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Detectability of ten invasive mammal pests in New Zealand: a synthesis of spatial detection parameters

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Abstract: Management of invasive mammal pests plays an integral role in the conservation of New Zealand's native flora and fauna. Models fitted to pest capture data can guide conservation managers by providing estimates of pest densities within a management area, or probabilities of absence for declaring local eradication. A key parameter of these models is the detectability, i.e. the probability of an animal being detected by a surveillance device for a given amount of survey effort. In this paper, we conduct a comprehensive review of both spatially explicit capture-recapture and home-range studies reporting estimates of two commonly applied spatial detectability parameters for ten of New Zealand's invasive mammal pests. We summarise study attributes including habitat, season, and surveillance device type, to assess how detectability varies over different environmental, biological, and survey conditions, and to identify knowledge gaps for prioritising future research.

Keywords: capture probability, detectability, detection probability, home-range, invasive mammal pests, pest eradication, pest management.

Introduction

In New Zealand, invasive mammal pests are driving serious declines in native populations of birds (Innes et al. 2010), invertebrates (Watts et al. 2017), herpetofauna (Reardon et al. 2012) and plants (Holland et al. 2013). Ship rats (*Rattus rattus*), brushtail possums (*Trichosurus vulpecula*) and stoats (*Mustela erminea*) are generally considered a major threat to native flora and fauna because they are abundant, arboreal, and ubiquitous across mainland New Zealand; however, other rodent and mustelid species, European hedgehogs (*Erinaceus europaeus*) and feral cats (*Felis catus*) also impact native biodiversity (King 2023). To conserve threatened species, pest control programmes have been implemented across New Zealand's North and South Islands, and offshore islands. Suppression or eradication of mammalian pests is currently achieved by trapping and/or toxic baiting, where baits are applied across a grid of stations, usually over relatively small spatial areas, or delivered aerially over larger landscapes (Russell et al. 2015). The success of these programmes relies on having effective control and surveillance methodologies, underpinned by knowledge of the ecology of target species, for example, the dynamics of pest populations, how they disperse, their interactions with other species in New Zealand's ecosystems, and their behaviour around detection devices. For this reason,

it is crucial to collect and summarise information on animals' detectability in a range of different habitats, seasons and trapping designs, for pest managers to refer to when designing efficient eradication programmes. This paper aims to review and summarise detectability estimates from a range of spatially explicit capture-recapture (SECR) and home-range studies.

Information on pest detectability is often used to parameterise models used in surveillance programmes. Surveillance of pests guides conservation and wildlife disease management, both prior to pest control commencing (e.g. providing baseline data and planning optimal control strategy or eradication monitoring) and during, e.g. adaptive management (Parkes et al. 2006). After operations, surveillance also allows managers to assess whether targets for residual densities of pests have been achieved. If the goal is complete eradication, surveillance is required to confidently declare the absence of animals within the management area and to monitor for future incursions (Russell et al. 2017; Gormley et al. 2021). Pest surveillance systems often employ stationary detection devices such as live traps, trail cameras and tracking tunnels, which provide data (e.g. images of animals or live captures) on the presence or absence of an animal at the device's location. Trail cameras additionally allow recording of counts of animals detected within a specified timeframe. By utilising these surveillance data, quantitative models can make inferences

about the current state of a pest population or predict information ahead of time (e.g. simulation models). Key model variables include the densities of pest populations over space and time, the sensitivity of pest surveillance systems (i.e. device type, density and layout, and frequency or duration of surveillance operations), the probabilities of local eradication given animals are no longer detected during surveillance operations, or the time required to achieve complete eradication (Samaniego-Herrera et al. 2013; Russell et al. 2017; Kim et al. 2020; Gormley et al. 2021; Anderson et al. 2022a).

Models using surveillance data typically incorporate a parameter of pest detectability for a given surveillance method. Often, the goal is to infer population density or the probability of absence, while detectability is merely a nuisance parameter. In other contexts, detectability is the main parameter of interest, for example, when assessing the effectiveness or sensitivity of different surveillance systems for detecting target pests. Understanding how varying biological (e.g. sex, age) or environmental conditions (e.g. habitat type, seasonality) affect detectability also provides ecological insight into pest behaviour, critical for designing effective approaches to control (Duron et al. 2020). For some models, prior knowledge of detectability is required as a model input, while others may infer these parameters from data. SECR models allow joint estimation of both population density and spatial detectability parameters, using capture-recapture data of uniquely identifiable individuals (Borchers & Efford 2008; Efford & Fewster 2013). However, resource constraints frequently limit the feasibility of conducting regular capture-recapture studies within pest management programmes, particularly for long-term or large-scale surveillance. Other methods, such as spatial count models, estimate density from more readily available data on counts of unmarked individuals at detection devices. Both SECR and spatial count models benefit from having accurate and precise estimates of spatial detection parameters as informative model priors for unbiased estimation (Burgar et al. 2018). Proof-of-absence models, a decision-support tool for eradication programmes, also require detectability information as a model input to estimate the probability of eradication (given no animals are detected during surveillance) and surveillance system sensitivity (Anderson et al. 2013; Russell et al. 2017; Gormley et al. 2021). Finally, detectability parameters are key inputs for a plethora of simulation models (e.g. agent-based models, which simulate individual animals and track their numbers and/or movements over time) that support the planning of optimal surveillance or control systems.

The probability of a pest being detected by a stationary detection device (hereafter P_{detect}) can be expressed as a product of the probability of a pest encountering the device, and the probability of the pest interacting with that device given an encounter. For pests utilising a home-range area, the likelihood of a pest encountering a device may vary over space so P_{detect} also varies spatially. P_{detect} is often assumed to be highest if the device is located at the animal's home-range centre and declines for devices located nearer the home-range periphery or beyond. Detection probabilities are therefore commonly defined as decaying spatial detection functions $P_{detect}(d)$ of the distance d between an animal's home-range centre and the device location. A half-normal detection function is frequently assumed, though other functional forms including hazard-rate, negative exponential or uniform, may be more appropriate for certain species or detection methods.

A half-normal detection function comprises two parameters. The first, an intercept g_0, is the probability of an animal being detected by a device located at its home-range centre in a single unit of survey effort (often one trap night). That is, g_0 is a product of the probability of interaction and probability of encounter at $d = 0$ in a single trap night. The second parameter σ is a spatial-decay parameter that determines the spread of the detection function and how the probability of encounter declines with d, i.e. σ scales the detection function relative to an animal's home-range size. The half-normal detection function is therefore:

$$p_{detect}(d) = g_0 \exp(\frac{-d^2}{2\sigma^2}) \qquad (1)$$

There is a parametric inverse relationship between g_0 and σ (Ramsey et al. 2005; Sweetapple & Nugent 2018; Anderson et al. 2022b), such that an animal with a larger home range is less likely to encounter a device at its home-range centre because it spends less time there on average than an animal with a smaller home-range. Detectability parameters, g_0 and σ, can be inferred alongside population density by fitting SECR models (Efford & Fewster 2013), which assume home-range centres are Poisson-distributed with density D, to capture-recapture data. Readily available software, such as DENSITY (Efford et al. 2004) and the *secr* package (Efford 2023) in R statistical software (R Core Team 2021), has been developed for this purpose. Alternatively, parameters can be inferred using independent methods, such as direct observation of surveillance devices. Assuming an animal occupies its home-range, on average, according to a symmetric bivariate normal distribution, then the area the animal occupies 95% of the time is a circle of radius 2.45σ with area $\pi(2.45\sigma)^2$ (Efford 2004, Efford et al. 2004). Under this assumption, estimates of σ can be back-calculated from home-range area estimates obtained by animal telemetry or other methods. Note, however, that estimates of σ calculated using telemetry are not directly comparable to those calculated from capture-mark-recapture methods (Nathan 2016). Telemetry trackers do not impede movement and usually record a wider range of locations (total movement) than the live-trapping devices used in SECR studies. Values of σ extracted from the latter, on the other hand, describe the spatial scale of detection, record fewer location points, and are dependent on animal behaviour towards the detection devices (Efford & Hunter 2018). While it is possible to incorporate home-range estimates from telemetry data into SECR studies (Efford 2023), practitioners should be wary of the possible change in animal movement patterns when in the presence of detection devices. Estimates of σ can also be biased in shorter spatial-capture-recapture surveys (Harmsen et al. 2020), or by other aspects of sampling design like device layout and spacing (Harmsen et al. 2020; Schmidt et al. 2022). To minimise estimation bias, all spatial-capture-recapture studies should follow current best-practice sampling designs, such as using an optimised device grid distance and longer sampling periods (Freeman et al. 2022).

For many species, increases in population density are directly calculated (Anderson et al. 2022b) or associated with decreases in home-range size due to interactions (e.g. competition) between contiguous neighbours (Adams 2001). This inverse relationship between density and σ is well documented for possums in New Zealand habitats (Rouco et al. 2013; Efford et al. 2016; Anderson et al. 2022b). In New Zealand's beech forest and alpine grassland systems, populations of house mice, ship rats, and mustelids undergo sporadic irruptions driven by pulses of food resource during heavy masting events (synchronous production of large

amounts of seed) (Wardle 1984; Wilson & Lee 2010; Walker et al. 2019); these periodically high population densities are also likely associated with smaller σ. Environmental and biological factors that influence behaviour, home-range size, and/or density, including habitat, food supply, season, interactions among pest species, sex, and age, will affect both g_0 and σ. For instance, possum home-range sizes are known to increase during seasonal heavy fruiting of native tree species, as they forage a larger area to utilise this food resource (Ward 1978). In addition, interaction probability (given an encounter) depends on the efficacy of different detection devices or lure types, and therefore affects g_0 but not σ (Nathan 2016).

Estimates of g_0 and σ are reported in the literature, primarily in SECR studies and for individual pest species at a single study site. To date, there has been no attempt to collate detectability estimates for all of New Zealand's mammalian pest species across a variety of surveillance techniques; however, see single-species reviews by Glen and Byrom (2014) for possums, ferrets and stoats, and Nathan (2016) for ship rats. In this work, we conduct a comprehensive review of studies reporting spatially explicit detection parameter estimates, for ten of New Zealand's invasive mammalian pest species. We compute summary values and quantify the dependencies between g_0, σ, and density for application in future modelling (e.g. as model priors). We also assess how detectability varies under different biological, environmental, and surveillance conditions to provide insight into pest behaviour and efficacy of different surveillance methods. We discuss the correlation, or lack thereof, between detectability and habitat, season, surveillance device, and sex, as well as collating information on lure, trap grid spacing, masting, and population status. These data will be particularly valuable to pest managers during the design of an efficient pest control or surveillance operation. As New Zealand increasingly attempts landscape-scale elimination of key pest species under its national Predator Free 2050 programme (New Zealand Government 2020), these estimates will inform quantitative decision support tools for eradication (e.g. estimating probabilities of absence) (Gormley et al. 2021). For example, knowledge on the effect of surveillance device type, season, and vegetation on detectability can be used to evaluate population abundance (Yiu et al. 2022), and the information collected on detectability at different population densities and for different trapping designs can help identify the right time to switch to a more intensive strategy to target survivors at low densities (Gronwald & Russell 2020). Finally, we identify critical knowledge gaps to help prioritise future research.

