

Do high recapture rates indicate representative sampling? The relationship between recapture probability, risk-taking, and personality

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ABSTRACT

Context. Monitoring programs provide valuable information on wildlife populations, thereby underpinning strategies for conservation and control. For threatened species, where every animal represents a substantial portion of the population, representative sampling is vital. One fundamental challenge during sampling is understanding drivers of survey bias; for instance, behavioural heterogeneity in trap response. Methods such as capture–mark–recapture have long been used to estimate capture and recapture heterogeneity; yet, this method, like many others, is able to gather data only from the trappable and re-trappable portion of the population; a problem that presents a particular challenge for small or vulnerable populations. A greater understanding of why biases arise can result in improved survey methods, more reliable survey data and increased modelling accuracy. **Aims.** We focus on an endangered species with unusually high recapture probabilities (0.78–0.92), namely, the mountain pygmy-possum (*Burramys parvus*). Specifically, we examine whether, within a single trapping session, a recapture bias exists either as a function of past trapping experience or personality. **Methods.** We tested whether recapture probability differs among cohorts with different capture histories ('known' animals captured during trapping sessions in previous years vs 'new' animals trapped for the first time in this study). We also tested for individual personality, general risk-taking behaviour during foraging, and subsequent links to recapture probability. **Key results.** Recapture probability was significantly affected by cohort. New animals had lower probabilities of recapture and took fewer risks during foraging than did known animals. Although personality did not significantly influence recapture probability, it did influence risk-taking during foraging. **Conclusions.** Despite high recapture probability within the populations, captures were significantly skewed towards a subset of the population, likely being due to different perceptions of risk among individuals. **Implications.** Understanding potential sources of bias during live-capture surveys is the initial step towards modifying and improving surveys to reduce sampling biases and to ensure representative population sampling.

Keywords: *Burramys parvus*, personality, population estimates, recapture probability, risk and reward, risk-taking, survey bias, trapping.

Introduction

Robust and representative population estimates are vital for effective conservation actions, particularly for tracking population changes in endangered species, where every animal may represent a substantial portion of the extant population. Consequently, any bias has considerable implications for accuracy of population estimate and subsequent conservation decisions. For most species, it is impossible to count every individual in a population, and, so, total population size is estimated from capture or count data. For instance, the capture–mark–recapture method (and associated statistical models) often uses live-capture trapping results to estimate population size, survival rates, recruitment, and population growth (e.g. Otis *et al.* 1978; Besbeas *et al.* 2002; Wilson *et al.* 2007).

Recapture is crucial to population estimates and underpins many models used to estimate population parameters. Although algorithms can be used to account for heterogeneity in recapture (and initial capture), a more robust approach may be to understand and accommodate potential biases into the trapping method itself.

Importantly, the act of entering a trap is a decision made by an animal, and so animal behaviour is likely to play a central role in trappability (Garvey *et al.* 2020). Entering traps and other enclosed devices can be perceived as a risky behaviour, with animals responding in a risk-sensitive manner (Johnstone *et al.* 2021a). This risk-sensitive decision can also be influenced by prior trapping experience (Linhart *et al.* 2012; Roche *et al.* 2013; Camacho *et al.* 2017), and whereas some animals are likely to re-enter traps, others may take longer or may not be recaptured (Balph 1968) and can vary on the individual level. Animal personality, consistent, among-individual differences in behaviour (Gosling 2001), can influence risk-sensitive decisions (Carter *et al.* 2010; Cole and Quinn 2014). Traits, including boldness, activity and docility, are associated with life-history traits and individual fitness (see table 1 in Biro and Stamps 2008) and can drive heterogeneity in trappability, skewing population sampling. In some species, increased boldness and activity correlate with ease of capture, whereas extreme shyness can link with active avoidance of traps (Boon *et al.* 2008; Carter *et al.* 2012).

Although capture heterogeneity during surveys is a common occurrence, high recapture rates are often associated with (1) little potential for bias, and (2) robust population estimates with low error (Krebs 1999; O'Brien *et al.* 2005). However, these assumptions have not been properly tested and the potential for behavioural heterogeneity to drive differences in recapture probability has not been explored in the context of high recapture rates.

In this paper, we focus on the Endangered mountain pygmy-possum (*Burrhamys parvus*), a small (40 g) marsupial with reportedly high recapture probability (0.78–0.92; Broome 2001a). The mountain pygmy-possum (hereafter pygmy-possum) is endemic to the alpine and subalpine regions of south-eastern Australia (Happold 1989), and in New South Wales (NSW) it persists in isolated populations in Kosciuszko National Park. Here, we test for potential mechanisms affecting recapture within a single trapping session (i.e. four nights). We first tested whether trap response differs between population cohorts (differing in previous trapping experience). Such differences can arise due to age (Domènech and Senar 1997) or prior experience with traps (Linhart *et al.* 2012). Given that personality can influence individual responses to the perceived risks and rewards associated with traps (Garvey *et al.* 2020; Johnstone *et al.* 2021a), we quantified pygmy-possum personality and tested for any personality effect on trap response.

