; Scenarios 1 vs. 3, Table 1) and hares ($\approx 5.0\%$; Haydon *et al.* 1999). Given the general sensitivity of population projections to effects on adult survival, we suggest that any evidence of adverse effects of handling on adult survival, in particular, should raise alarm bells about the accuracy of estimated population growth rates and resulting conclusions about dispersal sinks (i.e. $r < 0$).

We examined 17 of the 22 animal studies cited in Diffendorfer's (1998) recent review of empirical studies of source-sink dynamics (the remaining five were either inapplicable or inaccessible) for any acknowledgement

that handling effects may have biased the results. Only four studies did acknowledge this (Southern 1970; Nettleship 1972; Grant 1975; Stearns & Sage 1980). Notably, those that did were significantly ($t_{15} = 2.78$, $P = 0.014$) older (mean publication date = 1974) than those that did not (mean publication date = 1986). Those that did also tended to be longer (mean length = 36 pages) than those that did not (mean length = 16 pages), but the difference was not significant ($t_{15} = 1.64$, $P = 0.122$). There are at least two explanations why more recent studies do not acknowledge handling effects: (1) improvements in techniques and procedures have eliminated handling effects; or (2) researchers are now more reluctant to report or discuss potential handling effects.

We have discussed how biases attributable to handling effects may lead to erroneous conclusions about ecological processes. If handling effects are not reported there will also be no way to anticipate them and thereby attempt to reduce potential harm (Sedinger *et al.* 1997). We chose to focus our analyses on handling *per se* since this was the most invasive procedure animals were subjected to. Of course trapping, independent of handling, may also have adverse effects. Even apparently healthy animals were significantly more likely (binomial $P < 0.001$) to have lost weight (32) than not (8) over a 3-night trapping session. Providing more bait and processing animals at night, rather than waiting until the next day, are both ways to reduce potential weight loss. Moreover, while it is necessary to sample several (3) times over a short period in order to accurately estimate population size (Krebs 1999), sampling every second or third night, with 'nights off' in between, ought to be just as effective. Viggers & Lindenmayer (1995) recommended the use of a sedative to reduce the level of stress induced when handling possums.

Our work addressed an important question in conservation biology regarding the role of immigration in 'rescuing' populations from extinction (Clinchy 1997; Sih, Jonsson & Luikart 2000). To answer this question properly will generally require extensive handling and disturbance of the study population(s) (Stenseth & Lidicker 1992; Watkinson & Sutherland 1995; Clinchy 1999). If the resulting effects on the health and well-being of the subjects are not considered this may lead to erroneous conclusions, and the wrong conservation actions being taken. Consequently, conservation and animal welfare concerns are both better served by the explicit reporting and discussion of the potentially adverse effects of measurement.

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