Methods

We collated information from New Zealand studies on spatial detectability parameters g_0 and σ for brushtail possum (*Trichosurus vulpecula*), four rodent species (ship rat *Rattus rattus*, Norway rat *R. norvegicus*, kiore *R. exulans*, and house mouse *Mus musculus*), three mustelid species (stoat *Mustela erminea*, ferret *M. furo*, and weasel *M. nivalis*), feral cat (*Felis catus*) and European hedgehog (*Erinaceus europaeus*). We included all studies where detection probability g_0 and spatial-decay parameter σ were estimated by fitting SECR models to capture-recapture data. We also included studies reporting empirical measures of g_0, based on field observations of pest behaviour in close proximity to detection devices, e.g. Nathan (2016), or estimates of home-range size, typically obtained

from telemetry data using minimum convex polygons (MCP) or kernel density estimation (KDE). Home-range size estimates were converted to a corresponding σ value using:

$$\text{HR size (in m}^2) = \pi(2.45\sigma)^2 \qquad (2)$$

where HR size is the area of the circular home-range occupied by an average animal 95% of the time, i.e. a circle of radius 2.45σ (Efford et al. 2016). We also summarised general trends emerging from the wider literature on which key factors are known to affect home-range size and population density (which determine probability of encounter), or the probability of interaction with devices for each species.

We reviewed published studies, unpublished contract reports, unpublished datasets, and theses. From each study, we extracted estimated values and associated uncertainty for g_0, σ and density. For studies that mentioned but did not report g_0 or σ, authors were contacted to request estimates. We also extracted information on the sex of the animal, dominant habitat type (classified as beech (*Fuscopora* and *Lophozonia* spp.) forest, mixed beech-podocarp-broadleaved forest, podocarp-broadleaved forest, kauri forest, exotic plantations, alpine grassland, open-country, urban, wetland, braided riverbed), device type (live traps, tracking tunnels, hair-snag tubes, snap trap tunnel, bait station, or camera traps), season, location, study type (SECR or home-range size), detection function (half-normal, negative exponential, hazard rate or uniform), and the software/model method used. For studies in New Zealand beech forest or alpine grassland systems, we recorded whether the study was conducted during or following a mast year to indicate whether populations were likely to be at low or high density. Where available, we also extracted details of the detection device model, device layout and spacing, bait/lure type, study location, and the survey month/year.

For species with sufficient data, we used SECR estimates to quantify relationships between g_0 and σ, and between population density and σ. This was done by comparing a linear regression on log transformed variables and a power law non-linear regression, then selecting the best-fit model with lowest Akaike Information Criterion (AIC). Confidence intervals were calculated for predicted curves using the predict function of the *stats* package (R Core Team 2021) and the predFit function of the *investr* package (Greenwell & Kabban 2014). We also assessed the effects of seasonality on g_0 and σ, and of sex on σ, by pooling estimates over studies and comparing group means using ANOVA and t-tests or Wilcoxon rank tests. Note, this approach does not account for potential confounding factors and group estimates may be biased where there is uneven representation of these other factors. When pooling estimates, if multiple models had been fitted to the same dataset we selected only the best model as determined by AIC. If AIC was not reported, we chose estimates from the null model with constant detection probability across individuals and across time, i.e. the spatially explicit analogue of the null M_0 model in Otis et al. (1978), using the maximum likelihood closed-population estimator of population size. The definition of g_0 and σ changes for different detection functions due to differing assumptions about the probability of an animal encountering a device. We only pooled and analysed parameter values reported for the half-normal function, which was most commonly applied across all studies.

Table 1. Summary of mean estimates of spatial detectability parameters g_0, σ (metres), and density (animals ha^{-1}) for New Zealand's key small mammal pest species, for different detection methods and habitat types. Note this does not capture parameter uncertainty; see Appendix S1 for full summary statistics and study attributes. Estimates were extracted from SECR studies (that used a half-normal detection function, unless otherwise specified), and Bayesian Inference (BI) studies, or home-range size (HR) studies. Detection methods: BS: Bait Stations, CT: Camera Traps, HT: Hair-snag Tube, KT: Kill Traps, LT: Live Ground Traps, STT: Snap Trap Tunnels, TT: Tracking Tunnels. Habitat types: AG: Alpine grassland, B: Beech forest, MB: mixed beech-podocarp-broadleaved forest, PB: Podocarp-broadleaved forest, K: Kauri forest, E: Exotic plantation, OC: Open Country, BR: Braided riverbed, U: Urban, W: Wetland or swamp.

Species	min-max of mean g_0	min-max of mean σ (m)	min-max of mean density (animals ha^{-1})	Study type	Detection Method	Habitat	Season	Reference
Possum	0.05	63.00	-	SECR	LT	OC / B	Sp/Su/A/W	Ball et al. (2005)
	0.14–0.30	24.55–28.64	8.33–9.84	SECR	LT	MB	Sp	Efford and Cowan (2004)
	0.13–0.30	25.91–34.39	9.66–15.91	SECR	LT	MB	Su	Efford and Cowan (2004)
	0.13–0.35	25.30–32.58	9.66–14.02	SECR	LT	MB	W	Efford and Cowan (2004)
	0.16–0.26	47.90–48.70	1.67–2.45	SECR	LT	E	A	Efford et al. (2005)
	0.06–0.12	55.24–66.58	-	BI	LT	U	-	Latham et al. (2022)
	0.0012–0.0069†	179.42†	0.079†	SECR	LT	PB	W/Sp	O'Malley (2022a)
	0.06*	40.94*	3.68*	SECR	LT	U	Su	Patterson (2020)
	0.17	35.00	-	SECR	LT	OC	-	Ramsey et al. (2005)
	0.08–0.13	27.00–31.00	-	SECR	LT	MB	-	Ramsey et al. (2005)
	0.19	31.00	-	SECR	LT	PB	A	Ramsey et al. (2005)
	0.03	50.00	-	SECR	LT	PB	-	Ramsey et al. (2005)
	0.24	50.00	-	SECR	LT	E	-	Ramsey et al. (2005)
	0.05–0.11	31.68–60.03	4.08–6.92	SECR	LT	MB	Sp/Su/A/W	Richardson et al. (2017)
	0.07–0.08	107.33–131.19	0.44–0.69	SECR	LT	OC	A	Rouco et al. (2013)
	0.05–0.08	72.00–155.00	0.18–2.24	SECR	LT	OC / PB	A	Sweetapple and Nugent (2018)
	0.319	43.00	1.55	SECR	LT	OC / PB	Su	Sweetapple and Nugent (2018)
	-	♀: 28.48; ♂: 47.53	-	HR	-	U	Sp/Su	Adams et al. (2014)
	-	♀: 128.22; ♂: 125.92	-	HR	-	OC	-	Brockie et al. (1987)
	-	♀: 47.19; ♂: 73.47	-	HR	-	OC	Sp/Su/A/W	Byrom et al. (2008)
	-	♀: 23.03; ♂: 27.25	-	HR	-	E	-	Clout (1977)
	-	♀: 16.28; ♂: 20.60	-	HR	-	MB	-	Crawley (1973)
	-	♀: 24.50; ♂: 40.05	-	HR	-	U	Sp	Fitzgerald and Innes (2017)
	-	♀: 98.51; ♂: 114.22	-	HR	-	OC / PB	Sp/Su/A/W	Green and Coleman (1986)
	-	♀: 21.85; ♂: 40.55	-	HR	-	OC	-	Jolly (1976)
	-	♀: 133.80; ♂: 214.48†	-	HR	-	PB	W/Sp	O'Malley (2022a)
	-	♀: 21.85; ♂: 27.25	-	HR	-	OC	Sp/Su/A/W	Paterson et al. (1995)
	-	42.90–73.55	-	HR	-	B	Su	Pech et al. (2010)
	-	38.26–71.09	-	HR	-	B	W	Pech et al. (2010)
	-	♀: 30.03; ♂: 54.49	-	HR	-	OC	-	Ramsey (unpubl. data, referenced in Table 3.1 of Cowan and Clout (2000))

Table 1. Continued.