As an indirect driver of trap response, we also tested whether risk-taking differed between cohorts or was influenced by personality. We quantified the risk-taking behaviour of

trapped and marked individuals that visited feeding stations (i.e. feeders) with different risk–reward treatments. We examined (1) variation among individuals in visit frequency, and (2) behaviour at feeders. We anticipated that visiting and foraging from feeders would present a perceived risk either comparable (risky feeders) or lower (safe feeders) than the perceived risk of entering a trap. We also anticipated that visit frequency would be greater at feeders with high-preference food than at feeders with low-preference food. As personality and experience can influence risk-taking, we also predicted that either factor may link with increased visits or increased foraging at risky feeders.

Materials and methods

Study area and species

This study was conducted in Kosciuszko National Park, NSW, Australia during the 2017 pygmy-possum survey. As part of the National Recovery Plan and Saving Our Species Recovery Project, the NSW Department of Planning, Industry and Environment run annual four-night surveys in November/December across multiple sites. To maximise our sample size, we surveyed subpopulations at two independent sites (8.5 km apart), namely, the first, at Charlotte Pass (3.4 ha, 1740–1765 m), and the second, at Lower Blue Cow (1.78 ha, 1800–1850 m). Both sites are rocky boulder-fields consisting of boulder piles reaching over 2 m deep, periglacial blockstreams, and other boulder formations (Rosengren and Peterson 1989; Broome 2001a). Crevices between boulders provide shelter from larger predators, including introduced cats (*Felis catus*) and foxes (*Vulpes vulpes*), and native raptors (Green and Osborne 1981; Broome *et al.* 2012). No movement between the two sites has been recorded (Broome 2001a) and, during the breeding season, when surveys are conducted, animals are reasonably sedentary (Broome 2001a). Young are born in November/December and are trappable by 12 months (Broome 2001b). With a life-span of roughly 3 years, individuals are trappable over multiple surveys, although males aged five and females reaching 11 years have been recorded (Broome 2001a).

Factors affecting recapture probability

To test whether trap response differed between the population cohorts or was influenced by individual personality, we surveyed sites over four consecutive nights (one annual monitoring session). Elliott traps (Charlotte Pass = 100, Lower Blue Cow = 35) baited with walnuts were set ~10 m apart in crevices between boulders. For each capture, we recorded existing microchip IDs of known animals (trapped in previous years) and microchipped all new animals (trapped for the first time in this session). Animals were sexed and weighed, but we did not estimate age as it is

difficult to differentiate between subadults (1 year old) and mature (>2 years) animals (Broome 2001a). Individuals were also uniquely fur clipped (Charlotte Pass = 25 of 38, Lower Blue Cow = 15 of 15) for later identification on camera. Because the number of clear, unique marks is limited, given the size of a pygmy-possum (40 g), at Charlotte Pass, 13 randomly selected individuals were given a common mark to identify them as a trapped animal on camera (Supplementary material Fig. S1). All Lower Blue Cow captures were uniquely marked.

Quantifying personality

At capture we also tested for personality by using the immobility test (Martin and Réale 2008). Individuals were tested once per capture, with a maximum of three tests per individual. Once the pygmy-possum was in a handling bag, the bag was suspended, and we calculated the cumulative time an animal spent immobile in 60 s. Limited access to this threatened species meant that all repeat tests were conducted within a four-night span. However, in other marsupials and small mammals, personality quantified in the short term has been consistent with traits quantified over weeks (Mella et al. 2016), or even months (Wat et al. 2020; Johnstone et al. 2021b).

Factors affecting risk-taking at feeders

To test whether risk-taking differed between cohorts or was influenced by personality, we ran an experimental feeding trial (1–2 days post-trapping) by using novel feeders

(constructed of chicken-wire; holes 10 mm × 10 mm, height 150 mm, maximum width 120 mm; Fig. S2). We presented four feeder treatments, differing in risk (two levels: exposed, sheltered) and reward (two levels: high-preference, low-preference). Eight replicates of each treatment (total number of feeders = 32) were set at Charlotte Pass and four replicates (total number of feeders = 16) at Lower Blue Cow. We manipulated feeder risk (Fig. 1) by setting feeders on the top of boulders (exposed feeders) where animals are at high risk of predation (Broome et al. 2012), or in the crevices between boulders (sheltered feeders), where feeders were likely to be perceived as safer. As novel objects, all feeders were likely to be perceived with some degree of risk, at least initially (Cowan 1977). The feeder design prevented the rapid removal of food, and animals had to make a risk versus reward trade-off to forage. We manipulated feeder reward by using either 40 g of walnuts (high-preference food) or raisins (low-preference food) mashed into 10 g bait balls. All feeders were set within 5 m of a previous trap position and left for three nights. A remote-sensing camera (SG560K-12mHD) was set ~1.5 m from feeders to film behaviour and help identify individuals (see Supplementary methods 1 – Camera set up). A pilot study conducted at a separate site tested feeder designs and food preferences, from which we selected the feeder and foods used in this study.