Species	min-max of mean g_0	min-max of mean σ (m)	min-max of mean density (animals ha^{-1})	Study type	Detection Method	Habitat	Season	Reference
	-	♀: 87.39; ♂: 116.51	-	HR	-	OC	Sp/Su/A/W	Rouco et al. (2016)
	-	♀: 31.74; ♂: 26.26	-	HR	-	E	-	Triggs (1982)
	-	♀: 19.27; ♂: 19.27	-	HR	-	E	-	Warburton (1977)
	-	♀: 37.13; ♂: 45.48	-	HR	-	MB	-	Ward (1978)
	-	♀: 25.23–54.49; ♂: 30.90–67.92	1.00–7.00	HR	-	E	Su	Whyte et al. (2013)
	-	♀: 63.90; ♂: 79.77	2.00	HR	-	E	Sp	Whyte et al. (2013)
	-	♀: 37.84; ♂: 28.20	-	HR	-	U	-	Winter (1963)
	-	♀: 90.66; ♂: 121.42	-	HR	-	OC	Sp/Su	Yockney et al. (2013)
Ship rat	0.06	24.42	4.02–4.74	SECR	LT	B	W	Carpenter et al. (2023b)
	0.03	35.17	4.29–5.48	SECR	LT	B	Sp	Carpenter et al. (2023b)
	0.03	29.70	6.25–10.58	SECR	LT	B	Su	Carpenter et al. (2023b)
	0.03–0.06	23.77–30.47	0.45–0.75	SECR	LT	B	A	Carpenter et al. (2023b)
	0.09–0.11	17.91–20.05	5.95–10.03	SECR	LT	MB	W	Carpenter et al. (2023b)
	0.04–0.05	21.30–28.87	0.47–17.66	SECR	LT	MB	Sp	Carpenter et al. (2023b)
	0.02–0.05	21.78–60.97	0.10–15.84	SECR	LT	MB	Su	Carpenter et al. (2023b)
	0.04–0.10	17.43–25.02	2.69–21.36	SECR	LT	MB	A	Carpenter et al. (2023b)
	0.29–0.51*	6.05–10.60*	21.60–33.90*	SECR	LT	B	Sp/Su/A/W	Efford and Hunter (2018)
	0.10–0.18*	14.00–24.00*	2.80–2.90*	SECR	LT	B	Sp	Byrom (2008)
	0.09*	12.00–25.00*	2.30–5.70*	SECR	LT	B	A	Byrom (2008)
	0.28–0.40*	19.00*	4.10–4.20*	SECR	LT	MB	Sp	Byrom (2008)
	0.33*	13.00*	10.50*	SECR	LT	MB	Su	Byrom (2008)
	0.20–0.22*	19.00–23.00*	4.30–6.00*	SECR	LT	MB	A	Byrom (2008)
	0.20–0.25*	15.00–18.00*	3.50–5.30*	SECR	LT	PB	Sp	Byrom (2008)
	0.06*	15.00*	2.00*	SECR	LT	PB	Su	Byrom (2008)
	0.05–0.15*	11.00–16.00*	4.00–11.00*	SECR	LT	PB	A	Byrom (2008)
	0.15	22.25	-	BI	LT	U	W/Sp	Mackenzie et al. (2022)
	0.1	28.95	-	BI	LT	U	W/Sp	Mackenzie et al. (2022)
	-	-	1.17	SECR	HT	MB	W	McCulloch (2009)
	♀: 0.04; ♂: 0.00	♀: 14.63; ♂: 31.45	♀: 13.62; ♂: 13.62	SECR	LT	K	A	Nathan (2016)
	♀: 0.12–0.47; ♂: 0.01–0.09	♀: 6.22–14.63; ♂: 13.37–31.45	9.16–19.96	SECR	LT	K	W	Nathan (2016)
	0.27	-	-	SECR	TT	K	A/W	Nathan (2016)
	0.29	-	-	SECR	BS	K	A/W	Nathan (2016)
	0.01	-	-	SECR	STT	K	A/W	Nathan (2016)
	0.03–0.16	22.24	14.15–25.84	SECR	LT	PB	A	O'Malley et al. (2022b)
	0.09†	22.24	0.73†	SECR	LT	PB	A	O'Malley et al. (2022b)
	0.03–0.12†	22.24	0.51–12.39†	SECR	LT	PB	W	O'Malley et al. (2022b)
	0.03–0.14†	22.24	0.77–11.76†	SECR	LT	PB	Sp	O'Malley et al. (2022b)
	0.04–0.15†	22.24	1.29–23.74†	SECR	LT	PB	Su	O'Malley et al. (2022b)
	0.08	21.12	23.74	SECR	LT	OC / PB	Su	Russell et al. (unpubl.

Table 1. Continued.

Species	min-max of mean g_0	min-max of mean σ (m)	min-max of mean density (animals ha^{-1})	Study type	Detection Method	Habitat	Season	Reference
								data[1])
	0.02–0.04	27.80–37.40	4.90–8.70	SECR	LT	MB	A	Wilson et al. (2007a)
	-	8.14	-	HR	-	PB	Sp/Su/A/W	Daniel (1972)
	-	21.42	2.9	HR	-	K	Sp	Dowding and Murphy (1994)
	-	♀: 10.38; ♂: 9.68	-	HR	-	U	Sp	Fitzgerald and Innes (2017)
	-	9.11–11.08	6.52–11.60	HR	-	PB	Su	Harper and Rutherford (2016)
	-	16.64	1.8–2.3	HR	-	PB	Su	Hickson et al. (1986)
	-	23.09	6.2	HR	-	PB	Su	Hooker and Innes (1995)
	-	18.85	-	HR	-	PB	Sp/Su	Innes and Skipworth (1983)
	-	11.51	6.73–22.43	HR	-	W / PB	Sp/Su	Latham (2006)
	-	♀: 24.80–27.92; ♂: 21.72–34.92	-	HR	-	K	W	Nathan (2016)
	-	♀: 11.97; ♂: 70.72	-	HR	-	B	A	Pryde et al. (2005)
Norway rat	-	♀: 52.16; ♂: 55.36	-	HR	-	OC	W/Sp	Bramley (2014)
	-	♀: 14.04; ♂: 15.37	-	HR	-	U	Sp	Fitzgerald and Innes (2017)
	-	31.57	-	HR	-	PB	Su	Hickson et al. (1986)
	-	25.23	-	HR	-	PB	Su	Moors (1985)
Kiore	0.03	14.51	10.9	SECR	LT	OC / PB	Su	Carter et al. (2021)
	0.05†	13.99†	2.9†	SECR	LT	PB	Su/A	Gronwald and Russell (2020)
	0.007†	13.99†	4.1†	SECR	LT	PB	A	Gronwald and Russell (2020)
	0.25–0.73†	13.99†	1.10–1.60†	SECR	LT	PB	W	Gronwald and Russell (2020)
	0.064†	13.99†	3.1†	SECR	LT	PB	Sp	Gronwald and Russell (2020)
	0.08	21.12	1.90	SECR	LT	OC	Su	Russell et al. (unpubl. data[1])
	-	♀: 9.77; ♂: 8.62	-	HR	-	OC	W/Sp	Bramley (2014)
House mouse	0.23–0.26‡	23.40–32.00‡	8.70–14.30‡	SECR	LT	OC	Sp	Efford (2004)
	0.08–0.465‡	11.10–25.60‡	27.80–70.40‡	SECR	LT	OC	Su	Efford (2004)
	0.41–0.53‡	9.10–20.70‡	26.30–71.00‡	SECR	LT	OC	A	Efford (2004)
	0.19–0.50‡	19.20–32.20‡	12.90–19.00‡	SECR	LT	OC	W	Efford (2004)
	♀: 0.06–0.16; ♂: 0.04–0.12‡	♀: 9.50; ♂: 15.70‡	74.00–104.00‡	SECR	LT	OC	W	Elliott et al (2015)

Table 1. Continued.

Species	min-max of mean g_0	min-max of mean σ (m)	min-max of mean density (animals ha^{-1})	Study type	Detection Method	Habitat	Season	Reference
	0.239‡	-	25.8‡	SECR	LT	PB	Sp	Goldwater (2007)
	0.30–0.42‡	-	97.90–156.70‡	SECR	LT	PB	A	Goldwater (2007)
	0.09–0.67‡	-	14.60–74.80‡	SECR	LT	PB	W	Goldwater (2007)
	0.00–0.24	9.37–76.68	3.61–8.92	SECR	LT	OC	Sp	Moinet (2020)
	0.01–0.15	8.33–34.87	27.06–55.85	SECR	LT	OC	A	Moinet (2020)
	-	-	102‡	SECR	BS	OC	A	Reynolds (2015)
	-	-	138‡	SECR	BS	PB	A	Reynolds (2015)
	-	-	34‡	SECR	BS	E	A	Reynolds (2015)
	-	-	102‡	SECR	STT	OC	A	Reynolds (2015)
	-	-	138‡	SECR	STT	PB	A	Reynolds (2015)
	-	-	34‡	SECR	STT	E	A	Reynolds (2015)
	-	-	102‡	SECR	TT	OC	A	Reynolds (2015)
	-	-	138‡	SECR	TT	PB	A	Reynolds (2015)
	-	-	34‡	SECR	TT	E	A	Reynolds (2015)
	0.03–0.21‡	3.75–13.16‡	5.00–83.00‡	SECR	LT	OC	Su	Russell (2012)
	0.07	10.70	<1	SECR	LT	OC	A	Russell et al. (2018)
	0.01	17.19	-	SECR	LT	OC	Su	Russell et al. (2019)
	-	-	28–104	SECR	LT	OC / PB	Su	Sagar et al (2022)
	-	-	76–104	SECR	LT	OC / PB	Su	Sagar et al (2022)
	-	-	12–24	SECR	LT	OC / PB	W	Sagar et al (2022)
	-	-	12–31	SECR	LT	OC / PB	W	Sagar et al (2022)
	-	-	13–19	SECR	LT	OC / PB	Sp	Sagar et al (2022)
	-	-	13–32	SECR	LT	OC / PB	Su	Sagar et al (2022)
	-	-	645	SECR	LT	OC / PB	A	Sagar et al (2022)
	-	-	4–31	SECR	LT	OC / PB	W	Sagar et al (2022)
	0.15–0.75	11.30–20.30	0.32–32.37	SECR	LT	AG	Sp	Wilson and Lee (2010)
	0.12	17.80	0.33–2.22	SECR	LT	AG	Su	Wilson and Lee (2010)
	0.08–0.62	10.00–19.10	2.69–55.93	SECR	LT	AG	A	Wilson and Lee (2010)
	0.28	24.20	0.02–0.28	SECR	LT	B	Sp	Wilson and Lee (2010)
	0.1	37.70	0.24–0.30	SECR	LT	B	Su	Wilson and Lee (2010)
	0.28	17.70	1.77	SECR	LT	B	A	Wilson and Lee (2010)
	0.06–0.14‡	13.16–17.94‡	-	SECR	LT	PB	Sp	Wilson et al. (2018)
	0.03–0.08‡	15.62–21.29‡	-	SECR	LT	PB	Su	Wilson et al. (2018)
	0.05–0.11‡	13.93–18.99‡	-	SECR	LT	PB	A	Wilson et al. (2018)
	0.05–0.12‡	14.33–19.54‡	-	SECR	LT	PB	W	Wilson et al. (2018)
	-	-	>150‡	SECR	LT	PB	A/W/Sp	MacKay et al. (2019)
	-	-	19.2‡	SECR	LT	OC	Su/A/W	MacKay et al. (2019)
	0.05–0.21	14.19–23.65	0.01–0.15	SECR	LT	MB	A	Wilson et al. (2007b)
	-	♀: 17.68; ♂: 18.70	0.78	HR	-	MB	Sp/Su	Fitzgerald et al. (1981)
	-	♀: 14.20; ♂: 19.37	0.54	HR	-	MB	Su	Fitzgerald et al. (1981)
	-	♀: 11.16; ♂: 15.75	2.93	HR	-	MB	W/Sp	Fitzgerald et al. (1981)

Table 1. Continued.

Species	min-max of mean g_0	min-max of mean σ (m)	min-max of mean density (animals ha^{-1})	Study type	Detection Method	Habitat	Season	Reference
	-	♀: 12.19; ♂: 11.04‡	13.025‡	HR	-	OC	Su/A/W	MacKay et al. (2011)
Stoat	0.016	355.29	-	BI	KT	MB	Sp/Su/W	Anderson et al. (2016)
	0.13*	397.00*	0.005*	SECR	HT	MB	A/W	Clayton et al. (2011)
	0.05	255.00	0.00025	SECR	HT	B	Su	Efford et al. (2009)
	0.02–0.05	521.00–726.00	0.01–0.016	SECR	LT	AG	Su/A	Smith et al. (2008)
	0.04–0.08	429.00–891.00	0.008–0.015	SECR	LT	B	Su/A	Smith et al. (2008)
	-	♀: 223.27; ♂: 343.88	-	HR	-	B	W/Sp	Alterio (1998)
	-	♀: - ; ♂: 91.79	-	HR	-	AG	Sp	Cuthbert and Sommer (2002)
	-	♀: 67.77; ♂: 159.46	-	HR	-	AG	Su	Cuthbert and Sommer (2002)
	-	♀: 259.51; ♂: 407.41	-	HR	-	BR	Sp	Dowding and Elliott (unpubl. data[2])
	-	♀: 248.02; ♂: 313.22	-	HR	-	BR	A	Dowding and Elliott (unpubl. data[2])
	-	♀: 207.25; ♂: -	-	HR	-	K / PB	Su/A	Gillies et al. (2007)
	-	♀: - ; ♂: 238.20	-	HR	-	K / PB	Sp/Su/A/W	Gillies et al. (2007)
	-	♀: 197.80; ♂: 360.73	-	HR	-	E	Sp	Miller et al. (2001)
	-	♀: 222.46; ♂: 300.34	-	HR	-	E	Su	Miller et al. (2001)
	-	♀: 198.67; ♂: 274.81	-	HR	-	E	A	Miller et al. (2001)
	-	♀: 255.32; ♂: 223.27	-	HR	-	E	W	Miller et al. (2001)
	-	♀: 211.06; ♂: 241.52–284.84	-	HR	-	OC	Sp/A	Moller and Alterio (1999)
	-	♀: 227.50; ♂: 283.98	-	HR	-	B	Sp/Su/A/W	Murphy and Dowding (1994)
	-	♀: 190.69; ♂: 207.31	-	HR	-	B	Su/A	Murphy and Dowding (1995)
	-	♀: 162.83; ♂: 259.51	-	HR	-	AG / B	Su	Smith and Jamieson (2003)
	-	♀: 145.64; ♂: 185.66	-	HR	-	PB	W	Young (1998)
Ferret	0.01–0.216	305.00–791.00	0.008–0.069	SECR	LT	OC	Su/A	Efford and Norbury (2005)
	-	♀: - ; ♂: 223.27	-	HR	-	OC	A/W/Sp	Baker (1989)
	-	♀: 167.71; ♂: -	-	HR	-	OC	Sp/Su/A/W	Byrom et al. (2008)
	-	♀: 349.24; ♂: 634.84	0.021	HR	-	OC	Su/A	Caley and Morriss (2001)
	-	♀: - ; ♂: 238.20	-	HR	-	OC	W/Sp	Dymond (1991)
	-	♀: 267.56; ♂: 294.00	-	HR	-	OC	Sp/A	Moller and Alterio (1999)
	-	♀: 200.75; ♂: 232.57	-	HR	-	OC	Sp/Su/A/W	Norbury et al. (1998b)
	-	♀: 242.62; ♂: 390.80	-	HR	-	OC	Sp/Su/A/W	Pierce (1987)
	-	♀: 154.48; ♂: 213.55	-	HR	-	OC	A/W	Ragg (1997)
	-	♀: 176.88; ♂: -	-	HR	-	OC	A/W/Sp	Ragg (unpubl. data[3])

Table 1. Continued.

Species	min-max of mean g_0	min-max of mean σ (m)	min-max of mean density (animals ha^{-1})	Study type	Detection Method	Habitat	Season	Reference
	-	♀: 229.13; ♂: 320.74	-	HR	-	OC	Su/A	Spurr et al. (1997)
	-	♀: 166.06; ♂: 307.23	-	HR	-	OC	Sp/Su/A/W	Yockney et al. (2013)
	-	♀: 260.53–282.97; ♂: 205.97 –271.50	-	HR	-	OC	Su/A	Young (1998)
Weasel		♀: 176.88; ♂: 239.40		HR		PB	-	[unpubl. data, referenced in King and Murphy (2021)]
Feral cat	0.07	188.21	0.05	SECR	CT	OC	A	Nichols (2018)
	0.01†	265.37†	0.004†	SECR	CT	OC	A	Nichols (2018)
	0.224	179.50	-	SECR	CT	OC	A	Nichols and Glen (2015)
	0.05	643	0.01	SECR	CT	PB	A	Glen et al. (2022a)
	0.015	842	0.01	SECR	CT	OC / PB	Su	Glen et al. (2022b)
	-	♀: 220.06; ♂: 317.31	-	HR	-	OC	Sp/Su/A/W	Baker et al. (1989)
	-	♀: 301.54; ♂: 861.85	-	HR	-	OC	Sp/Su	Cruz et al (2014)
	-	♀: 379.09; ♂: 553.43	-	HR	-	OC	A/W/Sp	Cruz et al (2014)
	-	♀: 291.29; ♂: 381.88	-	HR	-	K / PB	-	Dowding (unpubl. data[4])
	-	♀: 156.18; ♂: 159.54	-	HR	-	OC	-	Dowding (1998)
	-	♀: 201.57; ♂: 272.46	-	HR	-	OC / MB	Sp/Su/A/W	Fitzgerald and Karl (1986)
	-	♀: 249.09; ♂: 486.32	-	HR	-	K / PB	Sp/Su/A/W	Gillies et al. (2007)
	-	♀: 469.12; ♂: -	-	HR	-	U / OC	W/Sp/Su	Hansen (2010)
	-	♀: 766.88; ♂: 1051.00	-	HR	-	OC / PB	Sp/Su/A/W	Harper et al. (2007)
	-	♀: 219.67–285.77; ♂: 266.57–356.01	-	HR	-	OC	Sp/Su/A/W	Langham and Porter (1991)
	-	♀: 280.15; ♂: 331.32	-	HR	-	OC	Sp/A	Moller and Alterio (1999)
	-	♀: 363.38; ♂: 316.58	-	HR	-	OC	Sp/Su/A/W	Norbury et al. (1998b)
	-	♀: 580.29; ♂: 611.44	-	HR	-	OC	-	Pierce (1987)
	-	♀: 923.08; ♂: 610.03	-	HR	-	OC / B / E	A/W	Recio et al. (2010)
	-	♀: 487.96; ♂: 822.27	-	HR	-	PB	Sp/Su/W	Recio et al. (2022)
	-	♀: 253.10; ♂: 800.74	-	HR	-	OC	Sp	Recio and Seddon (2013)
	-	♀: 402.17; ♂: 682.23	-	HR	-	OC	Su	Recio and Seddon (2013)
	-	♀: 443.73; ♂: 509.59	-	HR	-	OC	A	Recio and Seddon (2013)
	-	♀: 360.96; ♂: 659.91	-	HR	-	OC	W	Recio and Seddon (2013)
	-	♀: 356.53; ♂: 523.10	0.0117	HR	-	K / PB / OC	Sp/Su/A/W	Strang (2018)
European hedgehog	0.51	119	0.15	SECR	CT	OC	A	Nichols (2018)
	0.55†	105†	0.054†	SECR	CT	OC	A	Nichols (2018)
	-	-	-	SECR	LT	OC	-	van Heezik (pers. comm.)
	-	♀: 32.49–37.80; ♂: 31.48–34.87	-	HR	-	OC	Su	Campbell (1973)
	-	99.58	-	HR	-	OC	Sp/Su/A/W	Brockie (1974)
	-	♀: 39.37–42.24; ♂: 31.82–35.03	-	HR	-	OC / E	Sp/Su/A/W	Parkes (1975)
	-	♀: 46.74; ♂: 71.00	-	HR	-	OC / PB	Sp/Su/A	Gorton (1998)

Table 1. Continued.

Species	min-max of mean g_0	min-max of mean σ (m)	min-max of mean density (animals ha^{-1})	Study type	Detection Method	Habitat	Season	Reference
	-	♀: 152.06; ♂: 223.27	-	HR	-	BR	Sp/Su	Moss (1999)
	-	♀: 77.75; ♂: 141.77	-	HR	-	BR	Su/A	Moss (1999)
	-	♀: - ; ♂: 121.51	-	HR	-	OC / PB	Su/A	Berry (1999)

* Negative exponential detection function.
† Post-control estimate
‡ Estimates from studies conducted in sites where all other pest mammals were absent, either due to pest elimination, or on offshore islands where other pest mammals hadn't invaded, except for occasional incursions
[1]Data from a 2018 unpublished report: "Rakitu Island terrestrial survey January 2018" authored by Russell J, Bodey T, Peace J, Veale A.
[2]Data from a 2003 unpublished report to the Department of Conservation: "Ecology of stoats in a South Island braided river valley", authored by Dowding J & Elliott M.
[3]Data from a 2002 unpublished report to the Animal Health Board: "Home range, movement and activity patterns of female ferrets: testing hypotheses relating to low trapability in winter and spring", authored by Ragg JR.
[4]Data from a 1997 unpublished report: "Feral cats in the Waitakere Ranges, Auckland: trapping and home range data.", authored by Dowding J.

Table 2. Parameter estimates, 95% confidence intervals (CI), p-values and R^2 for best-fit models (according to AIC); either non-linear power law regression using the nls function or linear log-log regression using the lm function of the *stats* package (R Core Team 2021), fitted to g_0 versus σ, and σ versus density, for species with sufficient studies/estimates for model fitting. Note that this analysis does not take into account the possible correlation between the reported values of density and σ introduced by the parameter estimation process. See the Appendix S5 for an analysis of estimation noise.

Species	Model	Predictor	Est.	95% CI	p-value
Possum	$g_0 = a\sigma^b + \epsilon$	a	5.67	−3.13–14.46	0.200
		b	−0.99	−1.44−−0.54	< 0.001
		R^2	0.457		
	$\ln(\sigma) = a + b\ln(\text{Density}) + \epsilon$	a	4.30	4.21–4.40	< 0.001
		b	−0.40	−0.45−−0.35	< 0.001
		R^2	0.888		
Ship rat	$g_0 = a\sigma^b + \epsilon$	a	3.73	1.75–5.71	< 0.001
		b	−1.34	−1.56−−1.12	< 0.001
		R^2	0.655		
	$\ln(\sigma) = a + b\ln(\text{Density}) + \epsilon$	a	3.41	3.24–3.57	< 0.001
		b	−0.17	−0.26−−0.09	< 0.001
		R^2	0.268		
House mouse	$g_0 = a\sigma^b + \epsilon$	a	1.97	−1.04–4.97	0.196
		b	−0.93	−1.52−−0.34	0.002
		R^2	0.143		
	$\ln(\sigma) = a + b\ln(\text{Density}) + \epsilon$	a	3.07	2.91–3.23	< 0.001
		b	−0.08	−0.14−−0.03	< 0.003
		R^2	0.105		

Results

Our literature search yielded 43 New Zealand studies that estimated spatial detectability parameters for the selected key pest species, resulting in 277 g_0 estimates and 265 σ estimates. An additional 63 studies provided a further 189 estimates of home-range size which we converted to σ. A full list of studies and their attributes is provided in Appendix S1 in Supplementary Material.