Quantifying visits to and behaviours at feeders

To analyse individual risk-taking behaviour, we quantified (1) the frequency of visits per feeder and (2) the proportion

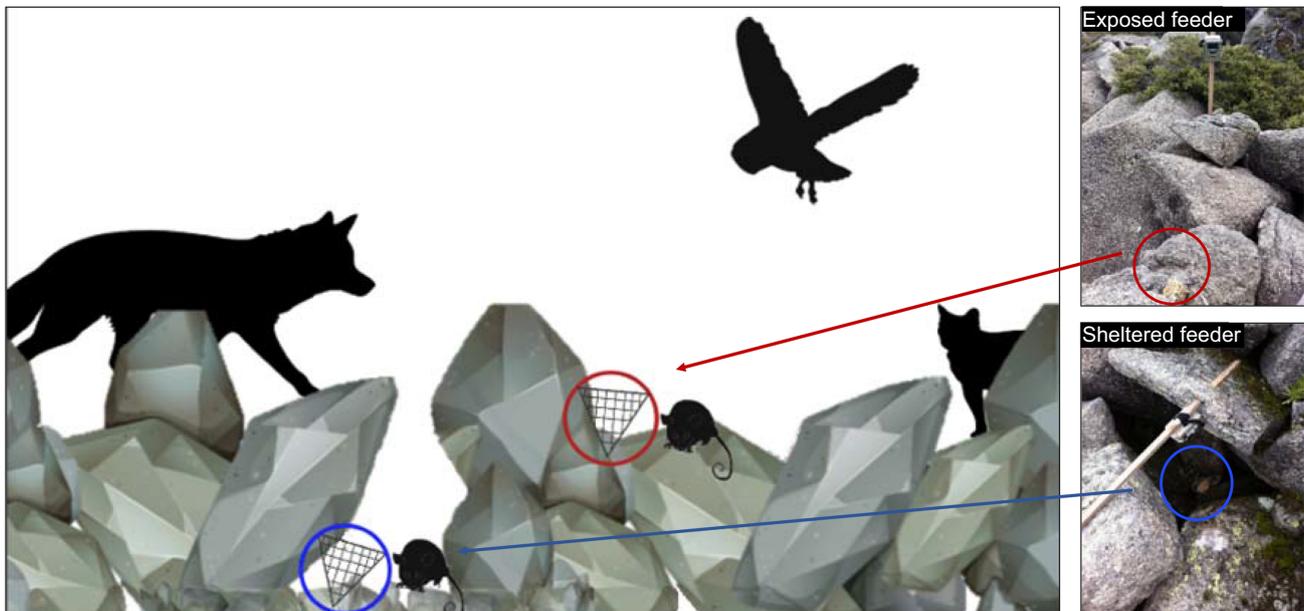


Fig. 1. The experimental design to test risk–reward trade-off decisions during foraging. Circles show feeders set in exposed (red) and sheltered (blue) microhabitats.

of time (in-sight) individuals allocated to different behaviours (Supplementary material Table S1), all as a function of feeder risk and reward. We measured behaviours related to risk-taking, namely, approach (in motion, approaches feeder or head is angled towards feeder), locomotion (in motion, but not focused on feeder), investigation (not in motion, focused on and within one body length of the feeder), and total time foraging (consuming or attempting to remove food from a device); and behaviours related to cautionary responses, including vigilance (not moving, but alert) and not moving (not moving but not vigilant). We included total time foraging (rather than the proportion of time) as a measure of the absolute value of time spent at a feeder. We scored video behaviours using the software JWatcher (Blumstein and Daniel 2007), and because pygmy-possums rarely remained at feeders for the full video duration (60 s), we considered each video to be a separate visit. (For full details, see Supplementary methods 2 – Quantifying behaviours at feeders).

Statistical analysis

Quantifying personality

All analysis was conducted in JMP Pro 13 (SAS Institute, Cary, NC, USA) unless otherwise specified. Behaviour from the immobility test was analysed as a potential personality trait by using the GLIMMIX procedure in SAS (following Dingemans and Dochtermann 2013). Models were fitted with a Gaussian distribution, and we checked for normality and homogeneity of variance. We compared two reduced models with fixed-effect assemblages (*sex*, *test order*), with the second including *individual identity* as a random factor. We used the -2Log-likelihood (-2LL) and Akaike information criterion corrected for small sample sizes (AICc) to determine whether including *individual identity* improved the model fit, and, if it did, the behaviour was considered a significant trait. To test for trait plasticity, we compared the second model with a third model, which included the interaction between *individual identity* and *test order* as a random effect. Finally, we calculated trait repeatability following Dingemans and Dochtermann (2013).

Ten individuals were tested only once (i.e. were not recaptured) and to determine whether they could be included in the analysis, we tested whether, in recaptured individuals ($n = 43$), immobility differed between repeat tests. A mixed model analysis with *test order* as a fixed effect and *individual identity* as a random factor showed no significant effect of *test order* on immobility ($P = 1.00$). Therefore, all individuals ($n = 53$) were included in the analyses.

Testing the influence of cohort and personality on the probability of recapture

To test whether personality (immobility) differed between the cohorts, we applied a square-root transformation to time

immobile and ran a general linear model with *cohort* as a fixed effect. We also tested whether the probability of recapture during our survey was influenced by population cohort (known vs new animals) or personality. We ran a logistic regression with a binary response variable (recaptured: yes, no) and included *cohort*, *immobility*, *sex* and *site* as fixed effects.

Testing the influence of cohort and personality on risk-taking at feeders

We tested whether cohort or personality influenced (1) visit frequency to feeders, and (2) behaviour at feeders. We included exposed and sheltered feeders with high-preference food (feeders with low-preference food had too few visits to gain meaningful data). We focused on the behaviour of animals in their initial interactions with a feeder by limiting our analysis to a maximum of the first three visits per feeder risk (i.e. a maximum of three visits to exposed feeders and three visits to sheltered feeders per individual). To examine whether marked (captured) animals were taking greater risks than were unmarked (not captured) animals, we looked at visit frequency to exposed and sheltered feeders (with high-preference food). We ran a relative risk test (calculated as the number of visits to feeders by marked pygmy-possums / number of visits to feeders by unmarked pygmy-possums, per feeder risk).