Table 1 summarises the ranges of mean estimates for g_0, σ, and density reported in each study for the ten pest species, along with the detection method, habitat type, and season. Most SECR studies were conducted for house mice ($n = 13$ studies), possums ($n = 10$) and ship rats ($n = 9$), while other species had four or fewer studies. Home-range size studies were most commonly conducted on possums ($n = 19$), feral cats ($n = 16$), ferrets ($n = 12$), stoats ($n = 10$) and ship rats ($n = 10$). Norway rats, kiore, and weasels were the least studied species, with only three SECR studies for kiore (none for Norway rats and weasels), four home-range studies for Norway rats, and one home-range study for kiore and weasels. Over all studies and species, the vast majority of detectability parameters were reported for live traps (273 g_0 estimates and 262 σ estimates), though device models, spacings, and baits/lures varied widely. We found five SECR studies reporting g_0 and σ for camera traps (for cats and hedgehogs), two for hair-snag tubes (stoats), and one reporting g_0 for bait stations, snap trap tunnels and tracking tunnels (ship rats). SECR studies were conducted in open country (dryland or modified/agricultural grassland, see Appendix S7, $n = 15$), alpine grassland ($n = 2$), urban environments ($n = 3$), and in five forest classes (podocarp-broadleaved forest $n = 14$, beech $n = 7$, mixed beech-podocarp-broadleaved $n = 10$, kauri $n = 1$, and exotic $n = 3$), but none in wetland habitats.

Brushtail possum (*Trichosurus vulpecula*)

Our search yielded ten published SECR studies of possum detection probabilities, reporting 53 estimates of g_0 and σ for live traps. Extracted mean estimates of g_0 ranged from 0.03 to 0.35; mean σ estimates ranged from 24.55 to 155.00 m, and mean density estimates from 0.079 to 15.91 possums ha^{-1} (Table 1). We found significant relationships between g_0 and σ and between density and σ (Table 2; Fig. 1), with higher densities occurring in February–May and lowest densities in September–October (Cowan & Glen 2021). However, there was high variability in g_0 for low values of σ. A further 19 studies reported 46 estimates of possum home-range size which we converted to σ ranging from 16.28 to 214.48 m.

Possum detectability and home range size are known to be highly dependent on habitat type and on the interannual variation in fruit abundance. For example, the highest estimate of $g_0 = 0.35$ was for wire mesh trapping during winter in mixed beech-podocarp-broadleaved forest where the estimated average density was 10.0 possums ha^{-1} and $\sigma = 25.3$ metres (Efford & Cowan 2004). In the following winter, g_0 decreased to 0.13 and possum density increased to 14.0 possums ha^{-1}
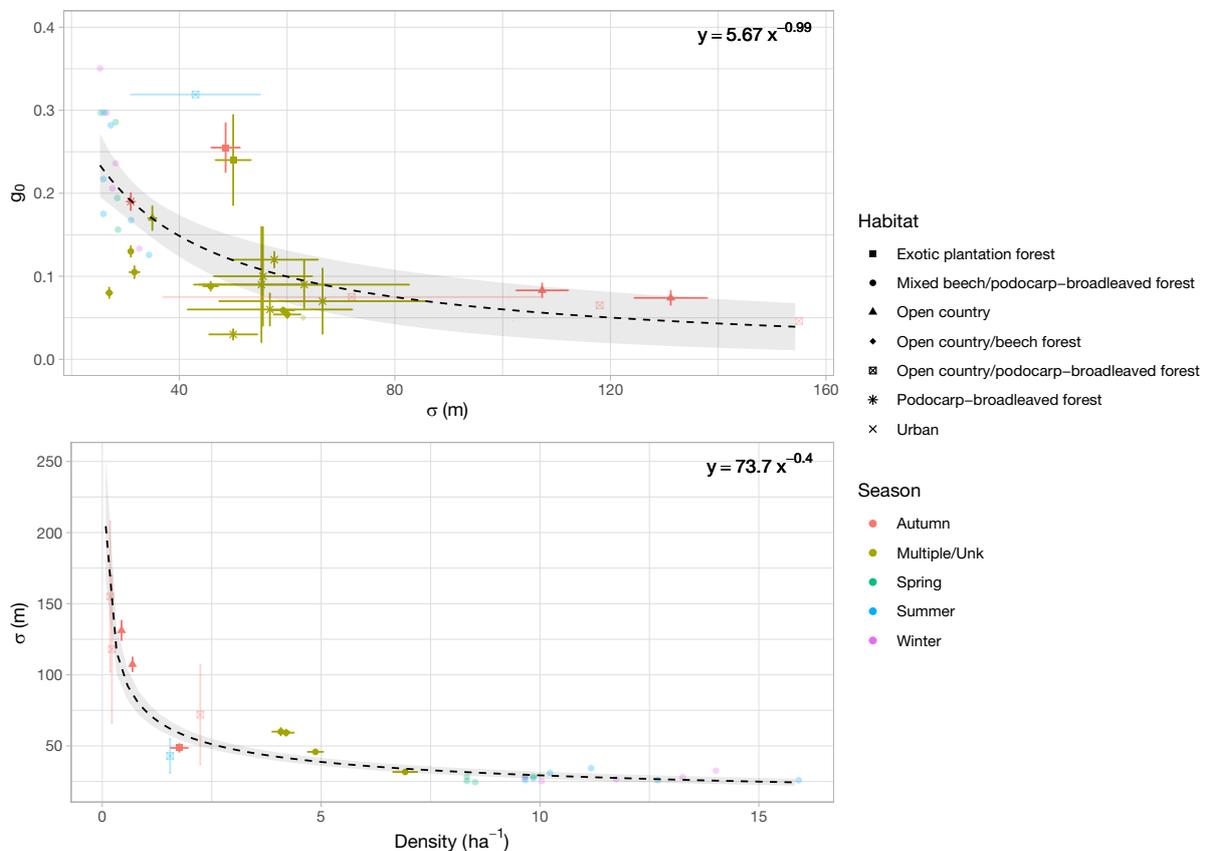
Figure 1. Estimates of g_0 versus σ (top) and σ versus density (bottom) for possums, with associated error bars. The error bars were calculated as ê ± SE, with ê being the mean reported estimate and SE being the associated standard error (where reported). Datapoints that didn't have a reported standard error in both dimensions are displayed with lower opacity. Data are labelled for dominant habitat type and season, and overlaid with regression lines (dashed, equations in top right corners; Table 2) and 95% confidence intervals (grey bands) resulting from the analysis presented in Table 2.
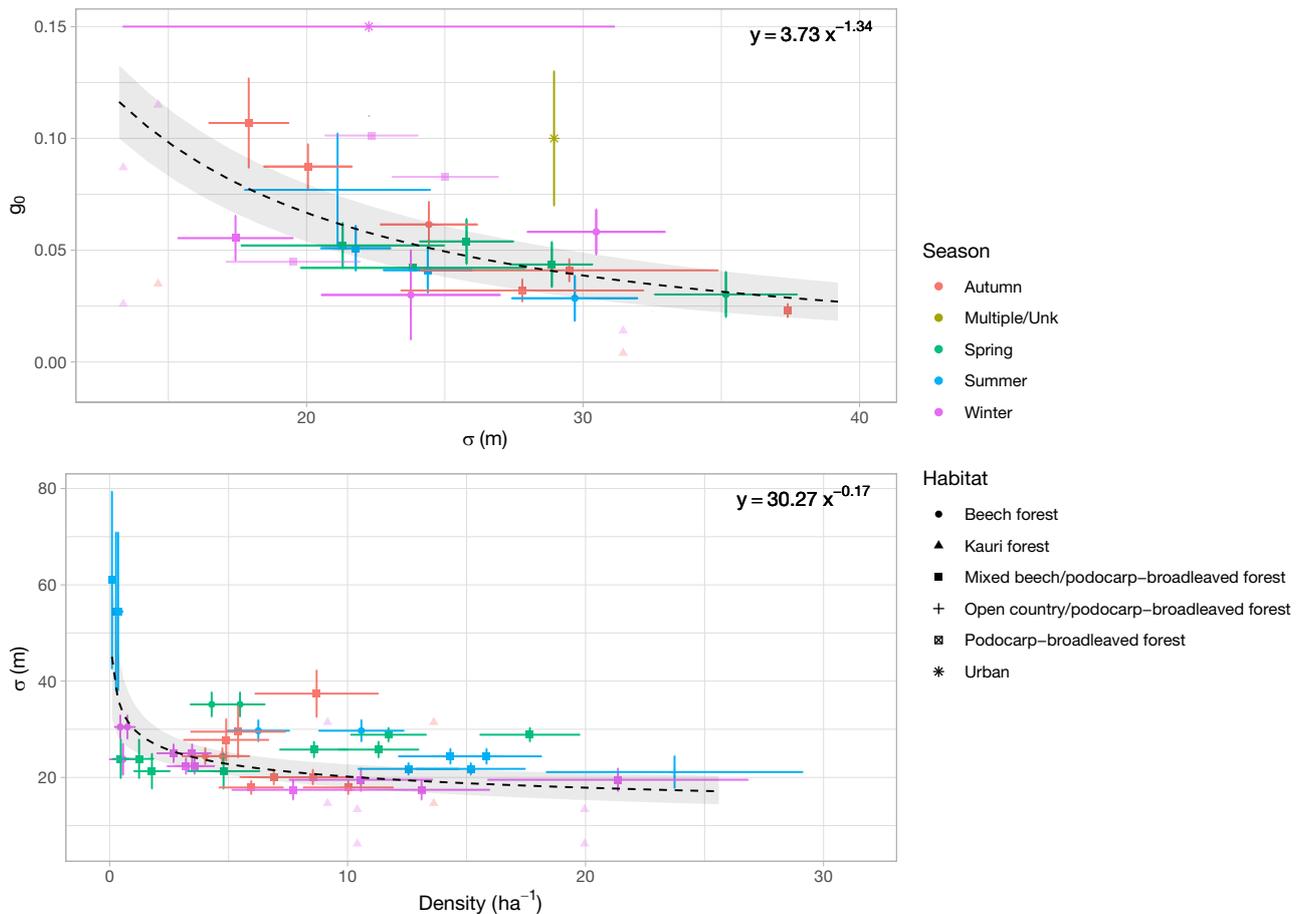
Figure 2. Estimates of g_0 versus σ (top) and σ versus density (bottom) for ship rats, with associated error bars. The error bars were calculated as $\hat{e} \pm SE$, with $\hat{e}$ being the mean reported estimate and SE being the associated standard error (where reported). Datapoints that didn't have a reported standard error in both dimensions are displayed with lower opacity. Data are labelled for dominant habitat type and season, and overlaid with regression lines (dashed, equations in top right corners; Table 2) and 95% confidence intervals (grey bands) resulting from the analysis presented in Table 2.

with $\sigma = 32.6$ metres; this inter-annual variation was possibly due to possums ranging further afield to exploit food resources during heavy fruiting of *Nothofagus truncata* and *Elaeocarpus dentatus* tree species in that year. The studies we reviewed were conducted in a range of habitats spanning four forest classes, open country, and an urban environment (Table 1; Fig. 1). However, not all habitats had been surveyed in all seasons so we were unable to quantify the relative effect of seasonality and habitat on density or σ. Appendices S2–S3 provide a visual representation of these effects, for species with enough data collected in a single season. The latter showed some differences between mean σ across seasons with the autumn measurements being significantly higher (F = 9.497, p = 0.0001) than the other three (Appendices S1–S2).