We also tested whether visit frequency to (high-preference food) feeders by identified (i.e. uniquely marked) pygmy-possums ($n = 40$) was influenced by feeder risk (two levels: exposed, sheltered), cohort (two levels: known, new), personality, or the interaction between feeder risk and cohort or personality. We used a linear mixed model approach and included *individual identity* as a random factor, because individuals could visit exposed and sheltered feeders. For each model, we checked for normality and homogeneity of variance. For significant effects we ran pair-wise comparisons using a Tukey–Kramer adjustment. As a complementary test, we tested whether capture frequency affected the relative visits to exposed and sheltered feeders (using the difference in total number of visits between exposed and sheltered feeders, with high-preference food feeders only). We ran a one-way ANOVA and included all visits from identified individuals that visited at least one feeder ($n = 32$), with *number of times trapped* and *relative visits* as fixed effects. For individuals ($n = 13$) that visited exposed and sheltered feeders with high-preference food, we also tested whether risk-taking (approach, locomotion, investigation, total time foraging) and cautionary behaviours (vigilance and not moving) were influenced by feeder risk, either cohort or personality, or the interaction. We used the mean proportion of time an individual allocated to behaviours across all (maximum of three) visits, per feeder risk. For total time foraging, we used the mean time individuals spent foraging across all (maximum of three) visits, per feeder risk.

To test whether the population cohorts differed in their overall behaviour at feeders, we used a permutational multivariate ANOVA (PERMANOVA, in Primer ver. 6 and PERMANOVA+) and included *feeder risk*, *cohort* and the interaction as fixed factors, and *individual identity* nested in *cohort* as a random factor. We used the conservative Type III sums of squares, with fixed effects summed to zero and permutation of residuals under a reduced model, with 9999 permutations. To test whether personality influenced behaviour, we used a general linear model with a Poisson distribution and log-link function for non-gaussian data. We ran a separate model for each behaviour at exposed and sheltered feeders and included *immobility* as a fixed effect.

Ethics approval

All research was conducted in accordance with The University of Sydney Animal Ethics (Permits: 2017/1247, 991129/01) and NSW National Parks and Wildlife Service Scientific Licence (SL100835).

Results

We captured 53 pygmy-possums (29 females, 24 males) over the four trapping nights, and, as expected, a high proportion (0.81, $n = 43$) was recaptured during the survey (Fig. 2a, b, Table S2). Similarly, of the 40 uniquely marked individuals, most were recaptured (0.88; Table S2). In total, 25 of the 40 marked individuals were new animals (trapped for the first time in this session) and 15 were known animals (trapped in previous years). Overall, most (58%) individuals were captured in the first night (Fig. 2a, b), after which additional captures declined (over the four trapping nights, 31, 11, 7 and 4 individuals respectively, were captured for the first time in this session). Similarly, most (47%) individuals were recaptured on the second night; over the second, third and fourth nights, 25, 13 and 5 individuals were recaptured respectively. Because this was a short survey, recaptures might have increased, given additional trapping nights, although this would have limited impact on our findings.

Mean body weight (\pm s.e.) was similar between the sexes (mean female = $39.3 \text{ g} \pm 0.89 \text{ g}$, mean male = $39.3 \text{ g} \pm 0.93 \text{ g}$) and there was no sex bias in the group of animals that was not recaptured (female $n = 5$, male $n = 5$). On average, females were captured 3.2 times and males 2.5 times. Captures of known animals were skewed slightly (0.7) towards females (14/21), whereas captures of new animals were roughly equal (15 females, 17 males). Known animals were also slightly heavier than were new animals (mean weight (\pm s.e.): $42.5 \text{ g} \pm 0.71 \text{ g}$ and $37.3 \text{ g} \pm 0.75 \text{ g}$ respectively).

Personality, quantified through the immobility test (i.e. time spent immobile in the handling bag), was a

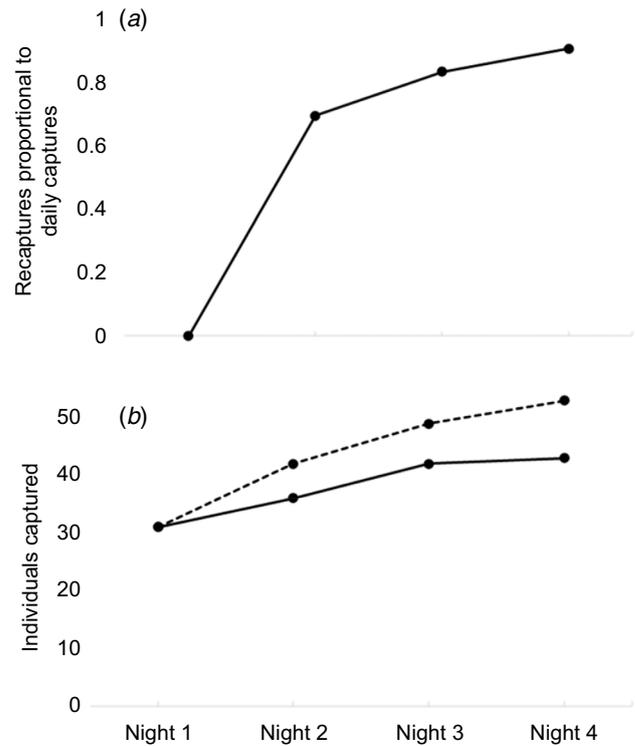


Fig. 2. Captures of mountain pygmy-possums over four trapping nights with (a) recaptures proportional to daily captures and, (b) the daily (solid line) and cumulative (dotted line) number of individuals caught.

significant (LRT = 18.51, $P < 0.001$) and repeatable ($r = 0.40$) trait. Although males spent more time immobile than did females (mean time \pm s.e.: males = 3.00 ± 1.61 , females = -2.61 ± 1.52 , $F_{1,51} = 7.70$, $P = 0.01$), personality did not differ between the population cohorts ($F = 3.20$, $P = 0.90$). The recapture probability being significantly influenced by cohort was greater for known animals than for new animals (likelihood ratio $\chi^2 = 5.24$, $P = 0.02$; Table S2). Recapture probability was not significantly influenced by personality (LR $\chi^2 = 0.05$, $P = 0.83$), sex (LR $\chi^2 = 0.01$, $P = 0.94$) or site (LR $\chi^2 = 0.05$, $P = 0.82$).

We analysed 1566 videos (i.e. visits) of pygmy-possums at feeders. Overall, there was a clear rank preference (in number of visits) among the four risk-reward treatments (Fig. 3). Feeders were ranked first by reward, then by risk, with visit number being greatest at sheltered, high-preference feeders and lowest at exposed, low-preference feeders. Of these visits, 746 were by marked (unique and common marks) animals trapped in this session. However, 312 visits were by unmarked animals (i.e. not trapped in this session), and 508 visits were by animals where the presence/absence of a mark could not be confirmed. Whereas visits to exposed feeders (with high-preference food) by marked and unmarked animals was comparable (relative risk = 1.1), marked animals

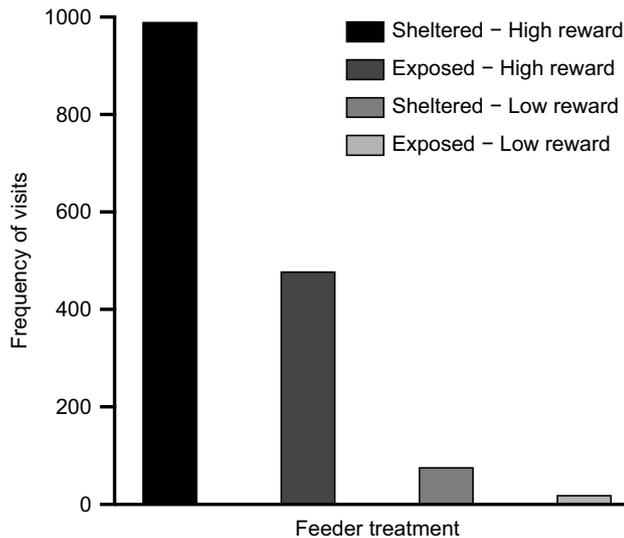


Fig. 3. Frequency of visits to feeder treatments by all mountain pygmy-possums.

were twice (relative risk = 2.0) as likely to visit sheltered feeders (with high-preference food) than were unmarked animals. Of the 40 uniquely marked individuals, 32 visited a feeder at least once (range = 1–45; mean = 15.44, s.e. \pm 2.31), and 13 visited both exposed and sheltered feeders.

Visit frequency to feeders was influenced by the interaction between population cohort and feeder risk ($F_{1,36} = 6.51$, $P = 0.02$). Known animals revisited exposed and sheltered feeders similarly, whereas new animals were more risk-averse and tended to revisit only sheltered feeders (Fig. 4).

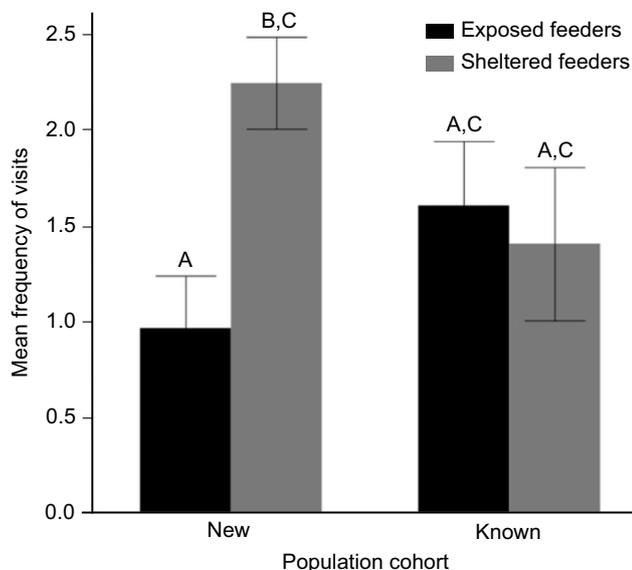


Fig. 4. The frequency (mean \pm s.e.) of visits to exposed and sheltered feeders by known ($n = 15$) and new ($n = 27$) animals. Different letters indicate significant differences at $P = 0.05$.

We found no significant effect of personality on visit frequency ($F_{1,36} = 1.09$, $P = 0.30$) or interactive effect of personality and feeder risk ($F_{1,36} = 1.26$, $P = 0.27$). There was also no significant effect of capture frequency on the relative frequency of visits to feeders ($F_{3,28} = 0.15$, $P = 0.93$).