Possum home range size is generally larger for males than females, and for older animals. Averaging over home-range size studies, the mean σ value was found to be larger for male possums than for females (Appendix S1), however this difference was not statistically significant ($t_{(df = 38)} = 1.150$, p = 0.257).

Rodents

Ship rat (*Rattus rattus*)

We found seven SECR studies and one unpublished capture-recapture dataset (see Appendix S4) of ship rat detectability, reporting 90 estimates of g_0 and 85 estimates of σ for live traps in four forest classes (including mast years and inter-mast years for beech or mixed beech-podocarp-broadleaved forest), and for tracking tunnels, bait stations, and snap-trap tunnels in kauri forest. One further study performed Bayesian inferential modelling of kill-trap capture data to estimate two values of g_0 and σ. For the five SECR studies that used a half-normal detection function, extracted estimates for g_0 ranged between 0.004 and 0.47, σ between 6.22 and 37.40 m, and density between 0.45 and 21.36 rats ha^{-1} (Table 1). Generally, home range size is inversely related to density (Nathan 2016; Innes & Russell 2021). Indeed, we found some evidence of weak inverse relationships between g_0 and σ and between density and σ (Table 2; Fig. 2).

Ship rats exhibit strong exploratory behaviour within their home-range but can be neophobic (i.e. avoid strange objects in familiar environments such as traps and baits), which could result in lower interaction probabilities and lower g_0 (Innes & Russell 2021). In a comprehensive study of ship rat detectability, Nathan (2016) showed that the probability of ship rat interaction varies by device type, with highest detectabilities for bait stations ($g_0 = 0.29$) and tracking tunnels ($g_0 = 0.27$) and lowest for snap trap tunnels ($g_0 = 0.01$). At low population

densities, consistent individual variation in behaviour is also likely to affect detectability (Innes & Russell 2021).

A further 10 studies reported 16 home-range size estimates, which we converted to σ, for four forest classes and an urban habitat. Estimates of σ ranged from 5.61 m in urban environment to 70.72 m in masting beech forest. Estimates of σ from the single study in urban gullies were at the lower end of this range, with $\sigma = 9.7$ (SE = 1.25) m in spring for male ship rats compared to $\sigma = 10.4$ (SE = 0.55) m for females (Fitzgerald & Innes 2017). Generally, home range size is known to be larger for male ship rats than females (Innes & Russell 2021). Three of the 10 studies found approximately similar home-range sizes for male and females in winter, but an increase in size for males in the breeding season (Dowding & Murphy 1994; Hooker & Innes 1995; Pryde et al. 2005). Averaging over all SECR and home-range studies we found higher mean σ estimates for males than females (Appendix S1), though this difference was not statistically significant ($t_{(df = 14)} = 1.83$, p = 0.09). Nathan (2016) reported that σ estimates were consistently higher for males compared to females, while g_0 estimates were correspondingly higher for females than males, which is expected given the inverse relationship between g_0 and σ.

Ship rat populations show seasonal and annual variation in density due to seasonal breeding, as shown in the summary of density estimates in Table 1. Averaging over all SECR and home-range studies we found a non-significant difference (F = 1.301, p = 0.283) between mean σ for studies carried out over a single season (Appendices S1–S2). Other studies have found some of the lowest densities occurring in spring-early summer, and highest densities in autumn (Innes & Russell 2021). In colder, beech forest environments, ship rat population dynamics are typically irruptive, while warmer, podocarp-broadleaved forests can sustain continuously high densities (Walker et al. 2019). However, densities of other predator species, such as stoats and feral cats, can also affect ship rat populations.

Norway rat (R. norvegicus)
We found no SECR studies reporting g_0 estimates for Norway rats. Four studies of home- range sizes provided estimates of σ; one in open country, one in an urban environment, and two in podocarp-broadleaved forest on offshore islands (Table 1). Mean σ estimates ranged from 14.04 to 55.36 m. Norway rats are distributed predominantly in New Zealand's urban and farmland habitats, and around waterways and wetlands. They exhibit a strong exploratory drive but are also highly neophobic. Exploratory movement during colonisation of new areas differs from movement in established populations; the area covered by colonising individuals increases most rapidly in the first week after introduction and is larger than home-range sizes in established high density populations (Russell et al. 2010). Population densities vary seasonally, tending to be lower in spring and peaking in autumn to early winter, when many juveniles are present. With abundant food supply, vegetation cover, and in the absence of predators, populations can reach very high densities. Studies of farmland in the United Kingdom found home-range areas were generally larger for males than females and varied with availability of food and vegetation cover offering protection from predators (Russell & Innes 2021). Smaller home-ranges have been observed in areas with rich food supplies relative to areas with low food supply (Hardy & Taylor 1979).

Kiore (*Pacific rat,* R. exulans)
We found three SECR studies of kiore detectability, reporting seven estimates of g_0 and σ for live traps in podocarp broadleaved forest and open country. Extracted estimates for g_0 ranged between 0.007 and 0.73, σ between 13.99 and 21.12 m, and density between 1.1 and 4.1 rats ha^{-1} (Table 1). Kiore population densities and home-range sizes follow strong seasonal trends. The rodents tend to occupy small home-range areas in winter but much larger areas in spring, especially for males, and in summer when kiore move from forested areas to grassland during seeding. In pure forest habitats densities are generally lower and more stable, except following mast events. Kiore densities are also strongly impacted by densities of other predators and are higher in the absence of feral cats, stoats, and other rodents. Home range sizes tend to be larger for males than females, and for adults compared to juveniles (Wilmshurst & Ruscoe 2021). We found one study reporting home-range sizes for kiore in winter–spring, in a high-density population living in open country on Kāpiti Island (Bramley 2014); mean estimates of σ were 8.62 m (ranging from 4.0 to 12.6 m, $n = 6$) for males and 9.77 m (ranging from 5.2 to 12.8 m, $n = 5$) for females.

House mouse (Mus musculus)
Ten SECR studies estimated density and associated detection parameters for live trapping of house mice in open country, alpine grassland, and three forest classes (podocarp-broadleaved, beech and mixed beech). We found three further SECR studies that did not report either detection parameter, only density (Table 1). In a comparison of three device types, Reynolds (2015) estimated highest probabilities of interaction, given encounter, for snap traps (ranging from 0.56–0.59 for open country habitat, podocarp-broadleaved forest, and exotic plantation forest), followed by tracking tunnels (0.51–0.54) and bait stations (0.43–0.46).

House mouse populations exhibit strong seasonal and interannual variability in density, as shown in Appendix S3. Higher densities are generally found in environments with dense ground cover. In beech or mixed beech forest (or forest with masting rimu), and in alpine grasslands, population dynamics tend to be highly irruptive. Following sporadic masting events in certain years, pulses of highly abundant food resource can drive extremely high mouse densities between autumn and winter, or even into spring-summer (King 1983; Wilson & Lee 2010). As food supply decays, populations undergo a crash to low densities and predation by stoats may also be affecting populations during this period. In other habitats, population densities generally peak between summer and autumn, then decrease in winter, in response to seasonal variations in food supply (Murphy & Nathan 2021). The limited data available did not allow separation of masting and non-masting years in our analysis; however, Appendices S2–S3 provide a visual representation of the effect of season on both σ and density. Distributions of house mice and ship rats are generally spatially reciprocal in New Zealand's forests (Walker et al. 2019), and mice tend to be more active if not abundant at low ship rat densities which likely affects the probability of encountering surveillance devices (Murphy & Nathan 2021). Meso-predator and competitor release of mice often occurs in areas where other pest species have been eradicated (Wilson et al. 2018). House mice can maintain individual or group territories and home-range size is likely related to food supply, and to behavioural or social factors (Murphy & Nathan 2021).