Of the behaviours recorded at feeders, locomotion and approach were positively correlated ($r = 0.65$), and total time spent foraging was negatively correlated with approach ($r = -0.74$), locomotion ($r = -0.63$), and investigation ($r = -0.51$). Our PERMANOVA showed that behaviour at feeders was not significantly affected by population cohort, feeder risk, or the interaction (pseudo $F_{1,11} \geq 0.13$, $P \geq 0.28$). However, in analysing behaviours separately by using general linear models, personality significantly affected risk-taking behaviour, but only at exposed feeders. Individuals that were more immobile also spent more time being vigilant ($F_{1,11} = 9.09$, d.f. = 1, $P = 0.003$) and less time in locomotion ($F_{1,11} = 8.96$, $P = 0.01$), than did less immobile individuals (Fig. 5a, b). There was no significant effect of personality on any other behaviour at feeders (Fig. 5c–f; Table 1).

Discussion

Determining the mechanisms underpinning differences in trap response following initial capture is one step towards addressing a substantial source of bias in live-capture surveys. Recapture rates during our trapping session were high, suggesting that most of the populations had been caught. However, recapture probability differed by cohort, and known animals trapped in previous years had a significantly greater recapture probability than did new animals trapped for the first time. We anticipated risk-assessment as a potential mechanism underpinning recapture probability (e.g. [Johnstone et al. 2021a](#)) and the cohorts, indeed, differed in risk-taking behaviours. Known animals visited exposed (risky) and sheltered (safe) feeders similarly, whereas new animals were more risk-averse, visiting exposed feeders far less frequently than sheltered feeders. Although personality (immobility) did not influence recapture, it did influence general risk-taking behaviours at exposed feeders. Individuals that were more immobile spent more time vigilant and less time in locomotion than did individuals that were less immobile. Notably, where recapture history could be determined (i.e. an animal was marked or unmarked), 29.5% of visits to feeders were by unmarked (i.e. not captured) animals. Together, our findings suggest that despite high recapture rates, within a single trapping session (1) differences in risk-taking proclivity between cohorts may influence recapture probability to drive a sample bias, and (2) a substantial portion of the population may go unsampled.

Despite our high recapture rates, the probability of recapture within our trapping session was substantially

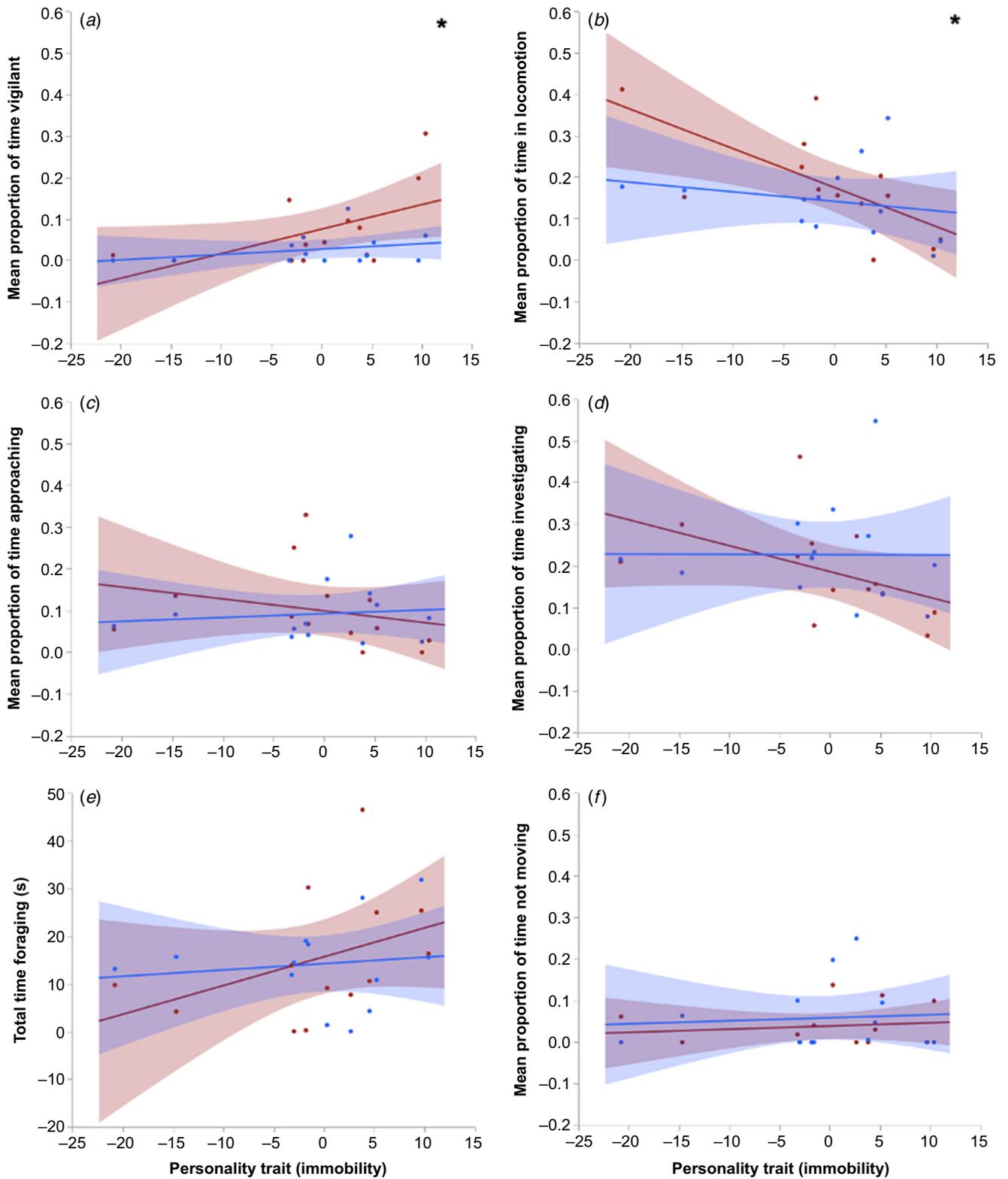


Fig. 5. The relationship between personality (immobility) and the mean proportion of time in-sight that individuals ($n = 13$) spent (a) vigilant, (b) in locomotion, (c) approaching, (d) investigating, (e) foraging (total time), and (f) not moving, at exposed (red) and sheltered (blue) feeders. Dots indicate individual values, lines indicate the predicted relationship, and shaded areas show 95% confidence interval. Asterisk indicates a significant effect at exposed feeders, at $P = 0.05$.

Table 1. Results of the general linear modelling analysis, showing the influence of personality (immobility) on the proportion of time (in-sight) that individuals ($n = 13$) allocated to risk-taking and cautionary behaviours.

Item	Risk-taking behaviour				Cautionary behaviour	
	Approach	Locomotion	Investigation	Foraging (total time)	Vigilance	Not moving
Exposed feeders (high risk)	LR $\chi^2 = 0.73$ d.f. = 1 $P = 0.34$	$F_{1,11} = 8.96$ $P = 0.01$	LR $\chi^2 = 2.81$ d.f. = 1 $P = 0.09$	LR $\chi^2 = 2.49$ d.f. = 1 $P = 0.11$	LR $\chi^2 = 9.09$ d.f. = 1 $P = 0.003$	LR $\chi^2 = 0.23$ d.f. = 1 $P = 0.63$
Sheltered feeders (low risk)	LR $\chi^2 = 0.15$ d.f. = 1 $P = 0.70$	$F_{1,11} = 0.59$ $P = 0.46$	LR $\chi^2 = 0.0003$ d.f. = 1 $P = 0.99$	LR $\chi^2 = 0.20$ d.f. = 1 $P = 0.66$	LR $\chi^2 = 1.45$ d.f. = 1 $P = 0.23$	LR $\chi^2 = 0.07$ d.f. = 1 $P = 0.79$

Significant effects are indicated in bold.

LR, likelihood ratio.

lower for new animals (trapped for the first time) than for known animals (trapped in previous years). Known animals were adults with prior trapping experience and had persisted in the population for at least 1 year. In contrast, new animals would have consisted mostly of subadults with no prior experience with traps, along with a small proportion of adults (Broome 2001a). Age and prior trapping experience can influence trap response (Camacho *et al.* 2017); adults are often more difficult to trap over time, whereas captures are greater for younger, trap-naïve animals (Daly 1980; Camacho *et al.* 2017). Interestingly, our short study found the opposite effect.

We considered several factors that may have contributed towards the differences in trappability between our cohorts. Differences may have been a function of low trap sensitivity to the lighter weight of young new animals (e.g. Anthony *et al.* 2005). However, because subadult pygmy-possums often weigh the same as adults (Broome 2001a), trap sensitivity was unlikely to influence our study. Second, competition for a high-value food (walnuts) during a period when animals are building fat reserves for hibernation may have led to known adults dominating traps. However, traps were not saturated and any resource guarding would have been negated once the dominant animal was captured. Individuals also had opportunity to encounter multiple traps (Broome 2001a) and, throughout our trapping session, individuals were often caught in different traps. Third, we considered the timing of the survey and the possibility that new adults may have avoided capture in previous years by dispersing before surveys began or recently entered the populations from unsurveyed sites. However, animals are generally trapped at the same site each year (Broome 2001a), and within the scope of our study. It was not possible to explore any effects of annual dispersal. Finally, we considered the potential for increased trappability, given a longer trapping session. Although the annual trapping survey (as with this study) only spans four nights, by mid-way, 72% of animals were recaptured and 81% were recaptured after four nights. This outcome suggested that few (but potentially some) additional animals would have been recaptured if the

survey were extended. Accounting for the above factors, we considered it to be most likely that the differences in recapture between the cohorts arose from behavioural differences.

Contrary to our prediction, we found that personality, *per se*, did not significantly affect recapture probability. Even though immobility can negatively correlate with boldness (Réale *et al.* 2000), activity, and aggression (Taylor *et al.* 2012), traits that can directly influence trappability (Boon *et al.* 2008; Carter *et al.* 2012), we found no evidence of a personality bias. However, not all traits influence trappability (Garamszegi *et al.* 2009) and some studies have found no discernible effect of personality on trappability (Michelangeli *et al.* 2016; Jolly *et al.* 2019). Considering our high recapture rates, it is possible that traps are not perceived as risky and there is no link between personality and recapture probability. But as we measured personality only along a single trait axis, the influence of additional traits would need to be assessed before we could conclude that personality, in general, does not drive a sample bias in this species.