In accordance with these trends, house mice showed the greatest variability in g_0 and population density, out of all ten species reviewed. Over all seasons and habitat types combined,
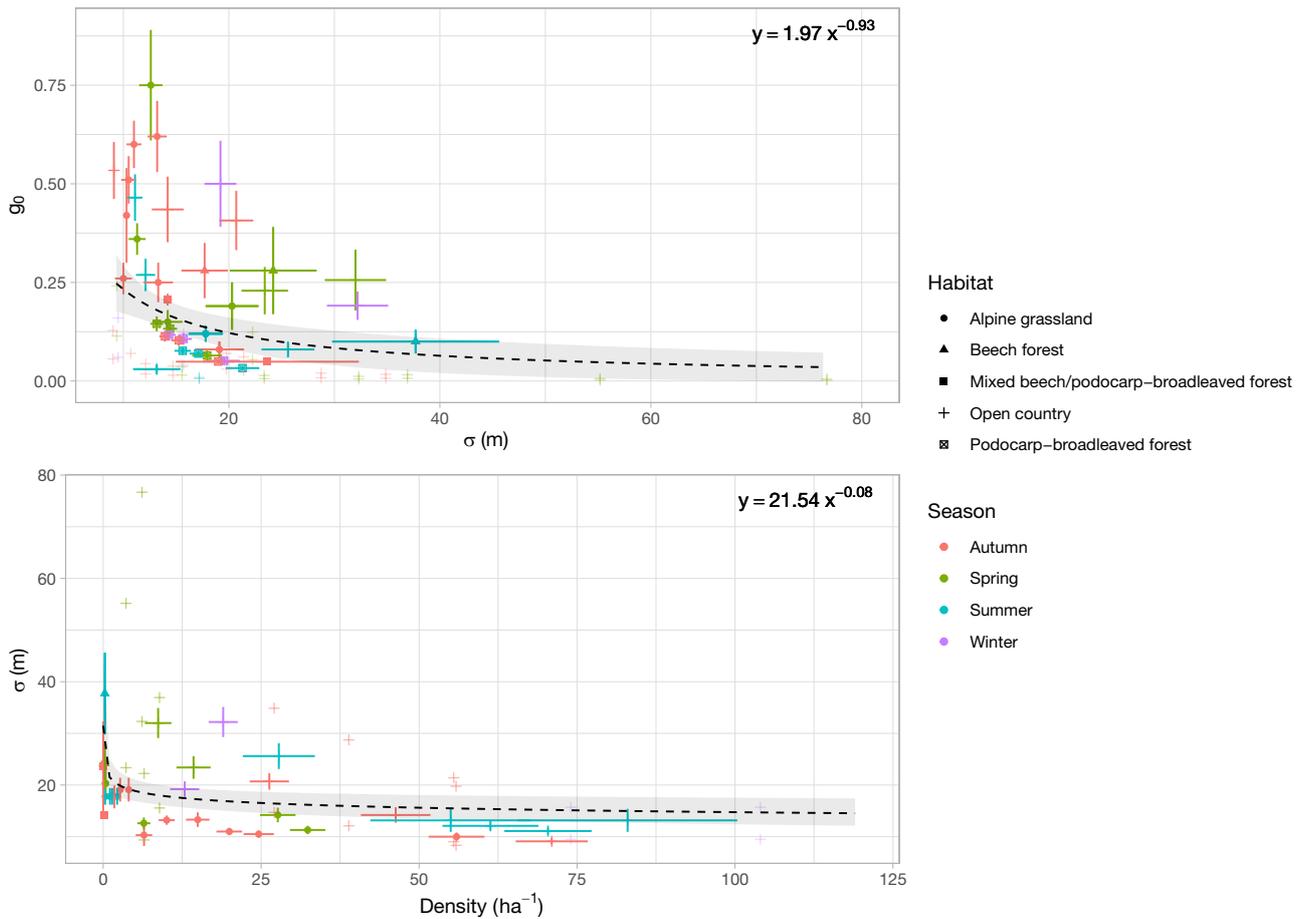
Figure 3. Estimates of g_0 versus σ (top) and σ versus density (bottom) for house mice, with associated error bars. The error bars were calculated as $\hat{e} \pm SE$, with $\hat{e}$ being the mean reported estimate and SE being the associated standard error (where reported). Datapoints that didn't have a reported standard error in both dimensions are displayed with lower opacity. Data are labelled for dominant habitat type and season, and overlaid with regression lines (dashed, equations in top right corners; Table 2) and 95% confidence intervals (grey bands) resulting from the analysis presented in Table 2.

estimates for g_0 (92 estimates) ranged from 0.002 to 0.75, σ (100 estimates) between 3.75 and 76.68 m, and densities (97 estimates) between 0.01 mice ha^{-1} and 156.70 mice ha^{-1} (Table 1). We found a significant inverse relationship between g_0 and σ and between density and σ (Table 2; Fig. 3). Two further studies reported 8 estimates of home-range size and density for house mice; corresponding σ estimates ranged from 11.2 to 19.4 m (at densities of 0.54 to 2.93 mice ha^{-1}) in a mixed beech- podocarp-broadleaved forest, and from 11.0 to 12.2 m (at 13.03 mice ha^{-1}) in open country on an offshore island. We also found a difference between mean σ for studies carried out over a single season, with measurements taken in spring being significantly higher (F = 4.919, p = 0.003) than those in the other seasons (Appendices S1–S2).

Mustelids

Stoat (Mustela erminea)

Three SECR studies reported stoat detectability for live traps in beech forest and alpine grassland, and for hair-snagging tunnels in beech and mixed beech forest. One further study performed Bayesian inferential modelling of kill-trap capture data to estimate g_0 and σ. Six estimates of g_0 were obtained using a half-normal function and were generally low, ranging from 0.016 to 0.077. Corresponding estimates of σ ranged between

255 and 891 m, and density between 0.000 and 0.016 stoats ha^{-1}. We found no correlation (at the $\alpha = 0.05$ significance level) between g_0 and σ, or between density and σ; however, the small sample size for this species means there was likely insufficient statistical power to detect any relationship.

Stoat trappability generally decreases over sequential recaptures. In a high density stoat population in a post-seedfall year in beech forest, King et al. (2003) reported a (non-spatial) probability of first capture (0.17 [95% CI 0.12–0.24]) that did not depend on age or sex. After the first capture, there was evidence of a reduction in trappability for both adults and young, likely due to trap avoidance. Young-of-the-year female stoats had the lowest recapture probability (0.07 [0.04–0.11], approximately half of probability of first capture), while young-of-the-year males were less likely to develop trap shyness. Activity of females reduces during the spring breeding season, which also has implications for the probability of encounter (King & Veale 2021).

Stoat home range size also depends strongly on density and distribution of prey. In masting beech forest, high stoat densities occur during the summer following a mast year, due to high prey abundance and a delayed breeding season (King 1983; White & King 2006). During these periods, stoats occupy smaller home ranges (Murphy & Dowding 1995); however,

associated estimates of g_0 remain a knowledge gap. Male stoats typically occupy larger home ranges than females and during spring may travel large distances in search of mates (King & Veale 2021). We found ten studies reporting 30 home-range size estimates for stoats, for habitats of open country, braided riverbed, alpine grassland, and four forest classes. Mean σ estimates ranged from 68 to 407 m (average σ = 233 m) and were significantly higher ($t_{(df = 26)}$ = 2.5, p = 0.019) for males than females (Appendix S1). We also found a non-significant difference (F = 0.772, p = 0.526) between mean σ for studies carried out over a single season (Appendices S1–S2).

Ferret (Mustela putorius furo)

We found only one SECR study reporting 11 detectability estimates for ferrets, using live trapping in open country in summer-autumn. Estimates for g_0 ranged between 0.014 and 0.216, σ between 305 and 791 m, and densities between 0.008–0.069 ferrets ha^{-1}. Efford and Norbury (2005) reported an inverse relationship between g_0 and σ, but found no correlation between g_0 and density.

Ferrets are known to have seasonal patterns of trappability with highest capture rates in summer and autumn and lowest in late winter and spring, especially for females during the spring breeding season (King et al. 2009; NPCA 2009). However, this effect varies between sites and years. Seasonally low detectabilities do not seem to be explained by a preference for live prey, reduced activity, or reduced home-range size, but could be attributed to seasonal neophobic behaviour (Byrom et al. 2015). We would therefore expect estimates of g_0 to be lower in winter-spring, although no SECR studies have been conducted in these seasons to date. Further, King et al. (2009) found clear evidence of individual variation in ferret interactions with traps and bait dispensers on pastoral farmland, likely related to sex, activity, and prior experience. Some ferrets demonstrated active avoidance of devices, or alternatively, avoidance of the infra-red illumination emitted by cameras used for field observations.

Ferret home-range sizes tend to increase when food becomes very scarce and are larger for males than females. Population densities are dependent on season, prey (e.g. rabbit) abundance and elevation, and may be inversely related to home-range size. Highest densities are found in open country, wetlands, river valleys and forest edges, and generally peak between late summer and early winter (Garvey & Byrom 2021). A previous review by Byrom et al. (2015) found 12 studies reporting home-range sizes for ferrets in open country, which we converted to 22 estimates for σ, with study means ranging from 154.5 to 634.8 m (Table 1). For these studies, mean estimates of σ were larger for males than females (Appendix S1), although this difference was not statistically significant (W = 88, p = 0.076). Each study presented in this review spanned multiple seasons, therefore we cannot comment on the effect of season on home range size using this dataset.

Weasel (Mustela nivalis)

There have been no New Zealand SECR studies reporting detectability for weasels. One unpublished study measured home-range areas for four weasels in podocarp-broadleaved forest when mouse abundance was low (E. Murphy, DOC, pers. comm.; referenced in King & Murphy 2021), corresponding to an average σ = 239.4 (SE = 27.84) m for males (n = 3) and lower σ = 176.9 m for females (n = 1). Studies in other countries have shown that weasels expand their home-ranges during periods of low prey availability, such as during rodent

population crashes (Jędrzejewski et al. 1995). Home-range areas are therefore expected to be larger in New Zealand compared to Europe due to small rodents being typically scarce. Sex ratios of trapped weasels are biased towards males; this is likely due to their larger home-ranges and higher chance of encountering a trap, differences in activity and behaviour, and lighter body weights of females making them less likely to trigger a kill-trap. Population densities can undergo rapid fluctuations in New Zealand owing to their unstable distribution and changes in abundance of small rodent prey, for example during mast events (King & Murphy 2021).

Feral cat (Felis catus)

We found four SECR studies for feral cats in New Zealand, all conducted using camera traps in either open country or podocarp-broadleaved forest habitat. Mean g_0 ranged between 0.015–0.224, σ = 188.21–842.00 m and density 0.01–0.05 cats ha^{-1}. Following cat removal, density decreased to 0.004 (0.001–0.240) cats ha^{-1}, corresponding to a decreased mean g_0 = 0.013 (0.000–0.121) and increased σ = 265.4 (52.01–623.29) m.

Home-range size of male cats is likely determined by the density and distribution of females, related in turn to prey abundance. Home-range size can vary seasonally, be highly variable among individuals, and may be inversely related to prey abundance and cat population density (Gillies & van Heezik 2021). We extracted 41 σ estimates, with means ranging from 156.2 m to 1051 m from a further 16 studies of home-range size in open-country, five forest classes, and an urban habitat. For these studies, mean estimates of σ were significantly larger (W = 125, p = 0.026) for males than females (Appendix S1). The limited number of studies performed on feral cats in a single season did not allow analysis of the effect of season on home range size.