Personality did influence behaviour in a high-risk context (i.e. at exposed feeders). But rather than driving avoidance of high-risk scenarios, personality influenced how individuals managed the risk, and immobility was associated with vigilant and explorative behaviours. More immobile individuals were risk adverse and these individuals were more vigilant, a cautionary behaviour often measured in response to predation risk (Brown 1999), and less active (less time in locomotion) at feeders, a response associated with risk-taking (Wat *et al.* 2020). To manage foraging risk–reward trade-offs, animals can decide where to spend their foraging time (i.e. selecting safe over risky patches), or can allocate different amounts of time to vigilance depending on the patch risk (Brown 1999). We found that patch selection differed between cohorts, and mitigating risk at risky patches (i.e. exposed feeders) was influenced by personality. Fundamentally, wildlife detection is dependent on animals visiting a given device (e.g. live traps), and subsequently interacting with it (i.e. entering the trap). Given that personality influenced cautionary and

investigative behaviours at high-risk exposed feeders, our results lend support to other research (Carter et al. 2012; Johnstone et al. 2021a) that has demonstrated the influence of personality on detection probability when using approaches that detect specific animal behaviours.

More generally, our results suggest that risk-taking behaviour may explain the differences in recapture probability between the cohorts. Overall, pygmy-possums visited sheltered feeders significantly more often than they did exposed feeders (Fig. 3), suggesting that they perceived sheltered feeders as safer microhabitats. These responses are consistent with other prey species. Both house mice (*Mus musculus*; Ylönen et al. 2002) and field voles (*Microtus agrestis*; Korpimäki et al. 1996) favour vegetated or sheltered microhabitats under potential or realised levels of predation risk. Importantly, whereas known individuals revisited exposed and sheltered feeders similarly, new individuals revisited sheltered feeders, but typically visited exposed feeders only once, suggesting that these animals were reducing their risk-taking, despite the great reward.

Although younger animals are typically less risk-averse than are adults (Fairbanks 1993; Bergman and Kitchen 2009), in some cases, this pattern may be reversed. For example, in the endangered alalā (*Corvus hawaiiensis*), younger individuals are more neophobic than are adults (Greggor et al. 2020), likely owing to heightened predation risk (e.g. at fledging). Similarly, nestling pygmy-possums are at risk from nest raiding by *Antechinus* sp. (NSW National Parks and Wildlife Service 2002), and inexperienced subadults may initially avoid unfamiliar or potentially risky situations (such as traps and exposed feeders). Risk aversion can dissipate with age (Greggor et al. 2020), because time and experience allow animals to make more informed decisions (Trimmer et al. 2011), and risk avoidance may decrease in pygmy-possums as they mature and trappability may subsequently increase in future trapping sessions. Together, our results suggest that exposed feeders and, to a lesser degree, live-traps were perceived as risky by pygmy-possums, at least following the first encounter. However, we surmise that known animals with greater life experience either associated traps and exposed feeders with little risk or were generally less risk-averse, resulting in a greater recapture probability.

Importantly, we noted that a larger-than-expected proportion (~0.30) of visits to feeders were by unmarked pygmy-possums (i.e. untrapped in this session). Although these animals may have been trapped in previous years and may be captured in future surveys, when a large part of a population goes undetected, the accuracy of population estimates decreases, and if many animals have capture probabilities close to zero, the actual population size may be greatly underestimated (Pollock and Otto 1983). Trapping the untrappable has long been a wicked problem in wildlife management (Bisi et al. 2011; Biro 2013; Garvey et al. 2020) and was observed here only because of our

use of wildlife cameras. How much this untrappability was driven by personality or risk aversion is unknown because these individuals were not assessable within this trapping session. Although additional trapping sessions may alleviate some bias, novel or complementary (Garvey et al. 2020) methods of capture or monitoring could be useful to address this knowledge gap.

As with all short studies, the interpretation of our results would benefit from replication. Although it is likely that a substantial number of animals went undetected during this survey, these individuals may have been trappable in previous (or in subsequent) years. Long-term surveying (as is conducted on these populations) is crucial for providing robust and reliable population data for wildlife managers to act on. However, experimental studies such as ours provide useful insights that may benefit from further investigation. For instance, although a single monitoring method is beneficial in providing consistent and comparative long-term data, no method is without bias (Biro 2013) and complementary or comparative methods may more effectively provide representative population samples, a factor that should never be discounted, especially when working on endangered species.

Our results indicated that even for species with high recapture rates, heterogeneity in trappability can arise during population sampling, likely owing to risk-sensitive decision-making by individuals. This heterogeneity can bias population estimates towards the most detectable individuals and overlook those that avoid capture. To address these biases during survey sessions, wildlife managers can seek to accommodate the different motivations of individuals that vary in experience and personality (Garvey et al. 2020), for instance, by using a suite of traps or sampling methods (Wilson et al. 2011; Johnstone et al. 2021c), running extended sessions where possible to account for trap-shy animals, and conducting repeated trapping sessions over multiple seasons or years. Understanding drivers of detection biases is a crucial step towards reducing sample bias during surveys and to increase representative population sampling.

Supplementary material

Supplementary material is available [online](#).

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Data availability. The data used to generate the results in this paper are available and accessible via figshare.com (<https://doi.org/10.6084/m9.figshare.21598899>).

Conflicts of interest. The authors declare no conflicts of interest.

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