European hedgehog (Erinaceus europaeus)

We found one SECR study on European hedgehogs in pastoral farmland, using camera traps in autumn. Following pest control, g_0 increased from 0.51 (95% CI 0.31–0.77) to 0.55 (0.25–0.90), σ decreased from 119 (74.0–197.0) m to 105 (51.2–118.0) m estimates, and density from 0.15 (0.04–0.26) hedgehogs ha^{-1} to 0.054 (0.01–0.15) hedgehogs ha^{-1}. One further unpublished mark-recapture study had been conducted in high-producing exotic grassland but results from a SECR analysis of these data were not yet available (Y van Heezik, University of Otago, pers. comm.). Six studies on hedgehog home-range areas in open country, braided riverbed, and exotic or podocarp-broadleaved forest provided 16 estimates for mean σ, ranging from 31.5 to 223.3 m, with an average σ = 76.17 (SE = 14.21, n = 16) m. Home-range areas of male hedgehogs are known to be generally larger (2–3 times) than females (Jones 2021). Across all studies, adult males had a larger but not statistically different average σ (Appendix S1), ranging from 20.60 to 323.13 m, compared to σ for females, which ranged from 23.03 to 197.83 m. Moss (1999) found that both sexes expand their home-ranges in spring-summer, corresponding to a mean σ = 187.66 (SE = 35.61, n = 2) m, compared to late summer-autumn where mean σ = 109.76 (SE = 32.01, n = 2) m.

Discussion

Reliable estimates of spatial detection parameters for invasive mammalian pest species are important for informing

conservation and pest management in New Zealand. In particular, spatial detection parameters inform design and planning of optimal surveillance systems and improve unbiased estimation of pest density or eradication probability to determine success of control operations. Our comprehensive review of SECR and home-range size studies, collates all g_0 and σ estimates reported to date for detectability of New Zealand's key mammalian pests. We provide an easily accessible reference for parameterising future models, and for assessing performance of current pest surveillance techniques under a range of biological, environmental, and surveillance conditions.

We quantified strong inverse relationships between g_0 and σ, and between σ and density, for possums, ship rats, and house mice. Further studies are required to assess relationships between these parameters for other species. Ship rats in particular remain a priority given they are a key target for control and eradication on the New Zealand mainland and are especially challenging to control to low abundance for sustained periods of time and at large spatial scales. The dependencies between g_0 and σ, and between density and σ mean that care must be taken when interpreting or re-applying the estimates collated in this review. When using this review to inform model priors, we recommend that estimates are always considered as dependent g_0-σ pairs and never as independent parameters. Managers and modellers should first consider the population densities, ecological conditions, habitat types, and (where practicable) seasons particular to their target species and sites, then extract the g_0-σ estimate pairs that are most representative of those conditions. Alternatively, we recommend using a weak prior distribution from either Table 1, Appendix S7, or the inverse relationship curves in Figs 1–3. However, the reader should note that the regression analysis presented was performed on SECR estimates of detection parameters, not on true values.

The SECR estimation process can itself introduce an artificial correlation between estimates, which could contribute to the negative relationship observed. We carried out a post-hoc analysis (Appendices S5–S6) which demonstrates that it is unlikely that the observed relationships for possums, ship rats, and house mice can be explained solely by noise in the estimation process. Similar relationships have been observed between density and sigma in some rodent species including invasive house mouse populations in Australia (Van de Weyer 2022) and for possums (Anderson et al. 2022b). It is possible that the observed relationships are a combination of a true relationship, plus correlated noise introduced by the estimation process.

In general, we found large variability in estimates of g_0 and σ, within and between species. Studies that measure the probability of encounter independently from the probability of interaction (given an encounter), such as cameras, are needed to unravel the mechanisms by which different biological and environmental factors affect the overall probability of detection. For instance, factors such as age may affect the probability of detection either via variation in home-range size (i.e. probability of encounter and σ) or via differences in probability of interaction (e.g. age-related variation in boldness) or both. Season and habitat are important factors affecting population density and probability of encounter, related primarily to the breeding biology of pest species and abundance of food resource. For example, our analysis suggests that possums have a higher mean home-range size in autumn than all other seasons (Appendix S2). Food supply is likely a key factor affecting detectability for all rodent species, as a driver of population abundance and home-range size, but also indirectly

determining the probability of interaction with poison baits and devices that use food lures (Weerakoon & Banks 2011). For most pest species, σ is also influenced by sex, with males generally occupying larger home-ranges than females.

Neophobic behaviour towards new devices is a factor to consider as it might have an effect on the probability of interaction, and therefore g_0, for ship rats (Cowan & Barnett 1975) and Norway rats (Inglis et al. 1996; Byers et al. 2019), and possibly for ferrets exhibiting seasonal neophobic behaviour (Byrom et al. 2015). Consistent individual differences in behaviour will also affect detection probability; ship rats, for example, exhibit high variation in individual exploratory behaviour (Cooper et al. 2018). The impacts of individual variation become especially important at low population densities such as those arising during eradication programmes (Innes & Russell 2021; Vattiato et al. 2021). The degree to which behaviour, like neophobia, may affect detection probability can easily be assessed in the SECR modelling framework, using an Mb model (Otis et al. 1978) to allow the capture probability parameter to change after first capture.

The issue of detectability is further complicated by competitive or predatory interactions with other pest species. Changes in abundance of target species due to control operations are often associated with subsequent changes in densities, home-range sizes, or behaviour of other pest species. For instance, on the New Zealand mainland there is a strong reciprocal relationship between distributions of ship rats and mice (Bridgman et al. 2018). Following possum control in podocarp-broadleaved forest, ship rat abundance can also increase due to decreased competition for fruit and seeds (Sweetapple & Nugent 2007; Ruscoe et al. 2011). Detection probability may be reduced, at least at certain times, for species that exhibit behavioural avoidance in the presence of predators. In contrast, the threat of predators can be exploited to increase detection probability in mesopredators; for instance, adding ferret odor (an apex predator) to conventional rabbit meat lures increases detection rates for stoats and hedgehogs (mesopredators) (Garvey et al. 2017).

In general, there was insufficient representation and replication of studies to draw reliable conclusions about the relative effects of different habitats, seasons, or other covariates on detection parameters and density. Sample sizes were generally too small and heterogeneous to perform multiple regression analyses on estimates of g_0 and σ, or to perform matching when comparing group means for different sexes and seasons. Our group mean estimates of g_0 and σ for each sex and season may therefore be biased where there is uneven representation of other confounding factors between these comparison groups. Nonetheless, our collated estimates are a comprehensive stocktake from which to build and are useful for guiding future research priorities.

While commonly used forms of the detection function, such as the half-normal, assume animals spend most of their time around a central den in the middle of their home-range, some animals might behave differently. For example, they could display a more patchy space use and travel across several dens scattered throughout their home-range. Efford (2004) highlighted how population density estimates using g_0 and σ are likely to be affected by non-circular home-ranges and individual variation in g_0. However, the SECR density estimator has been shown to be largely robust to non-circularity when detectors are spread in two dimensions (Efford 2019).

Our literature search also yielded several occupancy modelling studies (such as MacKenzie et al. 2002). This

alternative approach employs a "probability of detecting a species given presence at a site", i.e. a probability of at least one animal being present (Efford & Dawson 2012). This parameter is not spatially explicit and the concept of detection probability in occupancy models relates to the occupancy-abundance relationship (Steenweg et al. 2018). While these studies were not included in our collated dataset, they did offer general insights into detectability trends. For instance, occupancy modelling by Christie et al. (2014) showed that, on average, increased rainfall was associated with a higher probability of detecting rats in tracking tunnels. More generally, weather can affect detection probability due to changes in animal behaviour. Weather conditions were rarely described in the studies we reviewed, however certain surveillance methods, such as tracking tunnel monitoring, require surveys to be conducted on fair weather nights as standard operating procedure.

Our review revealed some important knowledge gaps. Of greatest note was the sparsity of studies reporting g_0 and σ for pest populations at extremely low densities, such as those achieved by control operations aimed at eradication. In particular, field measurement of detectability and movement of stoats, possums and especially ship rats at near-zero densities remains a critical research need, given these species are targets for eradication by Predator Free 2050 (New Zealand Government 2020). In the eradication context, there are two main situations in which extremely low densities occur that warrant further investigation. First, when a resident pest survives an eradication attempt but its neighbours in the population have been removed; and second, when a pest reinvades an eradicated area from an adjacent area. There have been four experimental studies for the latter context, involving release of individuals into a pest-free area: one for ship rats in a pest-fenced ecosanctuary (Innes et al. 2011), two for Norway rats (Russell et al. 2008, 2010), and one for house mice (Nathan et al. 2015) on small offshore islands. Another study by Nathan et al. (2020) reported movements of a ship rat mother and litter released into an area with very low rat density following treatment with 1080 toxin, and Carpenter et al. (2023a) recorded movements of reinvading ship rats on the edge of a 1080 zone. In these contexts, behaviour can differ dramatically from that of higher density populations, with large line movements of over 1000 m documented for ship rats (Innes et al. 2011; Carpenter et al. 2023a). Sample sizes were small in these studies as such approaches generally require animals to be released and monitored one at a time. Replication of detectability studies at near-zero densities and under a range of conditions will be essential for reliable estimation of probability of absence and to achieve successful landscape-scale eradications. We recommend rodent detectability at near-zero density is considered a top priority, followed by possums and stoats, then other pest species.

We identified further knowledge gaps for certain species and habitat combinations. There were no SECR studies (only home-range studies) reporting detectability for feral cats in forest habitats (due to feral cats being perceived as being hard to trap and recapture), none for any species in wetlands, except for one study on possums. In particular, more detectability estimates are needed for Norway rats in urban, open country, and wet habitats where they are primarily found in New Zealand. Nearly all the reviewed studies described detectability for live traps, while camera traps, tracking tunnels, hair-snag tubes, bait stations, and snap trap tunnels have only been assessed in few studies and for a small subset of pest species. Advances in camera technology, along with a reduction in cost, mean

that camera traps are becoming an increasingly popular detection tool globally (Green et al. 2020). These tools are proving more promising for detecting species that currently have low detectability using other surveillance methods, particularly stoats, ferrets, and feral cats. Obtaining reliable detection parameter estimates for camera traps, for the full suite of invasive pests in a range of habitats and seasons should therefore be another priority for future research.

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Additional information and declarations

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Mean estimates of σ, with associated standard deviations and number of estimates for possums, ship rats, house mice, stoats, ferrets, feral cats, and hedgehogs, pooled over sex and season separately.

Appendix S2. Estimates of σ versus season for (a) possum, (b) ship rats, (c) house mice, and (d) stoats labelled for sex and for studies carried out over a single season

Appendix S3. Estimates of density versus season for (a) possum, (b) ship rats, and (c) house mice labelled for sex and for studies carried out over a single season.

Appendix S4. Spatially-explicit capture-recapture (SECR) analysis of unpublished dataset (Byrom 2008).

Appendix S5. Analysis of detectability parameter estimation noise.

Appendix S6. Comparison of observed and simulated σ-density datasets and corresponding R^2 distribution resulting from model fittings, used to reject the null hypothesis that the true values of σ and density are uncorrelated.

Appendix S7. Complete dataset compiled for this paper, including the filtered dataset used in the analyses presented.

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